MAXIMUM LIKELIHOOD ESTIMATION OF A SEQUENCE OF ANNUAL SURVIVAL RATES FROM A CAPTURE-RECAPTURE SERIES*

BU-116-M   D. S. Robson **   April 12, 1960

A homogeneous group of individuals such as a single year class in a fish population is sampled at successive points in time to determine the survival rate (or death rate) during each successive time interval. Survival rate for any time interval is simply defined to be the ratio of final to initial population size for that interval. With no loss of generality, we shall assume the intervals to be of equal length and shall refer to the survival rate s_k for the k'th interval as an annual survival rate. The problem of estimating population size and survival rate from this type of experiment is covered extensively in the literature (see, for example, Bailey (1951), Hamersley (1953)), but with the assumption of a constant annual survival rate. The present approach to the problem was also taken by Darroch (1958, 1959) who was concerned principally with estimating population size.

Sampling procedure. The sampling procedure at each anniversary consists of selecting a random sample from the existing population, tagging all untagged individuals (individuals not previously "captured") and noting the year of tagging on each tagged individual ("recaptured" individual) in the sample. At the start of this procedure the population contains no tagged individuals; the first step then consists of capturing, tagging and releasing, say M_1 individuals. After one year a sample is taken from the surviving population and contains, in the notation of Ricker (1958), R_{12} recaptures along with M_2 untagged individuals. These M_2 individuals are tagged and released; the R_{12} recaptures may or may not be released, depending upon the mechanics of the sampling operation -- if, for example, some of the recaptures represent tag returns by sportsmen then these recaptures will not be returned to the population. At the next anniversary the sample may contain tags from both the previous releases, as well as untagged individuals; the number of recoveries from the first year's release will be denoted here by R_{13} and the number from the second year by R_{23}, with M_3 new individuals being tagged and released. Continuation of this annual capture-recapture procedure then produces the recovery data shown in Table 1.

---

* This note is an expansion of an appendix from the paper under this title by Forney, Eipper and Robson.

**Biometrics Unit, Plant Breeding Department, Cornell University

Table 1. Tag recoveries classified according to year of tagging and year of recovery

Year of tagging	Number tagged	Year of recovery					Total recovery
		2	3	4	...	n+1	
1	M_1	R_{12}	R_{13}	R_{14}	...	$R_{1,n+1}$	R_1
2	M_2		R_{23}	R_{24}	...	$R_{2,n+1}$	R_2
3	M_3			R_{34}	...	$R_{3,n+1}$	R_3
⋮	⋮				⋱	⋮	⋮
n	M_n					$R_{n,n+1}$	R_n
Total recovery		C_2	C_3	C_4	...	C_{n+1}	

The parametric model. The survival rate s_k from year k to year k+1 is assumed to be the same for all individuals in this homogeneous population; that is, an individual's probability of survival is s_k, regardless of his tagging history. In year k+1 the expected number of survivors among the M_1 individuals tagged in year 1 is therefore $s_1 s_2 \cdots s_k M_1$; the expected number of survivors among the M_2 individuals tagged in year 2 is $s_2 \cdots s_k M_2$. In general, among the M_i individuals tagged in year i, the expected number of survivors in year k+1 is $s_i s_{i+1} \cdots s_k M_i$, and the probability of exactly $X_{i,k+1}$ survivors is a binomial probability

$$\binom{M_i}{X_{i,k+1}} (s_i s_{i+1} \cdots s_k)^{X_{i,k+1}} (1-s_i s_{i+1} \cdots s_k)^{M_i - X_{i,k+1}}$$

If f_{k+1} is the catch rate in year k+1; that is, f_{k+1} is the probability of capture for each individual in the population in year k+1, then the probability of recapture of exactly $R_{i,k+1}$ survivors is also binomial,

$$P(R_{i,k+1}) = \sum_{X_{i,k+1}} P(X_{i,k+1}) P(R_{i,k+1} | X_{i,k+1})$$

$$= \binom{M_i}{R_{i,k+1}} (f_{k+1} s_i \cdots s_k)^{R_{i,k+1}} (1 - f_{k+1} s_i \cdots s_k)^{M_i - R_{i,k+1}}$$

Since catch rate is small, however, we shall, following Chapman and Robson, approximate this binomial function by the Poisson function with parameter $f_{k+1}s_i \cdots s_k M_i$. The f_k parameters may then be eliminated from consideration by employing only the conditional distribution of recoveries for fixed total yearly catches; thus,

$$P(R_{1,k+1}, \cdots, R_{k,k+1} | C_{k+1}) = \frac{C_{k+1}!}{\prod\limits_{i=1}^{k} R_{i,k+1}!} \prod\limits_{i=1}^{k} \left(\frac{f_{k+1}s_i \cdots s_k M_i}{\sum\limits_{i=1}^{k} f_{k+1}s_i \cdots s_k M_i} \right)^{R_{i,k+1}} \tag{1}$$

Notice that both f_{k+1} and s_k cancel out of this expression.

