

An Overview of Closed Capture–Recapture Models

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This article reviews various models for both discrete-time and continuous-time closed capture–recapture experiments. The traditional discrete-time models assume that the samples are independent. Dependence may be caused by local dependence (list dependence) within each animal or by heterogeneity among animals. Three different approaches that can incorporate dependence into models are reviewed, i.e., ecological models, log-linear models, and the sample-coverage approach. The statistical tools involved in population size estimation in these three approaches cover a wide range of methodologies. There has been relatively little published research for the continuous-time counterparts. The counting process approach, which is the framework for most existing estimation procedures for continuous-time models, is reviewed. The connection of continuous-time models to recurrent event analysis in the context of failure time inferences is discussed. The applications of capture–recapture models to other disciplines are briefly presented. Remarks about the limitations of the models are made and some future research directions are also suggested.

Key Words: Counting processes; Ecological models; Log-linear models; Mark–recapture; Population size; Sample coverage; Tag–recapture.

1. INTRODUCTION

The capture–recapture sampling and models have been widely used to estimate parameters of biological populations. In a closed capture–recapture model, we assume that there is no birth, death, or migration so that the population size is a constant over trapping times. The demographic closure assumption is usually valid for data collected in a relatively short time during a nonbreeding season. This article focuses mainly on population size estimation for closed models with emphasis on some recent developments. Seber (1982, 1986, 1992) and Schwarz and Seber (1999) provided excellent and comprehensive reviews of models for estimating animal abundance in general and on this topic in particular. Other important general references on closed models and applications include Otis, Burnham, White, and Anderson (1978), White, Anderson, Burnham, and Otis (1982), Pollock (1991), Hook

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and Regal (1995), and the two reviews by the International Working Group for Disease Monitoring and Forecasting (IWGDMF) (1995a,b). Recent encyclopedia articles include Cormack and Buckland (1997) and Chao (1998).

There are two types of models, i.e., discrete-time and continuous-time models. In a typical discrete-time model, the target population is sampled several times (or 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. We also assume that animals do not lose their marks and all marks are recorded correctly. Thus, at the end of the experiment, the complete capture history for each animal is known and the maximum count for each animal is the number of samples. In situations where only batch marks are feasible, some sophisticated models cannot be applied to estimate population size due to insufficient information (see Section 2.1).

Why is marking or tagging necessary? Biologists and ecologists have long recognized that it would be almost impossible to count every animal in order to obtain a census of the population. Marking or tagging is used to distinguish individuals caught in the samples, and thus the recapture information (overlap information) by marking or tagging can be used to estimate the number of missing animals in the experiment. Intuitively, for independent samples, when recaptures in the subsequent samples are few, we know that the size is much larger than the number of distinct captures. On the other hand, if the recapture rate is high, then we are likely to have caught most of the animals.

The use of discrete-time models has a long history for both animal and human populations. For historical development, see Seber (1982) and Manly and McDonald (1996). Darroch (1958) provided pioneering work on the statistical theory and mathematical framework. Since then, a large body of literature has been published in this area. Section 2 reviews three classes of discrete-time models that consider the dependence among samples.

For a continuous-time model, only one animal is caught at each trapping sample. In addition to the tagging process, we also record the exact capture times for each animal. Thus, any capture is 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 indicated by Wilson and Anderson (1995), typical applications of continuous-time models involve studies of insects, sperm whales, grizzly bears, and other large mammals.

Becker (1984) established a counting process approach for continuous-time models. Several authors have extended his approach to more general models. Section 3 provides a short review. The relationship between continuous-time models and recurrent event analysis is also discussed.

In addition to biological and ecological sciences, the closed capture–recapture technique has been applied to many other disciplines. Section 4 outlines the applications to epidemiology, health science, census undercount adjustment, software reliability, and oth-

ers. Section 5 concludes with some discussion and suggestions of directions for future research.

2. DISCRETE-TIME MODELS

Assume that the true population size is N , which is our parameter of interest. The animals are indexed by $1, 2, \dots, N$, and all animals act independently. Assume that there are t samples and they are indexed by $1, 2, \dots, t$. Presence and absence in any sample are denoted by one and zero, respectively. The capture data for all individuals can be conveniently expressed by an $N \times t$ matrix, $X = (X_{ij})$. Here $X_{ij} = I$ (the i th individual is caught in the j th sample) and $I(A)$ is the usual indicator function for the event A , i.e., $I(A) = 1$ if A is true and $I(A) = 0$ otherwise. A matrix row with all zeros means that this individual is not captured in any of the samples.

The traditional approach assumes that all animals have the same capture probability in each sample (equal-catchability assumption), although the probability can be allowed to vary among samples. The samples are independent under this assumption. Dependence among samples can be caused by the following sources: (i) local dependence (list dependence) within each animal, i.e., capture in one sample has a direct causal effect on this animal's capture in other samples; e.g., an animal might become either trap happy or trap shy because of the behavioral response to capture; (ii) heterogeneity among animals; even if there is no local dependence for each individual, the two samples may become dependent when the capture probabilities are heterogeneous. This phenomenon is similar to Simpson's paradox in categorical data analysis; i.e., aggregating two independent 2×2 tables might result in a dependent table. An illustrative example in epidemiology was given in Hook and Regal (1995, Table 4).

