

BAND RECOVERY MODEL INFERENCE WITH HETEROGENEOUS SURVIVAL RATES

Shen-Ming Lee, Li-Hui H. Huang and Shyh-Tyan Ou

*Feng Chia University, The Overseas Chinese Institute of Technology
and Center for Drug Evaluation, Taipei*

Abstract: In the context of band recovery models with heterogeneous survival rates, this paper estimates annual average survival rates by estimating the size of surviving population of banded birds. For the case of homogeneous survival rates, Brownie, Anderson, Burnham and Robson (1985) derived the relationship between the total number of surviving banded birds and annual average survival rates. However, their estimator of the total number of surviving banded birds is biased in the case of heterogeneous survival rates. We generalize their result to the case that annual average survival rates vary across individuals and years. In addition, the coefficient of variation for individual survival rates is used to reduce the estimation bias. The analytically intractable variances of proposed estimators are obtained by the bootstrap method. The proposed method is applied to data, and a simulation study is conducted to compare the performances of the estimators. Numerical results indicate that the proposed method works satisfactorily in general, and when there is a high degree of heterogeneity in particular.

Key words and phrases: Band recovery model, bootstrap sampling, coefficient of variation, heterogeneous survival rate, maximum likelihood estimation.

1. Introduction

In ecological research, it is important to estimate the survival probabilities of animals. Consequently, many techniques and sampling methods have been developed to estimate these quantities; see Seber (1970, 1982, 1986 and 1992), Burnham, Anderson, White, Brownie and Pollock (1987), Brownie and Pollock (1985), Pollock, Nichols, Brownie and Hines (1990) and Lebreton, Burnham, Clobert and Anderson (1992). In this line of research, models based on the release and recapture of a marked population have proven particularly useful for estimating the survival probabilities of free-ranging animals. One branch of this research, band recovery, is concerned with a single, terminal harvest recovery method, as synthesized by Brownie, Anderson, Burnham and Robson (1985). In a band recovery model, a sample of birds is captured, banded, and released into the population at roughly the same time each year for a number of successive

years. The banded population is assumed to be a representative sample of the population of interest.

Two common assumptions in the band recovery model are that marked birds have the same annual survival and recovery rates. Based on these assumptions, Seber (1970) and Robson and Youngs (1971) derived the maximum likelihood (ML) estimator for survival rate in the time-specific model. Brownie Anderson, Burnham and Robson (1985) derived the bias-adjusted ML estimator for survival probability. However, these two assumptions are not generally valid since survival probabilities can vary with individual effects (e.g., gender, weight and so on). Little work has been done with respect to heterogeneous survival probabilities. Pollock and Raveling (1982) and Nichols, Stockes, Hines and Conroy (1982) included heterogeneity in the band recovery model. They found that Seber's maximum likelihood estimator for the annual survival rate is positively biased when the band recovery rate and the survival rate are positively correlated or uncorrelated, and negatively biased when they are negatively correlated. Moreover, the bias increases with the degree of heterogeneity. Without a time effect, Burnham and Rexstad (1993) pointed out that ignoring heterogeneity may result in an incremental increase in annual average survival rate estimates throughout the study period, and proposed a parametric estimator for the expected survival rate during year one. In contrast, a nonparametric approach to estimate annual average survival rates with heterogeneous survival rates is considered in this paper.

Brownie, Anderson, Burnham and Robson (1985) have discussed the relationship between the survival rate and the total number of surviving banded birds for the marked birds having the same annual survival and recovery rates. The purpose of this paper is to consider a Taylor series expansion to obtain an expression for the bias in the estimation of the total number of surviving banded birds under homogeneity whenever the heterogeneity of survival rates exists in practice. Therefore an improved estimator of the total number of surviving banded birds under heterogeneity is obtained. In this paper, we define the annual average survival rate in terms of the expected total number of surviving banded birds under the assumption of heterogeneous survival rates, and thus estimate annual average survival rates by estimating the total number of surviving banded birds. Regarding the estimation of the total size of the population of interest, Chao, Lee and Jeng (1992) and Lee and Chao (1994) applied the coefficient of variation of individual capture probabilities to reduce the bias caused by estimating the closed population size. In a similar vein, the coefficient of variation of individual survival rates is used to reduce the bias caused by estimating the surviving banded bird population. In fact, the proposed estimator is the same as Seber's estimator if heterogeneity is not present.

A preliminary discussion of the banding experiment is given in the next section. In Section 3, annual average survival rates are estimated by estimating the total number of surviving banded birds. A simulation study provides a more detailed examination of the proposed estimator in Section 4. In Section 5, data are analyzed and a brief comparison of estimators is made. In Section 6, conclusions about the performance and validity of the proposed estimator are drawn.

2. Preliminary Discussion of the Banding Experiment

A description of the sampling process of banded birds in the band recovery model is in order. Samples of adult birds are captured, banded, and released into the population at roughly the same time each experimental year for a number of successive years. Here the banded population is assumed to be a representative sample of the population of interest, but survival rates can vary with individual effects (e.g., gender, weights and so on).

Bands are collected from hunters who report banded birds they have shot. Band collection may continue for several years after the last release of banded birds. A year is the period between successive releases of banded birds. The period of survival is the time from the banding in the i th year to the banding in the $(i + 1)$ th year.

For convenience, we let k represent the number of successive years in which banded birds are released and l represent the number of years during which recoveries are recorded. For most cases, band recovery model studies have $k \leq l$. In this paper, only $k = l$ is considered since after k years (including the k th year), annual average survival rates are not estimable. See Brownie, Anderson, Burnham and Robson (1985) for a detailed discussion. Suppose N_i banded birds are released in the i th experimental year, N_i^* banded birds survive up to the i th release, S_i^* is the annual average survival rate in the i th year, and $R_{i,j}$ is the number of birds banded in the i th year and recovered in the j th year, $i = 1, \dots, k$, $i \leq j$. With regard to individual and time effects, define $S_m^{(i)}$ as the individual effect associated with the survival rate of the m th bird banded in the i th year while e_r is the time effect associated with survival rates in the r th year. Finally the individual survival rate of the m th bird banded in the i th year for the r th year is defined as $S_{m,r}^{(i)} = S_m^{(i)} e_r$, $i < r$.

In this paper, we assume that the first two moments of $S_m^{(i)}$ are the same for each experimental year. There are two possible ways to treat the moments of $S_m^{(i)}$. Firstly, individual survival rates could be treated as parameters if individual effects are viewed as fixed. Secondly, individual survival rates could be treated as random variables if the individual effects for each year are ascribed to the whole population. From the viewpoint of the experimental design, the former and the

latter cases can be referred to as the fixed effects model and the random effects model, respectively. Moreover, the random effects model is the general case of the fixed effects model.

For the fixed effects model, the $S_m^{(i)}$ are parameters, the first two moments of $S_m^{(i)}$ are

$$\begin{aligned} \text{Assumption (A)} \quad & \sum_{m=1}^{N_i} S_m^{(i)} / N_i = \bar{S}, & i = 1, \dots, k, \\ \text{Assumption (B)} \quad & \sum_{m=1}^{N_i} (S_m^{(i)} - \bar{S})^2 / (N_i \bar{S}^2) = \gamma^2, & i = 1, \dots, k. \end{aligned}$$

In words, \bar{S} is the average of individual effects for each banding year and γ is the coefficient of variation for $S_m^{(i)}$ in the i th banding year, $m = 1, \dots, N_i$.

