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Inference for capture–recapture experiments in continuous time with variable capture rates

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SUMMARY

A two-step procedure based on a partial likelihood is proposed to estimate the size of a closed population for multiple recapture studies in continuous time when the capture rates are permitted to depend on covariates associated with individuals. The asymptotic and small-sample properties of the resulting estimators are investigated.

Some key words: Capture–recapture experiment; Covariate; Martingale; Partial likelihood.

1. INTRODUCTION

The analysis of capture–recapture experiments is often based on the assumption that capture probabilities are equal for all individuals in the population being caught. It has long been recognised that this assumption is often violated. Indeed, equal capture probability is only a convenient mathematical assumption with no empirical justification. Manly (1970), Gilbert (1973) and Carothers (1973) have shown that heterogeneity can cause substantial bias in commonly-used estimators. Burnham & Overton (1978) and Yip (1991) assumed a beta distribution to model the individual capture probabilities. Chao & Lee (1992) provided an estimator for a heterogeneous population using sample coverage. Seber (1982) and Otis et al. (1978) have pointed out that catchability may vary with characteristics of the individual such as age, with physical conditions, or with environmental factors. For the discrete case with distinct capture occasions, Huggins (1989) used covariates to model heterogeneity, a conditional argument to estimate the parameters associated with the model for the capture probabilities, and a method of moments to estimate the population size. Here we employ a similar two-step process in continuous time, first using a partial likelihood applied to the counting processes of recaptures of individuals already captured to estimate the parameters in the model for the capture intensity, then a method of moments to estimate the population size. The work here fits into the model \mathcal{M}_h classification of Pollock (1993). Also, Lee & Chao (1994) recently suggested a coverage estimator for the population size with heterogeneous and time-dependent and behaviour-dependent capture probabilities.

To motivate our work, consider a continuous time capture–recapture experiment for a closed population of a certain type of bird, where the capture intensities depend on covariates assumed to be time-independent during the experimental period. Simulated data from a population of 50 birds with captures occurring over a two-unit period, where the capture intensities depend on sex and weight, are given in Table 1.

Birds are marked at the time of their first capture and information regarding the covariates is

Table 1. *Simulated capture data based on $v = 50$ and $\tau = 2$*

Sex	Weight	Capture times				Sex	Weight	Capture times			
1	19.49	0.47				0	19.69	0.66			
1	14.89	0.53	0.95	1.06	1.28	0	20.79	0.81			
1	21.03	1.77	1.79			0	14.55	0.27			
1	26.73	0.57				0	21.16	0.11	0.68		
1	23.97	0.03	1.41	1.79		0	20.16	1.66			
1	23.04	0.75				0	20.01	0.73			
1	19.04	0.30				0	21.21	0.83	1.23		
1	19.41	1.96				0	18.40	0.48			
1	23.51	1.44				0	20.32	0.03	1.46		
1	19.56	1.43				0	19.81	0.22	0.78	1.31	1.45
1	22.17	1.03	1.46			0	24.09	1.21	1.39		
1	17.09	1.06				0	21.71	0.42	0.58	1.17	
1	17.11	1.98				0	22.05	0.70			
1	21.42	1.08	1.44			0	14.88	0.39	1.11	1.67	
1	20.82	1.70				0	19.93	0.23	0.41	1.69	
1	20.97	0.77	1.30	1.67	1.91	0	21.70	0.17	0.66		
0	20.90	0.99	1.47			0	21.29	0.56	0.57		
0	23.37	0.67	1.57			0	17.06	0.44	1.27		

noted. At subsequent captures their marks are noted. It is assumed that the birds do not lose their marks during the experimental period and that, apart from time allowed for marking or noting of the marks and information regarding the covariates, the captured birds are released immediately. Every individual is assumed to be catchable throughout the whole duration of the experiment. The birds are labelled $1, 2, \dots, v$. Let $N_i(t)$ denote the number of times bird i is caught in $[0, t]$, where $t = 0$ corresponds to the capture of the first bird. In this paper the time parameter t is assumed to vary in the finite interval $[0, \tau]$. Each $\{N_i(t); t \geq 0\}$ is a continuous time process with right-continuous sample path and assumed intensity function $\lambda_i(t) = \exp(\beta'Z_i)\lambda_0(t)$, where β is a vector of p unknown coefficients, $Z_i = (Z_{i1}, \dots, Z_{ip})'$ the vector of p time-independent covariates for the i th bird, and $\lambda_0(t) > 0$ for all t . We suppose that the birds behave independently, so that

$$(Z_i(t), \{N_i(t); t \in [0, \tau]\}) \quad (i = 1, \dots, v)$$

are independent and identically distributed. As the (Z_i) represent characteristics of birds, such as age or weight, there is no loss in supposing the (Z_i) are bounded.