Dependence among samples leads to a bias for the usual estimator derived under independence. We use a two-sample experiment to explain intuitively the direction of the bias. Assume that a first sample of n_1 animals is captured. Therefore, the marked rate in the population is n_1/N . A second sample of n_2 animals is subsequently captured and there are m_2 previously marked. The capture rate for the marked (recapture rate, overlap rate) in the second sample can be estimated by m_2/n_2 . If the two samples are independent, then the recapture rate in the sample should be approximately equal to the marked rate in the population. Therefore, we have $m_2/n_2 = n_1/N$, which yields an estimate of the population size under independence of $\hat{N}_P = n_1 n_2 / m_2$ (the well-known Petersen estimator or dual-system estimator). This estimator has been justified and modified under various statistical models (see Seber 1982, Chapter 3).

If the two samples are positively correlated due to heterogeneity or a trap-happy response, then those animals captured in the first sample are more easily captured in the second sample. The recapture rate in the second sample tends to be larger than the marked rate in the population, i.e., we would expect that $m_2/n_2 > n_1/N$, which gives $N > n_1 n_2 / m_2 = \hat{N}_P$. Thus, the Petersen estimator underestimates the true size if the two samples are positively dependent. Conversely, it overestimates for negatively dependent samples that may be due

to trap-shy responses to capture. A similar argument is also valid for any number of samples, i.e., a higher (lower) overlap rate is observed for positively (negatively) dependent samples, which implies fewer (more) estimated missing animals. Therefore, a negative (positive) bias arises for the estimate assuming independence.

A variety of models incorporating dependence among samples has been proposed in the literature. We classify these models into three categories: ecological models, log-linear models, and the sample-coverage approach. The latter two approaches can be used to provide estimates for some ecological models, but they are considered separately because they differ in their way of dealing with dependence.

2.1 ECOLOGICAL MODELS

This approach specifies various forms of capture probabilities based on empirical investigations of animal ecology. Two commonly used forms have been proposed—the multiplicative (or log-linear) form and the logistic form.

Pollock was the first to consider a sequence of models to relax the equal catchability assumption, and these models were reviewed in Pollock (1991) and fully discussed in Otis et al. (1978) and White et al. (1982). Three sources of variations in capture probability are considered: (i) model \mathcal{M}_t , which allows capture probabilities to vary by time; (ii) model \mathcal{M}_b , which allows behavioral responses to capture; and (iii) model \mathcal{M}_h , which allows heterogeneous capture probabilities. Various combinations of the above three variations (i.e., models \mathcal{M}_{tb} , \mathcal{M}_{th} , \mathcal{M}_{bh} , and \mathcal{M}_{tbbh}) and the model \mathcal{M}_0 , in which no variation exists, are also considered.

These types of ecological models specify $P(X_{ij} = 1 \mid \mathcal{F}_j)$, the conditional probability of capturing the i th animal in the j th sample given \mathcal{F}_j , the capture history of samples $1, 2, \dots, j - 1$. For notational simplicity, let $P(X_{ij} = 1 \mid \mathcal{F}_j) = P_{ij}$. A multiplicative form of model \mathcal{M}_{tbbh} is

$$P_{ij} = \begin{cases} p_i e_j & \text{until first capture,} \\ \tau p_i e_j & \text{for any recapture,} \end{cases} \quad (2.1)$$

where $0 < p_i e_j, \tau p_i e_j < 1$. Thus, the parameters $\{e_1, e_2, \dots, e_t\}$, $\{p_1, p_2, \dots, p_N\}$, and τ are used, respectively, to model the time effects, individual heterogeneity, and the behavioral response to capture. In this model, the recapture probabilities are assumed to be proportional to the initial capture probabilities. Define $\alpha_i = \log(p_i)$, $\mu_j = \log(e_j)$, $\alpha = \log(\tau)$, and $Y_{ij} = I$ (the i th animal has been captured before the j th sample); here the time-dependent variable Y_{ij} is used to denote the prior capture history of individual i for sample j . Then the multiplicative type of probability can be conveniently expressed in the following log-linear form:

$$\log(P_{ij}) = \alpha_i + \mu_j + \alpha Y_{ij}. \quad (2.2)$$

All submodels of this general model are formulated in Table 1.

The capture probability for the logistic model \mathcal{M}_{tbbh} can be written as (Huggins 1989, 1991; Alho 1990)