For the random effects model, the $S_m^{(i)}$ are random variables, the continuous versions of Assumptions (A) and (B) are

$$\begin{aligned} \text{Assumption (A}^*) \quad & \int s dF(s) = S_0, \\ \text{Assumption (B}^*) \quad & \int s^2 dF(s) / S_0^2 - 1 = \gamma_0^2, \end{aligned}$$

where $F(s)$ stands for the distribution of individual effects. Note that the form of the distribution of $S_m^{(i)}$ is not specified. In the following section, we show that the proposed method is valid under either Assumptions (A) and (B) or Assumptions (A*) and (B*).

3. Estimation of Annual Average Survival Rates

For convenience, we assume the i th band recovery rate, f_i , varies across years and is independent of individual survival rates; that is, recoveries are time-specific and there is no relationship between the survival rate and the recovery rate. In fact, a similar method can be applied to deal with heterogeneous recovery rates. The case of homogeneous survival rates for the band recovery model is considered first.

3.1. Homogeneous case

Suppose $S_m^{(i)} = \bar{S}$ for all $i = 1, \dots, k$ and $m = 1, \dots, N_i$, and the annual survival rate in the r th year is $S_r = \bar{S}e_r$. Here \bar{S} and e_r are not estimable. Based on the empirical definition of S_r , it can be rewritten as

$$S_r = \frac{\mathbb{E}(N_{r+1}^*)}{\mathbb{E}(N_r^*) + N_r}. \quad (1)$$

Seber (1970) derived the maximum likelihood estimator of S_r as

$$\hat{S}_r = \frac{R_r(T_{r+1} - R_{r+1})N_{r+1}}{N_r T_r R_{r+1}},$$

where R_r is the total number of birds banded in Year r and recovered at the end of experiment, and T_r is the total number of birds banded before Year r (including Year r) and recovered after Year r . If C_r is the total number of birds recovered in Year r , we can write $T_1 = R_1$, $T_r = T_{r-1} - C_{r-1} + R_r$, $r = 2, \dots, k$, and $T_{k+j} = T_{k+j-1} - C_{k+j-1}$, $j = 1, \dots, l - k$.

Because of the bias of \hat{S}_r , Brownie, Anderson, Burnham and Robson (1985) proposed the bias-adjusted maximum likelihood estimator of S_r as

$$\hat{S}_{r(b)} = \frac{R_r(T_{r+1} - R_{r+1})(N_{r+1} + 1)}{N_r T_r (R_{r+1} + 1)}.$$

3.2. Heterogeneous case

For the case of heterogeneous individual effects, define $I_{m,r}^{(i)} = I(\text{the } m\text{th bird banded in the } i\text{th year survives to the } r\text{th year})$, where $I(\cdot)$ is the indicator function. Empirically, the annual average survival rate in the r th year can be written as

$$S_r^* = \frac{\sum_{i=1}^r \sum_{m=1}^{N_i} S_m^{(i)} I_{m,r}^{(i)}}{\sum_{i=1}^r \sum_{m=1}^{N_i} I_{m,r}^{(i)}} = \frac{E(N_{r+1}^* | F_r)}{N_r^* + N_r}, \tag{2}$$

where F_r denotes the σ -field generated by $\{I_{m,j}^{(i)}; j = i, \dots, r, i = 1, \dots, j, m = 1, \dots, N_i\}$. Here $N_1^* = 0$. Seen this way, an accurate estimate of S_r^* depends on an accurate estimate of the number of surviving birds. Also notice that if $S_m^{(i)} = \bar{S}$ for $i = 1, \dots, k$ and $m = 1, \dots, N_i$, we obtain $S_{m,r}^{(i)} = \bar{S}e_r = S_r$. Therefore, S_r^* is indeed the extension of S_r to account for individual effects. For heterogeneous $S_m^{(i)}$, the expected values of $R_{i,j}$ are listed in Table 1, where $\phi_{i,r} = \prod_{t=i}^r e_t$.

Table 1. Expected recoveries $E(R_{i,j})$ for the fixed effects model.

Banding Year	Birds Banded	1	2	3	...	k
1	N_1	$N_1 f_1$	$\sum_{m=1}^{N_1} (S_m^{(1)}) \phi_{1,1} f_2$	$\sum_{m=1}^{N_1} (S_m^{(1)})^2 \phi_{1,2} f_3$...	$\sum_{m=1}^{N_1} (S_m^{(1)})^{k-1} \phi_{1,k-1} f_k$
2	N_2		$N_2 f_2$	$\sum_{m=1}^{N_2} (S_m^{(2)}) \phi_{2,2} f_3$...	$\sum_{m=1}^{N_2} (S_m^{(2)})^{k-2} \phi_{2,k-1} f_k$
3	N_3			$N_3 f_3$...	$\sum_{m=1}^{N_3} (S_m^{(3)})^{k-3} \phi_{3,k-1} f_k$
⋮	⋮				⋮	⋮
k	N_k					$N_k f_k$

Burnham and Rexstad (1993) found that if $e_r = \bar{e}$ for all r , then S_r^* increases with r ; our extension explains this phenomenon as will be described in Section 4. The band recovery model with time effects and heterogeneous survival rates is considered next.

Notice that N_r^* can be rewritten as $N_r^* = \sum_{i=1}^{r-1} \sum_{m=1}^{N_i} I_{m,r}^{(i)}$. Therefore,

$$E(N_r^*) = \sum_{i=1}^{r-1} \sum_{m=1}^{N_i} (S_m^{(i)})^{r-i} \phi_{i,r-1}. \tag{3}$$

Specifically, if $S_m^{(i)} = \bar{S}$ for all $i = 1, \dots, k$ and $m = 1, \dots, N_i$ (survival rates are homogeneous), then

$$E(N_r^*) = \frac{N_r E(T_r - R_r)}{E(R_r)}. \tag{4}$$

To reduce the estimation bias due to heterogeneity, we compute the difference between $E(N_r^*)$ and $N_r E(T_r - R_r)/E(R_r)$, in the following proposition.

Proposition 1. *Given (A) and (B) in the time specific band recovery model with heterogeneous survival rates, the expected value of the surviving population in the r th year is*

$$\begin{aligned} E(N_r^*) &= \frac{N_r E(T_r - R_r)}{E(R_r)} - \frac{g_r(\mathbf{S})}{E(R_r)} \\ &= \frac{N_r E(T_r - R_r)}{E(R_r)} - \frac{1}{E(R_r)} \left\{ \sum_{i=1}^{r-1} N_r (r-i) N_i \bar{S}^{r-i+1} \right. \\ &\quad \left. \phi_{i,r-1} [e_r f_{r+1} + \dots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k] \right\} \gamma^2 + \mathfrak{R}_2, \end{aligned} \tag{5}$$

where $\mathbf{S} = (S_1^{(1)}, S_2^{(1)}, \dots, S_{N_1}^{(1)}, \dots, S_{N_r}^{(r)})$,

$$\begin{aligned} g_r(\mathbf{S}) &= N_r \sum_{i=1}^{r-1} \sum_{m=1}^{N_i} (S_m^{(i)})^{r-i} \phi_{i,r-1} \{f_r + S_m^{(i)} e_r f_{r+1} + \dots + (S_m^{(i)})^{k-r} \phi_{r,k-1} f_k\} \\ &\quad - \left[\sum_{i=1}^{r-1} \sum_{m=1}^{N_i} (S_m^{(i)})^{r-i} \phi_{i,r-1} \right] \left[\sum_{m=1}^{N_r} (f_r + S_m^{(r)} e_r f_{r+1} + \dots + (S_m^{(r)})^{k-r} \phi_{r,k-1} f_k) \right]. \end{aligned} \tag{6}$$

$\mathfrak{R}_2 = -\mathfrak{R}_1/E(R_r)$ and \mathfrak{R}_1 is the error term in the Taylor expansion of $g_r(\mathbf{S})$. (The content of \mathfrak{R}_1 is seen in Appendix A.)