The history of the entire processes up to time t is represented by \mathcal{F}_t , the σ -field generated by the counting processes $\{N_i(s)\}$ up to time t and their associated covariate information (Z_i) over the time interval $[0, t]$. Note that \mathcal{F}_t contains the covariate information of captured individuals only.

By the Doob–Meyer decomposition,

$$\mathcal{M}_i(t) := N_i(t) - \int_0^t \lambda_i(u) du \tag{1.1}$$

is a zero mean martingale square integrable on $[0, \tau]$ (Andersen & Gill, 1982; Gill, 1984), with

$$\langle \mathcal{M}_i, \mathcal{M}_i \rangle(t) = \Lambda_i(t), \quad \langle \mathcal{M}_i, \mathcal{M}_j \rangle(t) = 0 \quad (i \neq j),$$

where

$$\Lambda_i(t) = \int_0^t \lambda_i(u) du,$$

as a consequence of the assumption that birds i and j cannot be caught at the same time.

2. ESTIMATING THE PARAMETERS IN THE MODEL

In order to estimate β we use a partial likelihood applied to the counting processes of recaptures. Let

$$Y_i(t) = \begin{cases} 1 & \text{if individual } i \text{ has been captured before } t, \\ 0 & \text{otherwise.} \end{cases}$$

Then $Y_i(t)$ is predictable with respect to \mathcal{F}_t and $\text{pr}\{Y_i(t) = 1, \text{ for all } t \in [0, \tau]\} > 0$. The recapture process $M_i(t)$, which counts the number of times that a captured individual i has been recaptured before time t , may be written as

$$M_i(t) = \int_0^t Y_i(u) dN_i(u).$$

Note that, for $N_i(t) > 1$, $M_i(t) = N_i(t) - 1$; otherwise $M_i(t) = 0$. Another zero mean martingale $\mathcal{M}_i^*(t)$ is constructed to estimate the capture probabilities:

$$\mathcal{M}_i^*(t) := M_i(t) - \int_0^t Y_i(u) \exp(\beta'Z_i) \lambda_0(u) du = \int_0^t Y_i(u) d\mathcal{M}_i(u).$$

Consider the partial likelihood

$$L(\beta) := \prod_{i=1}^v \prod_{0 \leq t \leq \tau} \left\{ \frac{\exp(\beta'Z_i)}{\sum_{k=1}^v Y_k(t) \exp(\beta'Z_k)} \right\}^{dM_i(t)}.$$

Following § 5 of Gill (1984), the derivative of the log partial likelihood with respect to β is the martingale

$$\begin{aligned} U(\beta) &:= \sum_{i=1}^v \int_0^\tau \left\{ Z_i - \frac{\sum_{k=1}^v Y_k(t) Z_k \exp(\beta'Z_k)}{\sum_{k=1}^v Y_k(t) \exp(\beta'Z_k)} \right\} Y_i(t) d\mathcal{M}_i(t) \\ &= \sum_{i=1}^v \int_0^\tau Q_i(\beta) Y_i(t) d\mathcal{M}_i(t). \end{aligned}$$

Standard arguments (Andersen & Gill, 1982; Andersen et al., 1993) show that under regularity conditions we have asymptotically

$$v^{\frac{1}{2}}(\hat{\beta} - \beta) = \Omega^{-1} v^{-\frac{1}{2}} U(\beta), \tag{2.1}$$

where, if $\mathcal{J}(\beta)$ denotes minus the first derivative of $U(\beta)$, we have, as $v \rightarrow \infty$,

$$v^{-1} \mathcal{J}(\hat{\beta}) \rightarrow \Omega$$

in probability, and in distribution

$$v^{-\frac{1}{2}} U(\beta) \rightarrow N(0, \Omega), \quad v^{\frac{1}{2}}(\hat{\beta} - \beta) \rightarrow N(0, \Omega^{-1}).$$

The underlying cumulative hazard rate

$$\Lambda_0(t) := \int_0^t \lambda_0(s) ds$$

may be estimated by

$$\hat{\Lambda}_0(t; \hat{\beta}) := \int_0^t \frac{d\bar{M}(s)}{\sum_{i=1}^v Y_i(s) \exp(\hat{\beta}'Z_i)},$$

where $d\bar{M}(s) := dM_1(s) + dM_2(s) + \dots + dM_v(s)$.