Table 1. Discrete-Time Models and Associated Estimation Approaches/Methods

<i>Model</i>	<i>Log-Linear/Logistic Form</i>	<i>Approaches/Methods</i>
\mathcal{M}_{tbh}	$\log(P_{ij}) = \alpha_i + \mu_j + \gamma Y_{ij}$ $\text{logit}(P_{ij}) = \alpha_i + \mu_j + \gamma Y_{ij}$	Conditional sample coverage (Lee 1996) MLE using mixture (Pledger 2000) Estimating function (Chao et al. 2001b) Generalized linear models using covariates (Huggins 1991; Evans et al. 1994) (All approaches are valid for the submodels given below; they are not repeated in each model)
\mathcal{M}_{bh}	$\log(P_{ij}) = \alpha_i + \gamma Y_{ij}$ (Generalized removal model) $\text{logit}(P_{ij}) = \alpha_i + \gamma Y_{ij}$	Generalized removal (Otis et al. 1978) Jackknife (Pollock and Otto 1983) Sample coverage ^a (Lee and Chao 1994) Nonparametric MLE (Norris and Pollock 1995, 1996b)
\mathcal{M}_{tb}	$\log(P_{ij}) = \mu_j + \gamma Y_{ij}$ $\text{logit}(P_{ij}) = \mu_j + \gamma Y_{ij}$	Martingale method (Lloyd 1994) Bayes approach (Lee and Chen 1998) MLE and maximum quasi-likelihood (Chao, Chu, and Hsu 2000) Log-linear models ^b (Cormack 1989)
\mathcal{M}_{th}	$\log(P_{ij}) = \alpha_i + \mu_j$ $\text{logit}(P_{ij}) = \alpha_i + \mu_j$ (Rasch model)	Sample coverage ^a (Lee and Chao 1994) Mixed logit models (Sanathanan 1972, Coull and Agresti 1999) Log-linear models ^b or latent class models (Darroch et al. 1993; Agresti 1994)
\mathcal{M}_{h}	$\log(P_{ij}) = \alpha_i$ $\text{logit}(P_{ij}) = \alpha_i$	Jackknife method (Burnham and Overton 1978) Bootstrap estimator (Smith and van Belle 1984) Martingale method (Lloyd and Yip 1991) Nonparametric MLE (Norris and Pollock 1995, 1996b) (All estimators listed for model \mathcal{M}_{th} are valid here)
\mathcal{M}_{b}	$\log(P_{ij}) = \alpha + \gamma Y_{ij}$ ($\alpha_i \equiv \alpha$) (Removal model) $\text{logit}(P_{ij}) = \alpha + \gamma Y_{ij}$ ($\alpha_i \equiv \alpha$)	MLE (Zippin 1956) Martingale method (Lloyd 1994) Log-linear models ^b (Cormack 1989)
\mathcal{M}_{t}	$\log(P_{ij}) = \mu_j$ $\text{logit}(P_{ij}) = \mu_j$	Binomial model (Schnabel 1938) MLE and conditional MLE (Darroch 1958; Otis et al. 1978; Sanathanan 1972) Log-linear models ^b (Fienberg 1972) Martingale method (Yip 1991) Bayes and empirical Bayes (Castledine 1981; Smith 1988, 1991; George and Robert 1992)
\mathcal{M}_0	$\log(P_{ij}) = \alpha$ $\text{logit}(P_{ij}) = \alpha$	(All estimators given above are valid here)

^a See Section 2.3.^b See Section 2.2.

$$P_{ij} = \begin{cases} p_i e_j / (1 + p_i e_j) & \text{until first capture,} \\ \tau p_i e_j / (1 + \tau p_i e_j) & \text{for any recapture,} \end{cases} \quad (2.3)$$

or equivalently,

$$\text{logit}(P_{ij}) \equiv \log[P_{ij}/(1 - P_{ij})] = \alpha_i + \mu_j + \alpha Y_{ij}, \quad (2.4)$$

where the parameters $\{\alpha_1, \alpha_2, \dots, \alpha_N\}$, $\{\mu_1, \mu_2, \dots, \mu_t\}$, and α denote, respectively, the heterogeneity, time effects, and behavioral response effect. It follows from (2.2) and (2.4) that the two types of models only differ in the link function. A class of eight logistic submodels, as in the multiplicative case, is also listed in Table 1. The well-known Rasch model corresponds to the special case of $\alpha = 0$ in (2.4), i.e., logistic model \mathcal{M}_{th} . The Rasch model has been extensively discussed in the context of educational testing and survey sampling. Sanathanan (1972) was the first to consider the Rasch model in population size estimation. We remark that the multiplicative models \mathcal{M}_b and \mathcal{M}_{bh} can also be applied to removal data because models \mathcal{M}_b (\mathcal{M}_{bh}) are statistically equivalent to the removal (generalized removal) model (see Otis et al. 1978). Also, the logit models \mathcal{M}_0 , \mathcal{M}_t , \mathcal{M}_b , and \mathcal{M}_h are equivalent to a reparameterization of their corresponding multiplicative models. For others, there are no equivalent models in the multiplicative models.

For both types of capture probabilities, only for models \mathcal{M}_0 and \mathcal{M}_t are the samples independent. Local dependence is induced for models \mathcal{M}_b and \mathcal{M}_{tb} in which the term αY_{ij} is considered; heterogeneity arises for models \mathcal{M}_h and \mathcal{M}_{th} ; and both types of dependencies exist for models \mathcal{M}_{bh} and \mathcal{M}_{tbh} .