Note that Proposition 1 is valid for the fixed effects model and Appendix A is the proof of Proposition 1, which includes a detailed expansion of $g_r(\mathbf{S})$ and the derivation of (5). Appendix B also shows that \mathfrak{R}_2 can be ignored in (5). The extension of Proposition 1 to the random effects case is the following.

Proposition 2. *Given (A^*) and (B^*) in the time specific band recovery model with heterogeneous survival rates, the expected value of the surviving population in the r th year is given by*

$$E(N_r^*) = \frac{N_r E(T_r - R_r)}{E(R_r)} - \frac{1}{E(R_r)} \left\{ \sum_{i=1}^{r-1} N_r (r-i) N_i S_0^{r-i+1} \phi_{i,r-1} [e_r f_{r+1} + \dots + (k-r) S_0^{k-r-1} \phi_{r,k-1} f_k] \right\} \gamma_0^2 + \mathfrak{R}_2, \tag{7}$$

$$\mathfrak{R}_2 = \frac{-1}{E(R_r)} \left\{ N_r \sum_{i=1}^{r-1} N_i \sum_{j=r}^k \phi_{i,j-1} f_j \left[\int s^{j-i} dF(s) - \left(\int s^{r-i} dF(s) \right) \left(\int s^{j-r} dF(s) \right) - (r-i)(j-r) S_0^{j-i} \gamma_0^2 \right] \right\}.$$

Note that the derivation of Proposition 2, obtained via a Taylor expansion, is valid for the random effects model. Since the derivation of Proposition 2 is similar to the case of Proposition 1 it is omitted here. If it is assumed that the recovery rates are heterogeneous and independent of the survival rates, the results of Proposition 2 still holds. Similar to the fixed effects case, \mathfrak{R}_2 in (7) can be ignored. Moreover, if $S_m^{(i)} \sim \text{Be}(\alpha, \beta)$, \mathfrak{R}_2 can be written as

$$\mathfrak{R}_2 = \frac{-1}{E(R_r)} \left\{ N_r \sum_{i=1}^{r-1} N_i \sum_{j=r}^k \phi_{i,j-1} f_j \left[\frac{\text{Beta}(\alpha + j - i, \beta)}{\text{Beta}(\alpha, \beta)} - \frac{\text{Beta}(\alpha + r - i, \beta) \text{Beta}(\alpha + j - r, \beta)}{(\text{Beta}(\alpha, \beta))^2} - (r-i)(j-r) \left(\frac{\alpha}{\alpha + \beta} \right)^{j-i} \frac{\beta}{\alpha(\alpha + \beta + 1)} \right] \right\}, \tag{8}$$

where $\text{Be}(\alpha, \beta)$ denotes the beta distribution, and $\text{Beta}(x, y)$ is beta function. Numerical results that show \mathfrak{R}_2 is negligible for a range of values of (α, β) are given in Appendix B. In general, there are no analytic results to show that \mathfrak{R}_2 is negligible under the fixed effects or the random effects model.

Next, we can estimate $E(N_r^*)$ with the help of Propositions 1 or 2. Based on (5) or (7) without \mathfrak{R}_2 , the proposed estimator of N_r^* is $\widehat{N}_r^* = [N_r(T_r - R_r) - \widehat{g}_r] / R_r$, where

$$\begin{aligned} \widehat{g}_r &= \left[\sum_{i=1}^{r-1} N_r (r-i) N_i \prod_{j=i}^{r-1} (\widehat{S}e_j) \right] \left[(\widehat{S}e_r) \widehat{f}_{r+1} + \dots + (k-r) \left[\prod_{t=r}^{k-r-1} (\widehat{S}e_t) \right] \widehat{f}_k \right] \widehat{\gamma}^2, \\ \widehat{S}e_r &= R_{r,r+1} / (N_r \widehat{f}_{r+1}), \quad \widehat{f}_r = R_{r,r} / N_r, \\ \widehat{\gamma}^2 &= \max \left\{ \frac{\sum_{i=1}^{k-2} R_{i+1,i+1} R_{i,i+2}}{\sum_{j=1}^{k-2} R_{j,j+1} R_{j+1,j+2}} - 1, \quad 0 \right\}. \end{aligned}$$

The derivation of \widehat{N}_r^* for the fixed effects model is given in Appendix C. For the random effects model, the expected values of $R_{i,j}$ can be expressed as $E(R_{i,j}) = N_i \phi_{i,j-1} \int s^{j-i} dF(s) f_j$, where $\phi_{i,j-1} = \prod_{k=i}^{j-1} e_k$. Apparently the expected values of $R_{i,j}$ for the fixed effects model (see Table 1) and for the random effects model are different. The terms $\widehat{S}e_r$ and $\widehat{\gamma}^2$ appearing in the fixed effects model will be replaced with $\widehat{S}_0 e_r$ and $\widehat{\gamma}_0^2$, respectively, in the random effects model. In fact, the moment estimators of $S_0 e_r$ and γ_0^2 are the same as $\widehat{S}e_r$ and $\widehat{\gamma}^2$.

With the help of \widehat{N}_r^* , the proposed estimator of S_r^* is defined as

$$\begin{aligned} \tilde{S}_r &= \frac{\widehat{N}_{r+1}^*}{\widehat{N}_r^* + N_r} \\ &= \frac{R_r \{N_{r+1}(T_{r+1} - R_{r+1}) - \widehat{g}_{r+1}\}}{R_{r+1}(N_r T_r - \widehat{g}_r)}. \end{aligned} \quad (9)$$

The analytically intractable variance of \tilde{S}_r is computed by the bootstrap sampling method. The variance estimates for \tilde{S}_r were derived as follows.

1. For given values of N_i and $R_{i,j}$, assume

$$\begin{aligned} &(R_{i,i}^*, R_{i,i+1}^*, \dots, R_{i,k}^*, N_i - R_i^*) \\ &\sim \text{Multinomial}\left(N_i, \frac{R_{i,i}}{N_i}, \frac{R_{i,i+1}}{N_i}, \dots, \frac{R_{i,k}}{N_i}, \frac{N_i - R_i}{N_i}\right). \end{aligned}$$

2. Generate the bootstrap data, $(R_{i,i}^*, R_{i,i+1}^*, \dots, R_{i,k}^*, N_i - R_i^*)$, from the distribution in Step 1 and compute \tilde{S}_r .
3. Repeat the first two steps 1000 times.
4. Use the 1000 estimates of \tilde{S}_r to obtain the variance of \tilde{S}_r .

Define the recovery rate as $f_r = E(C_r)/[E(N_r^*) + N_r]$, where C_r is the total number of birds recovered in Year r . This suggests an improved estimator of f_r is $\tilde{f}_r = C_r/[\widehat{N}_r^* + N_r]$. The variance of \tilde{f}_r is also obtained by the bootstrap method. However, we won't investigate the properties of \tilde{f}_r here since the performance of \tilde{f}_r depends on the performance of \widehat{N}_r^* .

4. Simulation Study

In this section, a simulation study is conducted to compare the performances of the bias-adjusted ML estimators $\widehat{S}_{r(b)}$ and the proposed estimator \tilde{S}_r . The combinations of (f_j, e_j, γ) conducted in the simulation are listed in the following.