The joint conditional distribution for the entire sample of R's is a product of distributions of form (1), since catches in successive years are statistically independent, so the log-likelihood function L takes the form

$$L = \text{constant} + (R_1 - C_2)\log s_1 + (R_1 + R_2 - C_2 - C_3)\log s_2 + \cdots + (R_1 + \cdots R_{n-1} - C_2 - \cdots - C_n)\log s_{n-1}$$

$$-C_3\log(s_1 M_1 + M_2) - C_4\log(s_1 s_2 M_1 + s_2 M_2 + M_3) - \cdots - C_{n+1}\log(s_1 \cdots s_{n-1} M_1 + s_2 \cdots s_{n-1} M_2 + \cdots + M_n)$$

or, letting

$$T_i = (R_1 + \cdots + R_i) - (C_2 + \cdots + C_i)$$

$$b_k = (s_1 \cdots s_{k-1} M_1 + s_2 \cdots s_{k-1} M_2 + \cdots + M_k) s_k s_{k+1} \cdots s_{n-1}$$

then

$$L = \text{constnat} + \sum_{k=1}^{n-1} (T_{k+1} - R_{k+1})\log s_k - \sum_{k=1}^{m-1} C_{k+2}\log \frac{b_{k+1}}{s_{k+1} \cdots s_{n-1}}$$

In this notation the maximum likelihood equations become

$$\frac{\delta L}{\delta s_k} = \frac{T_{k+1} - R_{k+1}}{s_k} - C_{k+2} \frac{\delta}{\delta s_k}\log \frac{b_{k+1}}{s_{k+1} \cdots s_{n-1}} - \cdots - C_{n+1}\frac{\delta b_n}{\delta s_k} = 0$$

or, since

$$\frac{\delta}{\delta s_k}\log b_{k+j} = \frac{(s_1 \cdots s_{k+j-1} M_1 + \cdots + s_k \cdots s_{k+j-1} M_k) s_{k+j} \cdots s_{n-1}}{s_k b_{k+j}}$$

$$= \frac{b_k}{s_k b_{k+j}}$$

then

$$\frac{\delta L}{\delta s_k} = \frac{T_{k+1} - R_{k+1}}{s_k} - \frac{b_k}{s_k}\left[\frac{C_{k+2}}{b_{k+1}} + \cdots + \frac{C_{n+1}}{b_n}\right] = 0 \qquad \ldots (2)$$

Multiplying both sides of equation (2) by s_k gives a recurrence relation for B_k, the maximum likelihood estimate of b_k, which may be written in the form

$$B_k = \frac{T_{k+1} - R_{k+1}}{\dfrac{C_{k+2}}{B_{k+1}} + \dfrac{C_{k+3}}{B_{k+2}} + \cdots + \dfrac{C_{n+1}}{B_n}}$$

$$= \frac{T_{k+1} - R_{k+1}}{\dfrac{C_{k+2}}{B_{k+1}} + \dfrac{T_{k+2} - R_{k+2}}{B_{k+1}}}$$

or, since $C_{k+2} = T_{k+1} - (T_{k+2} - R_{k+2})$,

$$B_k = \frac{T_{k+1} - R_{k+1}}{T_{k+1}} B_{k+1} \qquad\qquad (3)$$

The boundary condition on this system is $B_n = B_{n-1} + M_n$, or

$$Bn = \frac{M_n T_n}{R_n}$$

and, of course, $B_0 = 0$. Finally, we observe that

$$\frac{B_k - B_{k-1}}{M_k} = S_k S_{k+1} \cdots S_{n-1}$$

so the maximum likelihood estimate S_k of the survival rate s_k is

$$S_k = \frac{M_{k+1}}{M_k} \frac{B_k - B_{k-1}}{B_{k+1} - B_k}$$

$$= \frac{M_{k+1}}{M_k} \frac{B_k}{B_{k+1}} \frac{(1 - \dfrac{B_{k-1}}{B_k})}{(1 - \dfrac{B_k}{B_{k+1}})}$$

which, from (3), reduces to

$$S_k = \frac{M_{k+1}}{M_k} \cdot \frac{T_{k+1} - R_{k+1}}{R_{k+1}} \cdot \frac{R_k}{T_k}$$