To reduce the number of parameters and to remove the nonidentification caused by the numerous heterogeneity parameters, further assumptions about the heterogeneity are usually made. For example, Lloyd and Yip (1991), Sanathanan (1972), and Coull and Agresti (1999), respectively, used beta, gamma, and normal distributions to model either the effects $\{p_1, p_2, \dots, p_N\}$ or the logarithmic effects $\{\alpha_1, \alpha_2, \dots, \alpha_N\}$. Agresti (1994), Coull and Agresti (1999), and Pledger (2000) assumed a latent class or a finite mixture model, i.e., the heterogeneity effects were partitioned as two or more groups with homogeneous capture effects. Lee and Chao (1994) and Chao, Yip, Lee, and Chu (2001b) assumed that the heterogeneity effects can be summarized in terms of their mean and coefficient of variation (CV). Burnham and Overton (1978), Smith and van Belle (1984), and Norris and Pollock (1995, 1996b) did not make any assumption about the heterogeneity effects; these authors adopted nonparametric techniques such as the jackknife, bootstrap, and nonparametric maximum likelihood estimator (MLE) in their estimation procedures.

As noted in the reviews of Seber (1982, 1986, 1992) and Schwarz and Seber (1999), estimators for various models may be found in the literature. These estimators rely on many different approaches—maximum likelihood, the jackknife method, the bootstrap method, log-linear or generalized log-linear models, Bayesian methods, mixture models, sample-coverage procedures, and martingale estimating functions.

The bootstrap and related resampling procedures (Efron and Tibshirani 1993) are also applied to obtain variance estimates and confidence intervals (Buckland and Garthwaite 1991). Individual's covariates can be incorporated in the analysis. In most capture–recapture experiments, in addition to capture records, an individual's characteristics (age, sex, body weight, or wing length) are also recorded. Pollock, Hines, and Nichols (1984) were the first to use a logistic model to incorporate covariates in the analysis. If covariates can be used to account for heterogeneity, then the logistic model (2.4) becomes $\text{logit}(P_{ij}) = \mu_j + \alpha Y_{ij} + \beta' \mathbf{Z}_i$, where $\mathbf{Z}'_i = (Z_{i1}, Z_{i2}, \dots, Z_{ik})$ denotes the individual covariates for

the i th animal and $\beta' = (\beta_1, \beta_2, \dots, \beta_k)$ denotes the effects of the covariates. Since the covariates for the uncaptured animals are not available, the parameter estimates are obtained conditional on the captured animals. The population size is then estimated by the Horvitz–Thompson estimator. The above model can be extended to a more general form of $\text{logit}(P_{ij}) = \alpha_i + \mu_j + \alpha Y_{ij} + \beta' \mathbf{Z}_i$ (see Huggins 1991).

We use Table 1 to summarize all models and their appropriate estimators or methods. Generally, capture data collected from using batch marks can only be applied to models without heterogeneity. Individually identifiable marks are needed to fit heterogeneous models. Some estimators listed in Table 1 can be obtained using the comprehensive computer programs CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991) and MARK (White and Burnham 1999). These two programs are readily available from White's website (<http://www.cnr.colostate.edu/~gwhite/software.html>). The author and colleagues have also developed a program CARE (for CAPture–REcapture), which provides MLEs, jackknife estimators, and estimators using, respectively, sample-coverage, log-linear models, and estimating functions. Program CARE is described in a tutorial article by Chao, Tsay, Shau, and Chao (2001a) and will be available soon on the author's website at <http://www.stat.nthu.edu.tw/~chao/>.

2.2 LOG-LINEAR MODELS

The log-linear model approach was originally proposed by Fienberg (1972) and has been widely used in many applications (Cormack 1989; Agresti 1994; Evans, Bonett, and McDonald 1994; Coull and Agresti 1999; IWGDMF 1995a,b). In this approach, the data are regarded as a form of an incomplete 2^t contingency table (t is the number of lists) for which the cell corresponding to those individuals uncaptured by any of the samples is missing. Then various log-linear models are fitted to the observed cells and the chosen model is projected onto the unobserved cell by assuming that there is no t -sample interaction.

We use the three-sample case as an illustration. Extension to a general case is parallel. The individual capture data are first aggregated as a categorical data form, i.e., the frequencies of the same capture history are obtained. There are seven observed cells: z_{100} , z_{010} , z_{001} , z_{110} , z_{101} , z_{011} , and z_{111} , where z_{100} is the number of individuals captured in sample 1 only and z_{011} is the number of individuals caught in samples 2 and 3 but not in sample 1. A similar interpretation pertains to other capture histories. The missing cell z_{000} denotes the number of missed animals.

The log-linear approach models the logarithm of the expected value of each observable category. The most general log-linear model for the three-sample case is

$$\begin{aligned} \log E(z_{ijk}) = & u + u_1 I(i = 1) + u_2 I(j = 1) + u_3 I(k = 1) \\ & + u_{12} I(i = j = 1) + u_{13} I(i = k = 1) + u_{23} I(j = k = 1) \\ & + u_{123} I(i = j = k = 1), \end{aligned} \quad (2.5)$$

where $I(A)$ is an indicator function for event A . The above is a reparameterization of the eight expected values. We have seven observed cells, whereas there are eight parameters in

the right-hand side of (2.5). Therefore, a commonly adopted assumption is that there is no three-sample interaction term, i.e., $u_{123} = 0$, which allows an extrapolation formula for the missing cases using the fitted values of the observable cells. The independent model with main effect terms is equivalent to model \mathcal{M}_t in Table 1. The log-linear models corresponding to the multiplicative models \mathcal{M}_b and \mathcal{M}_{tb} are discussed in Cormack (1989), who also showed how to fit various models using the GLIM package.