- $(f_1, \dots, f_6) = (0.05, 0.05, 0.05, 0.5, 0.05, 0.05), (0.07, 0.03, 0.07, 0.3, 0.07, 0.03)$.
- $(e_1, \dots, e_6) = (0.99, 0.99, 0.99, 0.99, 0.99, 0.99), (0.81, 0.99, 0.81, 0.99, 0.81, 0.99)$.
- $0 \leq \gamma \leq 0.8$.

As mentioned in Section 2, individual effects can be treated as parameters (fixed-effect) or random variables (random-effect). Therefore two models for generating individual-effect factors are considered in the simulation. In the fixed-effect model, individual effects are specified. For each banding year, N_i individuals are divided into two equal groups. The two individual-effect factors, $S_1^{(i)}$ and $S_2^{(i)}$, are assigned to the two groups separately. Then the survival rates of the two groups are $S_1^{(i)}e_r$ and $S_2^{(i)}e_r$ in the r th year, respectively. Table 2 includes 13 different trials for the simulation. In the random-effect model, individual effects are generated from the Beta distribution; i.e., $S_m^{(i)} \sim Be(\alpha, \beta)$. Then the individual survival rates of the m th bird banded in the i th year and survived in the r th year will be $S_m^{(i)}e_r$. Simulations are conducted under these two models. For each trial, 1000 data sets are generated to compute $\hat{S}_{r(b)}$, \tilde{S}_r and S_r^* . The sample mean, the sample standard deviation, the sample root mean squared error (RMSE), and the relative bias are used to evaluate estimator performances. The sample standard deviations of \tilde{S}_r are computed by the bootstrap procedure described in Section 3.

Table 2. Description of the trial parameters ($N_i = 2000, i = 1, \dots, 6$).

Trial	1	2	3	4	5	6	7	8	9	10	11	12	13
$S_1^{(i)}$	0.30	0.25	0.20	0.15	0.50	0.40	0.30	0.20	0.10	0.60	0.50	0.40	0.30
$S_2^{(i)}$	0.30	0.35	0.40	0.45	0.50	0.60	0.70	0.80	0.90	0.60	0.70	0.80	0.90
\bar{S}	0.30	0.30	0.30	0.30	0.50	0.50	0.50	0.50	0.50	0.60	0.60	0.60	0.60
γ	0.000	0.167	0.333	0.500	0.000	0.200	0.400	0.600	0.800	0.000	0.167	0.333	0.500

Before comparing the performance of \tilde{S}_r and $\hat{S}_{r(b)}$, first we need to know the properties of S_r^* , and set these properties as the criteria for the comparisons. The properties of S_r^* are summarized corresponding to the 52 fixed-effect and random-effect models considered as follows.

1. With constant time effects e_i and homogeneous recovery rates f_j , S_r^* is an increasing function of the banding years and γ . This pattern coincides with the results of Burnham and Rexstad (1993). This phenomenon is considered as the criterion for evaluating the performances of estimators.
2. The values of S_r^* are not affected by time-specific recovery rates f_j , and S_r^* is still an increasing function of the banding years and γ .

It is reasonable to believe that a satisfactory estimator should provide a similar performance as S_r^* . The performances of the fixed-effect model and the random-effect model are investigated, and the robustness property for the proposed estimator is discussed in the following section.

4.1. Fixed-effect model

Due to space considerations, only trials 5, 7 and 9 are shown in detail in Table 3; other trials provide similar performances. The values of two individual-effect factors, $S_1^{(i)}$ and $S_2^{(i)}$, are determined before the experiment.

Table 3. Performance of $\hat{S}_{r(b)}$ and \tilde{S}_r .

Trial	Year	Relative Sample				Relative Bootstrap Sample				
		S_r^*	$\hat{S}_{r(b)}$	Bias	RMSE	\tilde{S}_r	Bias	S.E.	S.D.	RMSE
$\bar{S} = 0.5$ $\gamma = 0.0$	1	0.4049	0.4092	1.1%	0.0586	0.3837	-5.2%	0.0700	0.0703	0.0723
	2	0.4952	0.4946	0.1%	0.0561	0.4845	-2.2%	0.0592	0.0589	0.0594
	3	0.4048	0.4035	0.3%	0.0546	0.3823	-5.6%	0.0632	0.0615	0.0651
	4	0.4953	0.4973	0.4%	0.0615	0.5066	2.3%	0.0648	0.0642	0.0649
	5	0.4047	0.4038	-0.2%	0.0802	0.4140	2.3%	0.0879	0.0833	0.0835
$\bar{S} = 0.5$ $\gamma = 0.4$	1	0.4048	0.4596	13.5%	0.0821	0.4011	-0.9%	0.0764	0.0803	0.0792
	2	0.5176	0.5431	4.9%	0.0640	0.5186	0.2%	0.0619	0.0615	0.0603
	3	0.4385	0.4848	10.6%	0.0763	0.4392	0.2%	0.0712	0.0720	0.0710
	4	0.5432	0.5266	3.1%	0.0644	0.5452	0.4%	0.0684	0.0672	0.0662
	5	0.4515	0.4506	-0.2%	0.0866	0.4664	3.3%	0.0947	0.0919	0.0921
$\bar{S} = 0.5$ $\gamma = 0.8$	1	0.4050	0.6087	50.3%	0.2129	0.4313	6.5%	0.0837	0.0800	0.0831
	2	0.5864	0.6666	13.7%	0.1005	0.5906	0.7%	0.0661	0.0630	0.0625
	3	0.5322	0.6817	28.1%	0.1667	0.5500	3.3%	0.0818	0.0828	0.0838
	4	0.6720	0.6088	9.4%	0.0924	0.6746	0.4%	0.0823	0.0818	0.0811
	5	0.5746	0.5445	-5.2%	0.1051	0.5836	1.6%	0.1097	0.1114	0.1112

$\bar{S} = 0.5$ and $0 \leq \gamma \leq 0.8$, $(e_1, \dots, e_6) = (0.81, 0.99, 0.81, 0.99, 0.81, 0.99)$, $(f_1, \dots, f_6) = (0.07, 0.03, 0.07, 0.03, 0.07, 0.03)$, $N_i = 2000$, $i = 1, \dots, 6$.

With constant time effects e_i (compare Years 1, 3, 5 or Years 2, 4 in Table 3), \tilde{S}_r increases with the banding years and γ . In contrast, $\hat{S}_{r(b)}$ does not possess this property. With varying time effects e_i (Table 3), \tilde{S}_r and S_r^* have a similar pattern of change. With any value of γ , the relative bias of \tilde{S}_r is always less than 7%, but the relative bias of $\hat{S}_{r(b)}$ varies between 0.1% and 51%. This evidence indicates that \tilde{S}_r does a better job of estimating S_r^* than does $\hat{S}_{r(b)}$ in the presence of heterogeneity. The larger the value of γ is, the larger the relative bias of $\hat{S}_{r(b)}$. Notice also that bootstrap method works well for estimating the standard error of \tilde{S}_r . The estimated *s.d.* is quite close to the sample standard deviation of S_r^* . Regarding the sample RMSE, most of the time \tilde{S}_r produces smaller values of sample RMSE than $\hat{S}_{r(b)}$. The difference between them becomes more significant as the value of γ increases. Especially for $\gamma \geq 0.4$, the RMSE of \tilde{S}_r is much smaller than the sample RMSE of $\hat{S}_{r(b)}$. This indicates that \tilde{S}_r is preferable, particularly when the degree of heterogeneity is high. Moreover, we note that MSE(mean square error) is the sum of variance and the square of bias. The

estimator \tilde{S}_r generally reduces bias but increases the variance due to estimation of γ . Thus whether the reduction in the square of bias can compensate for the increase in variance clearly depends on the value of γ . When γ is relatively small, the usual estimators $\hat{S}_{r(b)}$ without estimating γ are not seriously biased, so the improvement in bias is quite limited. Thus our method cannot effectively reduce MSE. However if γ is relatively large the usual estimators $\hat{S}_{r(b)}$ have quite a large bias, warranting the use of the proposed procedure to reduce MSE.