Remark 1. The arguments of this section apply directly to the time-dependent case.

Remark 2. As we rely on recaptures to estimate the parameters in the model it is clear that we cannot estimate parameters corresponding to response to first capture. Nevertheless, we can estimate the parameters corresponding to the response to second or subsequent captures if necessary.

3. ESTIMATING THE POPULATION SIZE

We proceed following Huggins (1989). Let C_i denote the event that individual i is captured at least once in the course of the experiment. Given Z_i , the number of times individual i is captured in the course of the experiment has a Poisson distribution with mean $\exp(\beta'Z_i)\Lambda_0(\tau)$. Thus the probability of being caught in the course of the experiment is

$$p_i = 1 - \exp\{-\exp(\beta'Z_i)\Lambda_0(\tau)\}.$$

If the (p_i) were known, then the Horvitz–Thompson (1952) type estimator of ν would be

$$\sum_{i=1}^{\nu} \frac{I(C_i)}{p_i},$$

where $I(\cdot)$ denotes the indicator function. Thus, it is natural to estimate ν by

$$\hat{\nu} := \sum_{i=1}^{\nu} \frac{I(C_i)}{\hat{p}_i},$$

where $\hat{p}_i := 1 - \exp\{-\exp(\hat{\beta}'Z_i)\hat{\Lambda}_0(\tau; \hat{\beta})\}$. We show in the Appendix that, for large ν , the estimator $\hat{\nu}$ is approximately normal with mean ν and with variance estimated by

$$\begin{aligned} \hat{s}^2 := & \sum_{i=1}^{\nu} \frac{I(C_i)(1 - \hat{p}_i)}{\hat{p}_i^2} + \mathcal{D}'\mathcal{D}^{-1}(\hat{\beta})\mathcal{D} \\ & + \left\{ \sum_{i=1}^{\nu} \frac{I(C_i)(1 - \hat{p}_i) \exp(\hat{\beta}'Z_i)}{\hat{p}_i^2} \right\}^2 \int_0^{\tau} \frac{d\bar{M}(t)}{\{\sum_{j=1}^{\nu} Y_j(t) \exp(\hat{\beta}'Z_j)\}^2}, \end{aligned}$$

where

$$\mathcal{D} = \sum_{i=1}^{\nu} \frac{I(C_i)(1 - \hat{p}_i) \exp(\hat{\beta}'Z_i)}{\hat{p}_i^2} \left[Z_i \hat{\Lambda}_0(\tau; \hat{\beta}) - \int_0^{\tau} \frac{\sum_{j=1}^{\nu} Y_j(t) \exp(\hat{\beta}'Z_j) Z_j}{\{\sum_{j=1}^{\nu} Y_j(t) \exp(\hat{\beta}'Z_j)\}^2} d\bar{M}(t) \right].$$

4. SIMULATIONS

In order to examine the applicability of the asymptotic distribution in small samples and the validity of the estimated standard errors and the coverage probabilities of confidence intervals a simulation study was conducted. Four situations were considered which included two population sizes, 50 and 100 individuals, and two lengths of the experiment, 2 and 4 units of time. The simulation size was 10 000 per size-time combination. The baseline hazard $\lambda_0(t)$ was set to 1. The covariates considered were Z_1 , corresponding to sex, with half of the individuals assigned to each sex, and a continuous variable Z_2 , corresponding to weight, with a normal distribution of mean 20 and variance 4. We took $\beta' = (0.3, -0.02)$, so that males were more catchable than females and catchability declined with weight. For an average male, the probabilities of being caught at least once are 0.84 and 0.97 when $\tau = 2$ or $\tau = 4$ respectively. For an average female, the corresponding probabilities are 0.74 and 0.93.

Density estimates of the estimated population sizes are given in Fig. 1. When $\nu = 50$ and $\tau = 2$ the distribution is quite skewed (Fig. 1(a)); however, this skewness is reduced when $\tau = 4$ (Fig. 1(b)) or $\nu = 100$ (Fig. 1(c)) or both (Fig. 1(d)).