Interaction terms are used in the log-linear model approach to model the two types of dependencies. If local dependence arises in samples 1 and 2, then the interaction term u_{12} is included in the model. If local dependence also appears in samples 1 and 3, an additional term u_{13} is needed. The most commonly used models for heterogeneous populations in this approach are the Rasch model and its generalizations. Recall that the Rasch model specifies the following capture probability: $\text{logit}(P_{ij}) = \alpha_i + \mu_j$, where $i = 1, 2, \dots, N$, $j = 1, 2, \dots, t$, and P_{ij} is as defined in Section 2.1. A generalized Rasch model allows for the heterogeneity effects ($\alpha_1, \alpha_2, \dots, \alpha_N$) to be different for two or more separate groups of samples. It has been proved (cf., Darroch, Fienberg, Glonek, and Junker 1993) that the Rasch (generalized Rasch) model is equivalent to a quasi-symmetric (partial quasi-symmetric) model with proper moment restrictions. A quasi-symmetric model for the three-sample case with $\mu_{123} = 0$ means that all two-factor interactions are identical. A partial quasi-symmetric model assumes that some of the two-factor interactions are identical. Therefore, the dependence due to heterogeneity can be modeled by quasi-symmetric or by partial quasi-symmetric models. These two models can be fitted by using GLIM or other packages such as S-PLUS. More details are given in Agresti (1994) and the two recent review papers by IWGDMF (1995a,b). When both types of dependencies arise, these dependencies are confounded in the two-sample interaction terms.

Another approach for heterogeneity is to stratify the population into homogeneous subpopulations, where stratification is based on observable covariates. Evans et al. (1994) proposed a unified approach using log-linear models when the heterogeneity effects can be explained by the observable covariates. They also extended the approach to open populations as well as provided a model selection procedure.

2.3 SAMPLE-COVERAGE APPROACH

As discussed in the Introduction, overlap information plays an important role in estimating the number of missing animals. The main purposes of the sample-coverage approach are to provide a measure to quantify the overlap information and also to propose some parameters to quantify dependence among samples.

The concept of sample coverage is originally from I. J. Good and A. M. Turing, and it has been used to deal with species estimation for heterogeneous communities (see Bunge and Fitzpatrick 1993). The concept has also been modified to obtain population size estimators for multiplicative capture-recapture models (Table 1) and for the general dependent models (see Chao and Tsay 1998) for three samples and Tsay and Chao (2001) for any number of samples.

In this approach, the sample coverage is used as a measure of the overlap fraction. The basic idea is that the sample coverage can be well estimated even in the presence of two sources of dependencies. For example, the estimated sample coverage for the general dependent models is the average (over all available samples) of the fraction of animals captured more than once (Chao and Tsay 1998). Note that singletons clearly cannot contain any overlap information. Thus, an estimate of population size can be derived via the relationship between the population size and the sample coverage.

This approach aims to model dependence by coefficient of covariation (CCV) parameters based on either a fixed-effect or a random-effect model. To intuitively understand the CCV parameters, we consider a random-effect approach and assume for the moment that there is no list dependence but that there is heterogeneity. This random-effect approach assumes that the $\{(P_{i1}, P_{i2}, \dots, P_{it}), i = 1, 2, \dots, N\}$, where P_{ij} denotes the capture probability of the i th individual in the j th sample, are a random sample from a t -dimensional distribution $F_{P_1, P_2, \dots, P_t}(p_1, p_2, \dots, p_t)$. The CCV for samples j and k is defined as

$$\alpha_{jk} = \frac{E[(P_j - \mu_j)(P_k - \mu_k)]}{\mu_j \mu_k} = \frac{\text{cov}(P_j, P_k)}{\mu_j \mu_k} = \frac{E(P_j P_k)}{\mu_j \mu_k} - 1, \quad (2.6)$$

where $\mu_j = E(P_j)$ denotes the average capture probability for the j th sample.

The magnitude of α_{jk} measures the degree of the dependence of samples j and k . However, it is an overall measure of dependence since the two types of dependencies are confounded in this parameter and cannot be easily separated. If the two samples are independent, then $\alpha_{jk} = 0$. The two samples are positively (negatively) dependent if $\alpha_{jk} > 0$ ($\alpha_{jk} < 0$).

The CCV for more samples can be similarly defined. For example, the CCV for three samples under a random-effect model can be expressed as

$$\alpha_{jkm} = \frac{E[P_j - E(P_j)][P_k - E(P_k)][P_m - E(P_m)]}{\mu_j \mu_k \mu_m}.$$

In the independent case, all CCVs vanish. Under a multiplicative heterogeneous model that $P_{ij} = p_i$, the CCV for any two samples becomes the square of the CV of $\{p_1, p_2, \dots, p_N\}$ and thus any two samples are positively correlated. The parameter CV has been used to measure the extent of heterogeneity in ecological models (Lee and Chao 1994). When both types of dependencies exist, a fixed-effect model is needed (see Chao and Tsay 1998).