4.2. Random-effect model

In practice, it is reasonable to consider individual-effect factors as random variables generated from the Beta distribution. Assume $S_m^{(i)}$ is distributed as $Be(\alpha, \beta)$. To avoid rounding error, we consider the restriction $0.01 \leq S_m^{(i)} \leq 0.99$ in the simulation process. The simulation results when $\alpha = \beta$ are summarized in Table 4. The value of $E(S)$ in Table 4 is 0.5. Based on Table 4, it is apparent that the proposed estimator is superior to the bias-adjusted ML estimator when γ is large enough; for example, $\gamma \geq 0.4$. In addition, the proposed estimator and the bias-adjusted ML estimator provide similar performance when γ is small. Meanwhile, the proposed estimators of survival rates increase with the banding year and γ , which is consistent with the fixed-effect model. The other results for the fixed-effect model are provided in Table 4.

Table 4. Performance of $\hat{S}_{r(b)}$ and \tilde{S}_r .

Trial	Year	S_r^*	Relative Sample			Relative Bootstrap Sample				
			$\hat{S}_{r(b)}$	Bias	RMSE	\tilde{S}_r	Bias	S.E.	S.D.	RMSE
$(\alpha, \beta) = (0.2812, 0.2812)$ $\gamma = 0.6995$	1	0.4946	0.6617	33.8%	0.1788	0.5124	3.6%	0.0764	0.0759	0.0779
	2	0.5746	0.6923	20.5%	0.1340	0.5768	0.4%	0.0720	0.0699	0.0696
	3	0.6226	0.6940	11.5%	0.1007	0.6237	0.2%	0.0728	0.0731	0.0723
	4	0.6553	0.6667	1.7%	0.0743	0.6553	0.0%	0.0776	0.0750	0.0743
	5	0.6794	0.6360	-6.4%	0.0953	0.7108	4.6%	0.1051	0.0991	0.1038
$(\alpha, \beta) = (1, 1)$ $\gamma = 0.5654$	1	0.4953	0.6131	23.8%	0.1321	0.5062	2.2%	0.0764	0.0762	0.0759
	2	0.5478	0.6406	16.9%	0.1123	0.5549	1.3%	0.0719	0.0733	0.0728
	3	0.5809	0.6397	10.1%	0.0887	0.5866	1.0%	0.0701	0.0693	0.0688
	4	0.6043	0.6172	2.2%	0.0714	0.6075	0.5%	0.0729	0.0716	0.0702
	5	0.6219	0.5781	-7.1%	0.0933	0.6285	1.1%	0.0941	0.0946	0.0937
$(\alpha, \beta) = (2.6250, 2.6250)$ $\gamma = 0.3999$	1	0.4943	0.5597	13.2%	0.0905	0.4997	1.1%	0.0742	0.0780	0.0774
	2	0.5212	0.5737	10.1%	0.0804	0.5253	0.8%	0.0690	0.0707	0.0695
	3	0.5386	0.5713	6.1%	0.0691	0.5399	0.2%	0.0664	0.0652	0.0646
	4	0.5515	0.5613	1.8%	0.0691	0.5543	0.5%	0.0684	0.0702	0.0692
	5	0.5607	0.5398	-3.7%	0.0833	0.5688	1.4%	0.0873	0.0889	0.0882

$\bar{S} = 0.5$, $(e_1, \dots, e_6) = (0.99, 0.99, 0.99, 0.99, 0.99, 0.99)$, $(f_1, \dots, f_6) = (0.05, 0.05, 0.05, 0.05, 0.05, 0.05)$, $N_i = 2000$, $i = 1, \dots, 6$.

Table 5. Sensitivity analysis on $\hat{S}_{r(b)}$ and \tilde{S}_r .

Trial	Year	Relative Sample				Relative Bootstrap Sample				
		S_r^*	$\hat{S}_{r(b)}$	Bias	RMSE	\tilde{S}_r	Bias	S.E.	S.D.	RMSE
$\gamma = 0.0$	1	0.4948	0.4916	-0.7%	0.0549	0.4689	-5.2%	0.0641	0.0645	0.0688
	2	0.4949	0.4941	-0.2%	0.0522	0.4754	-3.9%	0.0598	0.0588	0.0615
	3	0.4944	0.4988	0.9%	0.0547	0.4859	-1.7%	0.0584	0.0578	0.0579
	4	0.4947	0.4931	-0.3%	0.0572	0.4900	-0.9%	0.0593	0.0587	0.0583
	5	0.4955	0.5000	0.9%	0.0699	0.5132	3.6%	0.0761	0.0739	0.0753
$\gamma = 0.4$	1	0.4946	0.5451	10.2%	0.0762	0.4818	-2.6%	0.0690	0.0705	0.0706
	2	0.5215	0.5609	7.6%	0.0672	0.5103	-2.1%	0.0644	0.0652	0.0654
	3	0.5386	0.5599	4.0%	0.0599	0.5275	-2.1%	0.0617	0.0621	0.0623
	4	0.5504	0.5474	-0.5%	0.0597	0.5390	-2.1%	0.0630	0.0612	0.0614
	5	0.5578	0.5213	-6.5%	0.0790	0.5492	-1.5%	0.0791	0.0781	0.0776
$\gamma = 0.8$	1	0.4950	0.6798	37.3%	0.19530	0.5025	1.5%	0.0657	0.0670	0.0669
	2	0.6000	0.7199	20.0%	0.13580	0.5854	-2.4%	0.0633	0.0618	0.0628
	3	0.6594	0.7167	8.7%	0.08950	0.6382	-3.2%	0.0670	0.0682	0.0708
	4	0.6957	0.6772	-2.7%	0.0712	0.6663	-4.2%	0.0732	0.0699	0.0750
	5	0.7197	0.5809	-19.3%	0.1574	0.6572	-8.7%	0.0891	0.0882	0.1077

$\bar{S} = 0.5$ and $\gamma = 0 \sim 0.8$, $(e_1, \dots, e_6) = (0.99, 0.99, 0.99, 0.99, 0.99, 0.99)$, $f_{m,j}^{(i)} = (1.0 - 0.3S_m^{(i)})\tilde{e}_j$, $N_i = 2000$, $i = 1, \dots, 6$, $(\tilde{e}_1, \dots, \tilde{e}_6) = (0.0667, 0.0667, 0.0667, 0.0667, 0.0667, 0.0667)$.

Table 6. Sensitivity analysis on $\hat{S}_{r(b)}$ and \tilde{S}_r .