A summary of the simulations is given in Table 2. There is a small positive bias for $\hat{\nu}$ when $\tau = 2$, due to the long right tail of the distribution (Fig. 1(a), (c)), which is reduced when $\tau = 4$. The

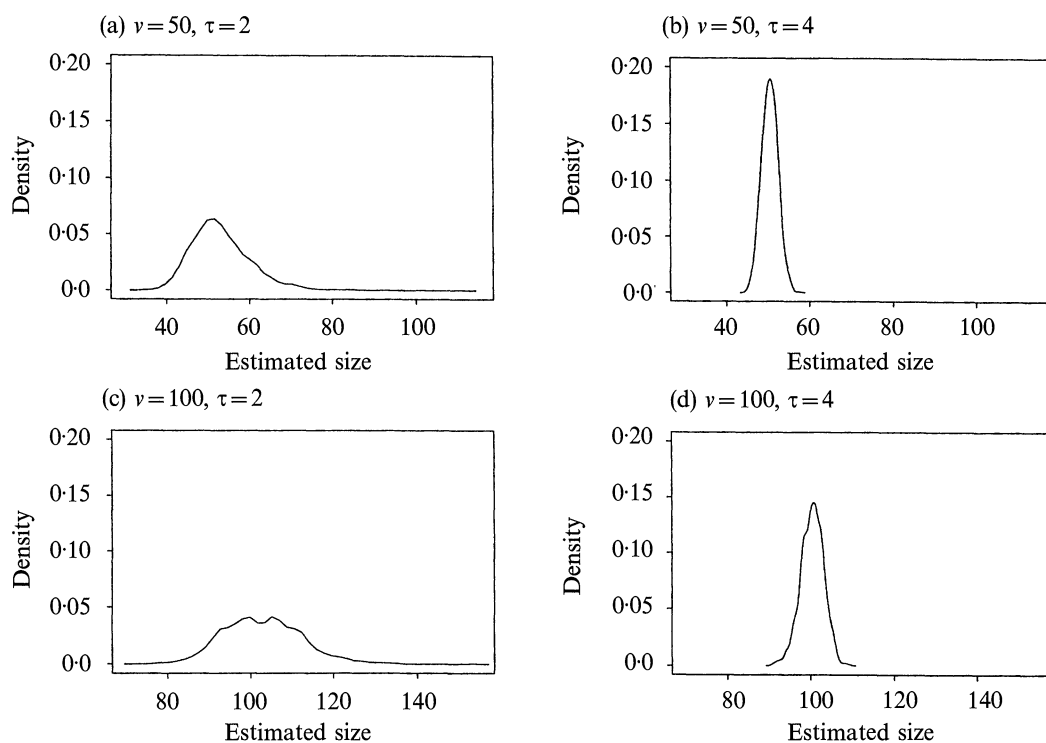


Fig. 1. Density estimates of simulated distribution of $\hat{\nu}$.

Table 2. Summary of simulation results

	$\nu = 50$		$\nu = 100$	
	$\tau = 2$	$\tau = 4$	$\tau = 2$	$\tau = 4$
Population size estimator, $\hat{\nu}$	53.17 (7.48)	50.50 (1.99)	102.87 (9.35)	100.48 (2.72)
Number of captured individuals	39.37 (2.86)	47.61 (1.50)	78.71 (4.05)	95.20 (2.11)
Standard error estimator, \hat{s}	7.19 (3.43)	2.07 (0.52)	9.07 (2.32)	2.78 (0.48)
Coverage probability of 0.95 confidence interval	0.964	0.959	0.953	0.959

Standard errors of the estimators are shown in parentheses.

mean of the standard error estimator \hat{s} is close to the true standard error of $\hat{\nu}$. The confidence interval has proper coverage probability.

The data of Table 1 were simulated from the above model with $\nu = 50$ and $\tau = 2$. In this case, $\hat{\beta} \approx (0.155, -0.022)$, $\hat{\nu} \approx 52.03$ and $\hat{s} \approx 7.36$.