In the two-sample case, there are three observable cells (animals captured in sample 1 only, animals captured in sample 2 only, and animals captured in both samples) whereas four parameters ($N, \mu_1, \mu_2, \alpha_{12}$) exist. Therefore, the data are insufficient for estimating dependence unless the dependence measure is set to some value or additional covariates are available. The usual independence assumption is equivalent to setting $\alpha_{12} = 0$, which implies the Petersen estimator given in Section 2.1. Seber (1982, p. 86) justified that the bias of the Petersen estimator due to heterogeneity in catchability could be reduced if two different sampling schemes were used (e.g., trapping and then resighting or netting and then angling). Note that, in such cases, the covariance of the two sets of catchabilities vanishes.

Consequently, the CCV in Equation (2.6) is zero and the two samples are independent, although catchabilities are allowed to vary among animals.

For the three-sample case, there are seven observable categories (i.e., z_{100} , z_{010} , z_{001} , z_{110} , z_{101} , z_{011} , and z_{111} defined in Section 2.2) and eight parameters (N , μ_1 , μ_2 , μ_3 , α_{12} , α_{13} , α_{23} , α_{123}). One constraint is still needed, yet it is possible to model dependence. Thus, at least three samples are required to reasonably estimate any dependence measures.

As shown in Chao and Tsay (1998) and Tsay and Chao (2001), when there are at least three samples and the overlap information is sufficiently high, the sample-coverage approach yields an estimate for the population size using estimated sample coverage and estimated CCVs. The constraint is satisfied when the heterogeneity effects follow a gamma type of distribution. However, if the overlap information is not high enough, which means the fraction of singletons is relatively large, the resulting estimated standard error (SE) might become quite large. Instead, the sample-coverage approach produces a stable lower bound for positively dependent samples when the above-mentioned estimated SE is not acceptable. We feel that, in this case, the data do not contain enough information so the undercount cannot be accurately measured due to insufficient overlapping. All the sample-coverage estimates can be computed from the program CARE mentioned previously in Section 2.1.

3. CONTINUOUS-TIME MODELS

Compared with discrete-time models, there has been relatively little published research for the continuous-time counterparts. The papers by Craig (1953) and Darroch (1958) dealt with homogeneous populations. Becker (1984) was the first to establish a counting process framework. Most subsequent authors have followed this approach, which will be outlined below.

Suppose that the experiment terminates at time τ and $C_i(t)$ denotes the number of times the i th animal has been caught in $[0, t]$, $0 \leq t \leq \tau$, $i = 1, 2, \dots, N$. Each $\{C_i(t); 0 \leq t \leq \tau\}$ is a continuous-time counting process with capture intensity $\lambda_i(t)$, which corresponds to the capture probability in the discrete-time case. The intensity for the i th animal, $\lambda_i(t)$, is defined as $\lambda_i(t)dt = P\{dC_i(t) = 1 \mid \mathcal{F}_{t-}\}$, where \mathcal{F}_t is the capture history that has occurred up to time t and $dC_i(t) = 1$ can be intuitively interpreted as capturing animal i in a small time interval around time t .

Becker's (1984) paper considered a continuous-time analog of \mathcal{M}_t , i.e., $\lambda_i(t) = \lambda_0(t)$, where $\lambda_0(t)$ is any arbitrary time-varying function in $[0, \tau]$. He constructed an estimating function based on a martingale method. For the same model, Becker and Heyde (1990) and Yip, Fong, and Wilson (1993) subsequently developed the MLE as well as a class of high-efficiency martingale-based estimators. Wilson and Anderson (1995) and Wilson and Collins (1992) provided simulation comparisons.

As in the discrete-time models, a general class of models can be similarly formulated. The intensity for model \mathcal{M}_{tbh} is given by

$$\lambda_i(t) = \begin{cases} \alpha_i \lambda_0(t) & \text{until first capture,} \\ \tau \alpha_i \lambda_0(t) & \text{for any recapture.} \end{cases} \quad (3.1)$$

Here $\lambda_0(t)$, $\{\alpha_1, \alpha_2, \dots, \alpha_N\}$, and τ represent the effects of time, heterogeneity, and behavioral response. Thus, all continuous-time analogs of \mathcal{M}_{tbh} , \mathcal{M}_{bh} , \mathcal{M}_{th} , \mathcal{M}_{tb} , \mathcal{M}_{t} , \mathcal{M}_{b} , and \mathcal{M}_{h} can be obtained. Becker (1984) developed a martingale estimator for model \mathcal{M}_{th} ($\lambda_i(t) = \alpha_i \lambda_0(t)$), where $\{\alpha_1, \alpha_2, \dots, \alpha_N\}$ are a random sample from a gamma distribution. However, this procedure might result in negative estimates, which motivated Chao and Lee (1993) and Yip and Chao (1996) to derive new estimators for model \mathcal{M}_{th} using the sample coverage and estimating function approach. For models \mathcal{M}_{b} and \mathcal{M}_{tb} , Yip, Xi, Chao, and Hwang (2000) proposed martingale-based estimators. There have been no estimators available for models \mathcal{M}_{bh} and \mathcal{M}_{tbh} .