Trial	Year	Relative Sample				Relative Bootstrap Sample				
		S_r^*	$\hat{S}_{r(b)}$	Bias	RMSE	\tilde{S}_r	Bias	S.E.	S.D.	RMSE
$\gamma = 0.0$	1	0.4948	0.4919	-0.6%	0.0459	0.4726	-4.5%	0.0549	0.0544	0.0572
	2	0.4949	0.4951	0.1%	0.0450	0.4794	-3.1%	0.0510	0.0517	0.0529
	3	0.4944	0.4979	0.7%	0.0469	0.4870	-1.5%	0.0495	0.0513	0.0505
	4	0.4947	0.4940	-0.1%	0.0489	0.4912	-0.7%	0.0501	0.0507	0.0493
	5	0.4955	0.5001	0.9%	0.0590	0.5105	3.0%	0.0640	0.0625	0.0626
$\gamma = 0.4$	1	0.4946	0.5684	14.9%	0.08770	.5038	1.9%	0.0619	0.0624	0.0620
	2	0.5215	0.5798	11.2%	0.07450	.5282	1.3%	0.0567	0.0576	0.0572
	3	0.5386	0.5804	7.8%	0.06320	.5476	1.7%	0.0534	0.0538	0.0537
	4	0.5504	0.5697	3.5%	0.05570	.5619	2.1%	0.0542	0.0540	0.0540
	5	0.5578	0.5448	-2.3%	0.06320	.5725	2.6%	0.0693	0.0686	0.0691
$\gamma = 0.8$	1	0.4950	0.7487	51.3%	0.25850	.5511	11.3%	0.0632	0.0626	0.0837
	2	0.6000	0.7758	29.3%	0.18310	.6250	4.2%	0.0584	0.0567	0.0614
	3	0.6594	0.7735	17.3%	0.12730	.6909	4.8%	0.0586	0.0579	0.0653
	4	0.6957	0.7387	6.2%	0.07310	.7381	6.1%	0.0646	0.0606	0.0733
	5	0.7197	0.6558	-8.9%	0.09470	.7454	3.6%	0.0844	0.0843	0.0876

$\bar{S} = 0.5$ and $\gamma = 0 \sim 0.8$, $(e_1, \dots, e_6) = (0.99, 0.99, 0.99, 0.99, 0.99, 0.99)$, $f_{m,j}^{(i)} = (1.0 + 0.3S_m^{(i)})\tilde{e}_j$, $N_i = 2000$, $i = 1, \dots, 6$, $(\tilde{e}_1, \dots, \tilde{e}_6) = (0.0667, 0.0667, 0.0667, 0.0667, 0.0667, 0.0667)$.

Tables 3–4 are set up under the assumption that survival rates are independent of recovery rates. Without this assumption, do their results still hold?

Assume recovery rates are heterogeneous and time-specific. Define $f_{m,j}^{(i)}$ as the individual recovery rate of the m th bird banded in the i th year and recovered in the j th year, and \tilde{e}_j as the time effect associated with the recovery rate in the j th year. The relationships between $f_{m,j}^{(i)}$ and $S_m^{(i)}$ include $f_{m,j}^{(i)} = (1 - aS_m^{(i)})\tilde{e}_j$ and $f_{m,j}^{(i)} = (1 + aS_m^{(i)})\tilde{e}_j$, where $a = 0.3, 0.5$. Tables 5–6 ($a = 0.3$) summarize the simulation results. Based on them, both of S_r^* and \tilde{S}_r increase with the banding years. The proposed estimator always underestimates the true survival rate in Table 5 and overestimates the true survival rate in Table 6, when $\gamma \geq 0.4$. The proposed estimator is superior to the bias-adjusted ML estimator if $\gamma \geq 0.4$, consistent with the results from Tables 3–4. Thus the proposed estimator is preferred whether independence of survival rates and recovery rates is assumed or not.

5. Data Analysis

With the band recovery data in Brownie, Anderson, Burnham and Robson (1985), we compare the performances of $\hat{S}_{r(b)}$ and \tilde{S}_r in estimating S_r^* . The data are listed in Table 7 ($k = l = 9$); adult male ducks were collected and banded in San Luis Valley (Colorado) from 1963 to 1971. From Table 8 we obtain $\hat{\gamma} = 0.5140$, which indicates heterogeneity of survival rates. Note that as $\hat{\gamma} > 0.4$, the simulation have demonstrated our method preferable. The results for the performances of $\hat{S}_{r(b)}$ and \tilde{S}_r are in Table 8.

Table 7. Band recoveries for adult male mallards.

Banding year	N_i	1963	1964	1965	1966	1967	1968	1969	1970	1971
1963	231	10	13	6	1	1	3	1	2	0
1964	649		58	21	16	15	13	6	1	1
1965	885			54	39	23	18	11	10	6
1966	590				44	21	22	9	9	3
1967	943					55	39	23	11	12
1968	1077						66	46	29	18
1969	1250							101	59	30
1970	938								97	22
1971	312									21

In Table 8, $\hat{S}_{r(b)}$ exceeds \tilde{S}_r from 1963 to 1968. This pattern was evident in the simulations. The sample standard deviations for $\hat{S}_{r(b)}$ are smaller than the bootstrap standard deviations for \tilde{S}_r due to the large value of $\hat{\gamma}$. Since the data suggest that $\gamma > 0.4$, it is expected that the proposed estimator \tilde{S}_r provides better performance than $\hat{S}_{r(b)}$. Therefore $\hat{S}_{r(b)}$ might overestimate the true annual survival rates.

Table 8. Estimates of annual average survival rates.

Year	1963	1964	1965	1966	1967	1968	1969	1970
$\widehat{S}_{r(b)}$	0.5756	0.6079	0.6642	0.7799	0.6351	0.5333	0.5855	0.5357
s.e.	0.1134	0.0777	0.0803	0.0978	0.0732	0.0586	0.0704	0.1305
\widetilde{S}_r	0.4171	0.4366	0.5101	0.6163	0.5475	0.5102	0.6157	0.5851
s.e.	0.1466	0.1452	0.1349	0.1575	0.0885	0.0667	0.0807	0.1664

6. Conclusions

The band recovery model considered here is based on the assumptions that individual survival rates are heterogeneous and the band recovery rate is independent of the individual survival rate. In this context, a new estimator of the annual average survival rate is proposed, and the following conclusions are obtained.

1. The bias-adjusted MLE derived under a homogeneous survival rate is recommended when the coefficient of variation of individual survival rate is relatively small, say $\gamma < 0.4$.
2. When the coefficient of variation of individual survival rate is relatively large, say $\gamma \geq 0.4$, the proposed estimator performs better than the bias-adjusted MLE since the effect of heterogeneity becomes significant. With the help of the bootstrap method, we can compute the sample variance of the proposed estimator for further statistical inference.
3. As the survival rates and recovery rates are negatively linearly correlated, the bias-adjusted MLE produces a negative bias on estimating the annual average survival rate only for the last experimental year. This phenomenon is consistent with the results in Pollock and Raveling(1982). Nevertheless the annual average survival rates for the first two or three years are overestimated by the bias-adjusted MLE. Based on the simulation set up in this paper, the proposed estimator has smaller bias and MSE on estimating the annual average survival rates.
4. As the survival rates and recovery rates are positively linearly correlated, the bias-adjusted MLE produces a negative bias on estimating the annual average survival rate only for the last experimental year. This phenomenon is not consistent with the results in Nichols, Stockes, Hines and Conroy (1982). Similarly, based on the simulation set up in this paper, the proposed method is recommended on estimating the annual average survival rates.

Acknowledgements

This research of S. M. Lee was supported by National Science Council of Taiwan under contracts NSC91-2118-M-035-002. We are thankful to an associate

editor and the referees for helpful comments and suggestions. This has led to a much improved manuscript. We thank the Editor for encouraging us to work on a revision.

Appendix A.