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APPENDIX

Asymptotic properties of \hat{v}

We make the following decomposition:

$$\begin{aligned} v^{-\frac{1}{2}}(\hat{v} - v) &= v^{-\frac{1}{2}} \sum_{i=1}^v \left[\frac{I(C_i)}{1 - \exp\{-\exp(\hat{\beta}'Z_i)\hat{\Lambda}_0(\tau; \hat{\beta})\}} - \frac{I(C_i)}{1 - \exp\{-\exp(\beta'Z_i)\hat{\Lambda}_0(\tau; \beta)\}} \right] \\ &= v^{-\frac{1}{2}} \sum_{i=1}^v \left[\frac{I(C_i)}{1 - \exp\{-\exp(\beta'Z_i)\hat{\Lambda}_0(\tau; \beta)\}} - \frac{I(C_i)}{1 - \exp\{-\exp(\beta'Z_i)\Lambda_0(\tau)\}} \right] \\ &\quad + v^{-\frac{1}{2}} \sum_{i=1}^v \left[\frac{I(C_i)}{1 - \exp\{-\exp(\beta'Z_i)\Lambda_0(\tau)\}} - 1 \right]. \end{aligned} \quad (\text{A}\cdot 1)$$

By Taylor series expansion, the first term on the right side of (A·1) is asymptotically

$$K'\Omega^{-1}v^{-\frac{1}{2}} \sum_{i=1}^v \int_0^\tau Q_i(\beta)Y_i(t) d\mathcal{M}_i(t), \quad (\text{A}\cdot 2)$$

where

$$K := - \lim_{v \rightarrow \infty} v^{-1} \sum_{i=1}^v \frac{I(C_i)(1 - p_i) \exp(\beta'Z_i)}{p_i^2} \left[Z_i \Lambda_0(\tau) - \int_0^\tau \frac{\sum_{j=1}^v Y_j(t) \exp(\beta'Z_j) Z_j}{\{\sum_{j=1}^v Y_j(t) \exp(\beta'Z_j)\}^2} d\bar{M}(t) \right].$$

Similarly, the second term on the right-hand side of (A·1) is asymptotically

$$hv^{\frac{1}{2}} \sum_{i=1}^v \int_0^\tau \frac{Y_i(t) d\mathcal{M}_i(t)}{\sum_{j=1}^v Y_j(t) \exp(\beta'Z_j)}, \quad (\text{A}\cdot 3)$$

where

$$h := - \lim_{v \rightarrow \infty} v^{-1} \sum_{i=1}^v \frac{I(C_i)(1 - p_i) \exp(\beta'Z_i)}{p_i^2}.$$

The third term on the right-hand side of (A·1) is

$$v^{-\frac{1}{2}} \sum_{i=1}^v \left\{ \frac{I(C_i) - p_i}{p_i} \right\}. \quad (\text{A}\cdot 4)$$

Note that (A·2) and (A·3) are martingale integrals while (A·4) is a sum of independent and identically distributed random variables with zero mean and infinite variance. Thus, it follows from the martingale and classical central limit theorems that the random variable $v^{-\frac{1}{2}}(\hat{v} - v)$ is asymptotically zero-mean normal. By standard counting process martingale arguments, the limiting variances of (A·2) and (A·3) are, respectively, $K'\Omega^{-1}K$ and $h^2\psi$, which can be consistently estimated by $\hat{K}'\hat{v}\mathcal{I}^{-1}(\hat{\beta})\hat{K}$ and $\hat{h}^2\hat{\psi}$, where

$$\psi := \lim_{v \rightarrow \infty} \int_0^\tau \frac{d\Lambda_0(t)}{v^{-1} \sum_{j=1}^v Y_j(t) \exp(\beta'Z_j)},$$

and where \hat{K} , \hat{h} and $\hat{\psi}$ are obtained from K , h and ψ by replacing β , $\Lambda_0(\tau)$, p_i and v by $\hat{\beta}$, $\hat{\Lambda}_0(\tau; \hat{\beta})$, \hat{p}_i and \hat{v} . A simple calculation shows that the covariance between (A·2) and (A·3) is zero. Furthermore, the covariances between (A·2) and (A·4), and between (A·3) and (A·4) are also zero because $I(C_i)Y_i(t) = Y_i(t)$. Finally, the variance of (A·4) is

$$v^{-1} \sum_{i=1}^v \frac{1 - p_i}{p_i},$$

which can be consistently estimated by

$$\hat{v}^{-1} \sum_{i=1}^v \frac{I(C_i)(1 - \hat{p}_i)}{\hat{p}_i^2}.$$

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