When the heterogeneity effects can be modeled as a function of the covariates, several authors have developed estimation procedures. Let the associated covariates for the i th individual be $\mathbf{Z}'_i = (Z_{i1}, Z_{i2}, \dots, Z_{ik})$. Letting $\alpha_i = \exp(\beta' \mathbf{Z}_i)$ and $\tau = \exp(\alpha)$ in (3.1), we have a proportional hazard (Cox 1972) model,

$$\lambda_i(t) = \lambda_0(t) \exp(\beta' \mathbf{Z}_i + \alpha Y_i(t)), \quad (3.2)$$

where $\beta' = (\beta_1, \beta_2, \dots, \beta_k)$ is a vector of unknown coefficient parameter and $Y_i(t) = I$ (the i th animal has been captured in $(0, t)$) denotes the prior capture history. Yip, Huggins, and Lin (1996) used a partial likelihood to get estimators of the coefficients first; then the Horvitz–Thompson estimator was employed to obtain an estimated population size. Lin and Yip (1999) assumed a parametric form for $\lambda_0(t)$, i.e., $\lambda_0(t) = \exp(\beta_0)$, and proposed a martingale-based method for this special parametric type of model \mathcal{M}_{tbh} .

We now link the continuous-time models to recurrent event analysis. In many studies, individual subjects may experience repeated events and times of each event, and related covariates are recorded. Examples in industrial reliability include the successive failure or repair times of a component or a system (see Lawless and Thiagarajah (1996) and references therein). The repeated events in medical studies include the recurrences of tumors, infection, or other diseases. There is rich literature on the recurrent event analysis in the context of engineering reliability and medical statistics. A collection of papers appears in a special 1997 issue of *Statistics in Medicine*. Wei and Glidden (1997) classified all the models into five families, including Andersen–Gill type models and frailty models (Andersen, Borgan, Gill, and Keiding 1993). Most of the approaches have adopted a form of Cox's model based on the counting process approach. If we regard each capture as a recurrent event, then the continuous-time capture–recapture time with intensity (3.2) can be treated as a special case of recurrent event analysis. Therefore, a variety of these models might be applied to capture–recapture data.

4. APPLICATIONS

In addition to biological and ecological sciences, the capture–recapture models have been applied to other disciplines. This section briefly reviews the applications of capture–recapture models to epidemiology, health sciences, the census undercount problem, software reliability, and others.

Epidemiology and Health Sciences. The purpose of many epidemiological surveillance studies is to estimate the size of a population by merging several existing but incomplete lists of names. For example, a recent study estimates the number of total infected in an outbreak of the hepatitis A virus in northern Taiwan (Chao et al. 1996) based on three sources. As shown in IWGDMF (1995a,b), other similar examples arise in various disease categories such as birth defects, cancer, diabetes, drug use, infectious diseases, injuries, and others. In a traditional approach, cases in various lists are merged and any duplicate cases are eliminated. This approach assumes complete ascertainment and does not correct or adjust for underascertainment. However, in most studies, complete ascertainment is a nearly unattainable ideal.

If each list is regarded as a trapping sample and identification numbers and/or names are used as tags or marks, then it is similar to a capture–recapture setup for wildlife population estimation. Two major differences between wildlife and human applications are noted: (i) there are usually more trapping samples in wildlife studies, whereas in most epidemiological surveys, only two to four lists are available; (ii) there is a natural time ordering in animal experiments, but generally no such order exists in epidemiological lists or the order may vary with individuals. Therefore, estimation procedures valid for wildlife populations may not be directly adapted for use in human populations. Hook and Regal (1995), IWGDMF (1995a,b), and Chao (1998) provided overviews of the models specifically for epidemiological applications.

Epidemiologists recently have shown renewed and growing interest in the use of capture–recapture models (see LaPorte, McCarty, Tull, and Tajima 1992; IWGDMF 1995a,b). Currently, only discrete-time models have been applied to this area. It is expected that continuous-time models will become potentially useful because of the availability of on-line disease monitoring systems.

Census Undercount Adjustment for Multiple-System Data. The census undercount problem has been extensively discussed in the literature. A series paper by Fienberg (1992) in *Chance* described the controversial issue of the adjustment of the U.S. census undercount. Using the capture–recapture approach, we can provide a view on a special type of census undercount problem from the standpoint of animal abundance estimation.

A capture–recapture approach involves the census data and postenumeration survey (PES) that is conducted after the census. As discussed in Section 2.3, for only two lists, there is no way to model the dependence between the census and its PES unless some covariates are used. If an additional list is available, models incorporating dependence are possible. Zaslavsky and Wolfgang (1993) considered the additional list compiled from the administrative records of state and federal government agencies. For this special type of census data, Darroch et al. (1993) used a log-linear approach and Chao and Tsay (1998) proposed the use of a sample-coverage method.