Proof of Proposition 1. Note that $E(R_r)$ and $E(T_r - R_r)$ can be expressed as

$$E(R_r) = \sum_{m=1}^{N_r} [f_r + S_m^{(r)} e_r f_{r+1} + \cdots + (S_m^{(r)})^{k-r} \phi_{r,k-1} f_k],$$

$$E(T_r - R_r) = \sum_{i=1}^{r-1} \sum_{m=1}^{N_i} (S_m^{(i)})^{r-i} \phi_{i,r-1} [f_r + S_m^{(i)} e_r f_{r+1} + \cdots + (S_m^{(i)})^{k-r} \phi_{r,k-1} f_k].$$

Then, when $S_m^{(i)} = \bar{S}$ for all $i = 1, \dots, k$ and $m = 1, \dots, N_i$, we obtain from (3) that

$$E(N_r^*) = \frac{N_r E(T_r - R_r)}{E(R_r)}.$$

When the $S_m^{(i)}$ are not the same, $E(N_r^*) \neq N_r E(T_r - R_r)/E(R_r)$. Naturally the next step is to find the discrepancy between $E(N_r^*)$ and $N_r E(T_r - R_r)/E(R_r)$ when $S_m^{(i)}$'s are different.

$$\frac{E(T_r - R_r)N_r}{E(R_r)} - E(N_r^*) = \frac{g_r(\mathbf{S})}{E(R_r)},$$

where $\mathbf{S} = (S_1^{(1)}, S_2^{(1)}, \dots, S_{N_1}^{(1)}, \dots, S_{N_r}^{(r)})$ and $g_r(\mathbf{S})$ is defined at (6).

Next we need to derive the first and second partial derivatives of $g_r(\mathbf{S})$ in order to obtain the Taylor expansion on $g_r(\mathbf{S})$.

$$\left. \frac{\partial g_r(\mathbf{S})}{\partial S_m^{(j)}} \right|_{\mathbf{s} = (\bar{S}, \bar{S}, \dots, \bar{S})} = N_r \bar{S}^{r-j} \phi_{j,r-1} [e_r f_{r+1} + \cdots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k], \quad j = 1, \dots, r-1,$$

$$\left. \frac{\partial g_r(\mathbf{S})}{\partial S_m^{(r)}} \right|_{\mathbf{s} = (\bar{S}, \bar{S}, \dots, \bar{S})} = - \left[\sum_{j=1}^{r-1} N_j \bar{S}^{r-j} \phi_{j,r-1} [e_r f_{r+1} + \cdots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k] \right],$$

$$\left. \frac{\partial^2 g_r(\mathbf{S})}{\partial S_m^{(j)2}} \right|_{\mathbf{s} = (\bar{S}, \bar{S}, \dots, \bar{S})} = 2N_r (r-j) \bar{S}^{r-j-1} \phi_{j,r-1} [e_r f_{r+1} + \cdots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k] + N_r \bar{S}^{r-j} \phi_{j,r-1} \times [2e_r e_{r+1} f_{r+2} + \cdots + (k-r)(k-r-1) \bar{S}^{k-r-2} \phi_{r,k-1} f_k], \quad j = 1, \dots, r-1,$$

$$\begin{aligned} & \frac{\partial^2 g_r(\mathbf{S})}{\partial S_m^{(r)^2}} \Big|_{\mathbf{s}=(\bar{S}, \bar{S}, \dots, \bar{S})} \\ &= - \left[\sum_{j=1}^{r-1} N_j \bar{S}^{r-j} \phi_{j,r-1} \right] [2e_r e_{r+1} f_{r+2} + \dots + (k-r)(k-r-1) \bar{S}^{k-r-2} \phi_{r,k-1} f_k], \\ & \frac{\partial^2 g_r(\mathbf{S})}{\partial S_m^{(j)} \partial S_t^{(i)}} \Big|_{\mathbf{s}=(\bar{S}, \bar{S}, \dots, \bar{S})} = 0 \quad i, j = 1, \dots, r-1, \quad i \neq j, \\ & \frac{\partial^2 g_r(\mathbf{S})}{\partial S_m^{(j)} \partial S_t^{(r)}} \Big|_{\mathbf{s}=(\bar{S}, \bar{S}, \dots, \bar{S})} \\ &= -(r-j) \bar{S}^{r-j-1} \phi_{j,r-1} [e_r f_{r+1} + \dots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k], \quad j=1, \dots, r-1. \end{aligned}$$

At the point $\bar{\mathbf{S}} = (\bar{S}, \bar{S}, \dots, \bar{S})$, the Taylor's expansion on $g_r(\mathbf{S})$ is given by

$$\begin{aligned} g_r(\mathbf{S}) &= g_r(\bar{\mathbf{S}}) + \sum_{i=1}^r \sum_{m=1}^{N_i} \left(\frac{\partial g_r(\mathbf{S})}{\partial S_m^{(i)}} \Big|_{\mathbf{s}=(\bar{S}, \bar{S}, \dots, \bar{S})} \right) (S_m^{(i)} - \bar{S}) \\ & \quad + \frac{1}{2!} \sum_{i=1}^r \sum_{j=1}^r \sum_{m=1}^{N_i} \sum_{t=1}^{N_j} \left(\frac{\partial^2 g_r(\mathbf{S})}{\partial S_m^{(i)} \partial S_t^{(j)}} \Big|_{\mathbf{s}=(\bar{S}, \bar{S}, \dots, \bar{S})} \right) \\ & \quad \times (S_m^{(i)} - \bar{S}) (S_t^{(j)} - \bar{S}) + \mathfrak{R}_1, \end{aligned}$$

where \mathfrak{R}_1 is the error term. Under Assumptions (A) and (B), $g_r(\mathbf{S})$ is rewritten as

$$g_r(\mathbf{S}) = \left\{ \sum_{i=1}^{r-1} N_r (r-i) N_i \bar{S}^{r-i+1} \phi_{i,r-1} [e_r f_{r+1} + \dots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k] \right\} \gamma^2 + \mathfrak{R}_1. \tag{10}$$

Appendix B.

To show the validity of ignoring \mathfrak{R}_2 , simulation work is provided in Tables 9 and 10. Table 9 contains the values of \mathfrak{R}_2 for three populations (see Table 2, trials 5, 7 and 9). Table 10 contains the values of \mathfrak{R}_2 for beta distributions. The possible values of e_j and f_j , $j = 1, \dots, 6$, are $(e_1, \dots, e_6) = (0.99, 0.99, 0.99, 0.99, 0.99, 0.99)$, $(f_1, \dots, f_6) = (0.05, 0.05, 0.05, 0.05, 0.05, 0.05)$. Numerical results for other values of e_j and k are quite similar and support the validity of ignoring \mathfrak{R}_2 , given $S_m^{(i)}$ and e_j, f_j and $E(N_r^*)$ can be calculated from (3).

Appendix C.

Equation (5) may be rewritten as

$$E(N_r^*) = \frac{N_r E(T_r - R_r)}{E(R_r)} - \frac{g_r(\mathbf{S})}{E(R_r)}$$

$$\begin{aligned}
 &= \frac{N_r E(T_r - R_r)}{E(R_r)} - \frac{1}{E(R_r)} \left\{ \sum_{i=1}^{r-1} N_r (r-i) N_i \bar{S}^{r-i+1} \phi_{i,r-1} \right. \\
 &\quad \left. \times [e_r f_{r+1} + \dots + (k-r) \bar{S}^{k-r-1} \phi_{r,k-1} f_k] \right\} \gamma^2 + \mathfrak{R}_2,
 \end{aligned}$$

where $\mathfrak{R}_2 = -\mathfrak{R}_1/E(R_r)$. Here \mathfrak{R}_2 is negligible (see Appendix B). With Assumption (B), for each i , the value of γ^2 is defined as

$$\begin{aligned}
 \gamma^2 &= \frac{\sum_{m=1}^{N_i} (S_m^{(i)} - \bar{S})^2}{N_i \bar{S}^2} = \frac{\sum_{m=1}^{N_i} (S_m^{(i)})^2}{N_i \bar{S}^2} - 1 \\
 &= \frac{N_{i+1} \sum_{m=1}^{N_i} (S_m^{(i)})^2}{(\sum_{m=1}^{N_i} S_m^{(i)}) (\sum_{m=1}^{N_{i+1}} S_m^{(i+1)})} - 1 \\
 &= \frac{(N_{i+1} f_{i+1}) [\sum_{m=1}^{N_i} (S_m^{(i)})^2 e_i e_{i+1} f_{i+2}]}{(\sum_{m=1}^{N_i} S_m^{(i)} e_i f_{i+1}) (\sum_{m=1}^{N_{i+1}} S_m^{(i+1)} e_{i+1} f_{i+2})} - 1 = \frac{E(R_{i+1,i+1}) E(R_{i,i+2})}{E(R_{i,i+1}) E(R_{i+1,i+2})} - 1.
 \end{aligned}$$

Considering the information from the whole experimental process, i.e., $i = 1, \dots, k$, we can get another form of γ^2 as

$$\gamma^2 = \frac{\sum_{i=1}^{k-2} E(R_{i+1,i+1}) E(R_{i,i+2})}{\sum_{i=1}^{k-2} E(R_{i,i+1}) E(R_{i+1,i+2})} - 1.$$

Table 9. Theoretical behavior of approximation (5), $N_i = 2000, i = 1, \dots, 6$.

Trial	Year	R.H.S of Eq.(3)	R.H.S. of Eq. (4)	Eq.(5) without \mathfrak{R}_2	\mathfrak{R}_2
$\bar{S} = 0.5$ $\gamma = 0$	1	990.0	990.0	990.0	0.0
	2	1480.0	1480.0	1480.0	0.0
	3	1722.6	1722.6	1722.6	0.0
	4	1842.6	1842.6	1842.6	0.0
	5	1902.1	1902.1	1902.1	0.0
$\bar{S} = 0.5$ $\gamma = 0.4$	1	990.0	1115.5	994.4	-4.4
	2	1558.5	1778.6	1561.6	-3.1
	3	1917.4	2159.9	1920.9	-3.5
	4	2155.9	2330.4	2162.0	-6.1
	5	2318.0	2318.0	2318.0	0.0
$\bar{S} = 0.5$ $\gamma = 0.8$	1	990.0	1439.5	1047.1	-57.1
	2	1793.7	2592.7	1837.2	-44.5
	3	2502.0	3450.0	2553.6	-51.6
	4	3132.5	3903.8	3230.4	-97.9
	5	3694.2	3693.9	3693.9	0.3

R.H.S.=Right Hand Side

Table 10. Theoretical behavior of approximation (7), $N_i = 2000, i = 1, \dots, 6$.

Trial	Year	R.H.S	R.H.S.	Eq.(7)	
		of Eq.(3)	of Eq. (4)	without \mathfrak{R}_2	\mathfrak{R}_2
$Beta(200., 200.)$ $\gamma = 0.05$	1	990.0	991.6	990.0	0.0
	2	1481.0	1483.9	1481.0	0.0
	3	1725.1	1728.1	1725.1	0.0
	4	1846.6	1848.7	1846.6	0.0
	5	1907.2	1907.2	1907.2	0.0
$Beta(2.625, 2.625)$ $\gamma = 0.4$	1	990.0	1121.0	1000.0	-10.0
	2	1558.5	1787.6	1570.5	-12.1
	3	1917.4	2169.7	1930.7	-13.3
	4	2159.8	2342.1	2173.7	-13.9
	5	2331.6	2331.6	2331.6	0.0
$Beta(0.2813, 0.2813)$ $\gamma = 0.8$	1	990.0	1456.1	1064.9	-74.9
	2	1793.7	2623.6	1868.0	-74.4
	3	2502.0	3486.9	2590.2	-88.2
	4	3147.9	3950.3	3276.9	-129.0
	5	3747.9	3747.9	3747.9	0.0

R.H.S.=Right Hand Side

Thus, the moment estimator of γ^2 is given as

$$\hat{\gamma}^2 = \max \left\{ \frac{\sum_{i=1}^{k-2} R_{i+1,i+1} R_{i,i+2}}{\sum_{i=1}^{k-2} R_{i,i+1} R_{i+1,i+2}} - 1, \quad 0 \right\}.$$

Ignoring \mathfrak{R}_1 in (10)(see Appendix A), we can estimate $g_r(\mathbf{S})$ as

$$\hat{g}_r = \sum_{i=1}^{r-1} N_r(r-i) N_i \left(\prod_{j=i}^{r-1} (\widehat{S}e_j) \right) [(\widehat{S}e_r) \hat{f}_{r+1} + \dots + (k-r) \left(\prod_{j=r}^{k-r-1} (\widehat{S}e_j) \right) \hat{f}_k] \hat{\gamma}^2,$$

where $\widehat{S}e_r = R_{r,r+1}/N_r$ and $\hat{f}_r = R_{r,r}/N_r$. Ignoring \mathfrak{R}_2 in (5), the proposed estimator of N_r^* is then

$$\hat{N}_r^* = \frac{N_r(T_r - R_r) - \hat{g}_r}{R_r}.$$

References

- Brownie, C. and Pollock, K. H. (1985). Analysis of multiple capture-recapture data using band-recovery methods. *Biometrics* **41**, 411-420.
- Brownie, C., Anderson, D. R., Burnham, K. P. and Robson, D. S. (1985). *Statistical Inference from Band-Recovery Data-A Handbook*. 2nd edition. Resource Publication No. 156. Washington, D.C.: Fish and Wildlife Service, U.S. Dept. of the Interior.
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. and Pollock, K. H. (1987). *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society Monographs **5**.

- Burnham, K. P. and Rexstad, E. A. (1993). Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* **49**, 1194-1208.
- Chao, A., Lee, S. M. and Jeng, S. L. (1992). Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* **48**, 201-216.
- Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. *Ecological Monographs* **62**, 67-118.
- Lee, S. M. and Chao, A. (1994). Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* **50**, 88-97.
- Nichols, J. D., Stockes, S. L., Hines, J. E. and Conroy, M. J. (1982). Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. *J. Wildlife Management* **46**, 953-962.
- Pollock, K. H. and Raveling, D. G. (1982). Assumptions of modern band recovery models, with emphasis on heterogeneous survival rates. *J. Wildlife Management* **46**, 88-98.
- Pollock, K. H., Nichols, J. D., Brownie, C. and Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**, 1-97.
- Robson, D. S. and Youngs, W. D. (1971). Statistical analysis of reported tag-recaptures in the harvest from an exploited population. Bu-369-m Biometrics Unit, Cornell University, Ithaca, New York.
- Seber, G. A. F. (1970). Estimating time-specific survival and reporting rates for adult birds from band returns. *Biometrika* **57**, 313-318.
- Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*. 2nd edition. Griffin, London.
- Seber, G. A. F. (1986). A review of estimating animal abundance I. *Biometrics* **42**, 267-292.
- Seber, G. A. F. (1992). A review of estimating animal abundance II. *Internat. Statist. Rev.* **60**, 129-166.

Graduate Institute of Statistics and Actuarial Science, Feng Chia University, 100 Wenhwa Road, Seatwen, Taichung, Taiwan 40724, R.O.C.

E-mail: smlee@fcu.edu.tw

Department of International Trade, The Overseas Chinese Institute of Technology, Taichung, Taiwan, R.O.C.

E-mail: hlh@ocit.edu.tw

Center for Drug Evaluation, Taipei, Taiwan, R.O.C.

E-mail: stou@cde.org.tw

(Received August 2001; accepted September 2003)