Software Reliability. The number of errors (bugs, faults) in software is an important criterion in evaluating software reliability. Before the release of a piece of software, it is usually debugged independently by several people. Traditional debugging removes any error when it is detected. However, Nayak (1988) found substantial information can be

gained if a recapture debugging process is applied. In a recapture debugging, errors can be redetected; a detected error is still removed but a counter is inserted to record each time the error would have recurred. If each software error is regarded as a bug, detection time is capture time, and each tester is regarded as a trapping sample, then a capture–recapture model can be applied to estimate the number of undetected bugs (see Nayak 1988; Yip 1995; Voas and McGraw 1997).

Others. Other interesting applications also include the estimations of plant populations (Alexander, Slade, and Kettle 1997), rare and elusive populations (e.g., homeless persons, disabled patients, or mentally ill people), and the number of species in a community (Colwell and Coddington 1994; Boulinier, Nichols, Sauer, Hines, and Pollock 1998). In a species problem, tagging or marking is not needed because presence–absence of species by sightings would suffice for providing information on species overlap. The software EstimateS, which provides various estimates of species richness, can be downloaded from Colwell’s website at <http://vicery.eeb.uconn.edu/estimates>.

5. DISCUSSION

In this article, closed capture–recapture models in both discrete and continuous time, together with their associated methods for estimating population size, are reviewed. We note that the number of catchable individuals is the target to be estimated. If it is impossible to capture some animals in any sample, precluding overlap information being obtained, then those animals cannot be included in the population. An extreme example is the case where the first trapping sample is conducted inside a fence and the second trapping sample is conducted outside the fence. In this case, there is no way to collect overlap information, and hence capture–recapture methods are not applicable to estimate the total number of animals in the area involved.

Another serious limitation of the capture–recapture methods is that a significant amount of overlapping information is required to model the dependence among samples and to obtain a precise estimator for the population size. Coull and Agresti (1999) demonstrated that the likelihoods under some random-effect models for severe heterogeneity and/or sparse data become quite flat and the resulting estimators become unstable; the associated confidence intervals also tend to be wide to reflect large amounts of uncertainty. They also cautioned that simpler models assuming homogeneity usually produce narrow but overly optimistic intervals, with the actual coverage probability being much lower than the nominal level. Chao et al. (1996) showed that the sample-coverage approach would yield estimators with large variances when there is insufficient overlap in samples. A general prescription of how large the overlap information should be is still unclear and remains an issue worthy of further study.

There are other interesting and promising directions for future research on closed models. Some topics that reflect the author’s interest and reading are suggested below.

Discrete Versus Continuous Time. Continuous-time models require that the time for each capture be recorded; thus, more efforts are usually needed. These models provide

more information than discrete-time models. We would expect that estimators based on continuous-time models are preferable, in some senses, to those based on their corresponding discrete-time models. However, Wilson and Anderson (1995) indicated for some special models that there was no reduction in the mean squared error for a continuous-time estimator over that for a discrete-time model on the same simulated data. More investigation is needed to compare the two types of models.

Combination of Closed and Other Models. Pollock (1982) proposed an important robust design that combines the features of both closed and open populations. This design has several advantages over the traditional Jolly-Seber models. Skalski and Robson (1982) considered the integration of mark and removal models. Recent developments include the combination of capture/recapture methods with line transect sampling (Manly, McDonald, and Garner 1996; Borchers, Zucchini, and Fewster, 1998). Similar types of integrated models have also been developed to cover other sampling methods, such as tag-recovery, tag-resight, catch-effort, and change-in-ratio studies (e.g., Barker 1997). Huggins and Yip (1999) proposed a weighted martingale method, akin to a moving average, to allow the use of closed models in the estimation of the size of a smoothly changing open population. Further developments are expected for both integrated models and moving-average approaches.

Bayesian Approaches. Complicated calculations in Bayesian approaches can now be handled by computer-intensive algorithms through the use of Gibbs sampling, a Markov chain Monte Carlo method. George and Robert (1992) and Lee and Chen (1998) have applied Gibbs sampling to capture-recapture models (see Table 1). One advantage of the Bayesian approaches, as shown in Lee and Chen (1998) for the multiplicative model, \mathcal{M}_{tb} , is that even nonidentifiable models can be treated without any restrictions on parameters. More research in this fruitful approach is anticipated.

Comparisons of Various Approaches. A wide range of statistical methods has been applied to the analysis of closed models. Several researchers have completed comparative studies based on either real data sets or simulations (Seber 1992; Schwarz and Seber 1999). More practical guidelines about the relative merits of various methods for point and interval estimation are still needed. Systematic comparisons between Bayesian and non-Bayesian approaches are also of interest.

Model Uncertainty and Model Selection. Model selection has played an important role in statistical inference. Information-theoretic approaches and likelihood-based procedures are usually adopted (Burnham and Anderson 1998). However, Stanley and Burnham (1998) noted that the likelihoods for some heterogeneous models are not computable. They also commented that the current model selection procedure in CAPTURE usually selects an inappropriate model in the simulations. Stanley and Burnham (1998) proposed the use of a model-averaging concept (Buckland, Burnham, and Augustin 1997), in which weighted estimates from competing models are combined. Norris and Pollock (1996a) also considered model uncertainty in the estimation of variances. The approach, which accounts for model uncertainty in inferences, merits more attention and use.

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