The inverse of the variance-covariance matrix of the asymptotic joint distribution of the statistics $S_1, \cdots, S_{n-1}$ is then given by the negative expectation of the second partial derivatives of the likelihood L as

$$\sigma^{k,k} = -E \frac{\delta^2 L}{\delta s_k^2} = E(\frac{T_{k+1} - R_{k+1}}{s_k^2}) + \frac{b_k}{s_k} \frac{\delta}{\delta s_k} \left[\frac{C_{k+2}}{b_{k+1}} + \cdots + \frac{C_{n+1}}{b_n} \right]$$

$$= \frac{b_k}{s_k^2} \left[\frac{C_{k+2}}{b_{k+1}} + \cdots + \frac{C_{n+1}}{b_n} \right] - \frac{b_k^2}{s_k^2} \left[\frac{C_{k+2}}{b_{k+1}^2} + \cdots + \frac{C_{n+1}}{b_n^2} \right]$$

$$= \frac{b_k}{s_k^2} \left[\frac{C_{k+2}}{b_{k+1}} (1 - \frac{b_k}{b_{k+1}}) + \cdots + \frac{C_{n+1}}{b_n}(1 - \frac{b_k}{b_n}) \right]$$

$$= \frac{b_k}{s_k^2} a_k \quad \text{(say)}$$

and

$$\sigma^{k-j,k} = -E \frac{\delta^2 L}{\delta s_{k-j} \delta s_k} = - \frac{\delta}{\delta s_{k-j}} \frac{b_k}{s_k} \left[\frac{C_{k+2}}{b_{k+1}} + \cdots + \frac{C_{n+1}}{b_n} \right]$$

$$= \frac{b_{k-j}}{s_{k-j} s_k} \left[\frac{C_{k+2}}{b_{k+1}} (1 - \frac{b_k}{b_{k+1}}) + \cdots + \frac{C_{n+1}}{b_n} (1 - \frac{b_k}{b_n}) \right]$$

$$= \frac{b_{k-j}}{s_{k-j} s_k} a_k$$

This symmetric matrix

$$[\sigma^{ij}] = \begin{bmatrix} \dfrac{b_1 a_1}{s_1^2} & \dfrac{b_1 a_2}{s_1 s_2} & \dfrac{b_1 a_3}{s_1 s_3} & \cdots & \dfrac{b_1 a_{n-1}}{s_1 s_{n-1}} \\[2em] \dfrac{b_1 a_2}{s_1 s_2} & \dfrac{b_2 a_2}{s_2^2} & \dfrac{b_2 a_3}{s_2 s_3} & \cdots & \dfrac{b_2 a_{n-1}}{s_2 s_{n-1}} \\[2em] \dfrac{b_1 a_3}{s_1 s_3} & \dfrac{b_2 a_3}{s_2 s_3} & \dfrac{b_3 a_3}{s_3^2} & \cdots & \dfrac{b_3 a_{n-1}}{s_3 s_{n-1}} \\[2em] \vdots & \vdots & \vdots & \ddots & \vdots \\[1em] \dfrac{b_1 a_{n-1}}{s_1 s_{n-1}} & \dfrac{b_2 a_{n-1}}{s_2 s_{n-1}} & \dfrac{b_3 a_{n-1}}{s_3 s_{n-1}} & \cdots & \dfrac{b_{n-1} a_{n-1}}{s_{n-1}^2} \end{bmatrix}$$

can be diagonalized by multiplying row k+1 by $b_k s_{k+1}/b_{k+1} s_k$ and subtracting from row k, k=1,$\cdots$,n-2, to give

$$\begin{bmatrix} \dfrac{b_1}{s_1^2}\left(\dfrac{b_2 a_1 - b_1 a_2}{b_2}\right) & 0 & 0 & \cdots & 0 \\[2em] \dfrac{b_1}{s_1 s_2}\left(\dfrac{b_3 a_2 - b_2 a_3}{b_3}\right) & \dfrac{b_2}{s_2^2}\left(\dfrac{b_3 a_2 - b_2 a_3}{b_3}\right) & 0 & \cdots & 0 \\[2em] \dfrac{b_1}{s_1 s_3}\left(\dfrac{b_4 a_3 - b_3 a_4}{b_4}\right) & \dfrac{b_2}{s_2 s_3}\left(\dfrac{b_4 a_3 - b_3 a_4}{b_4}\right) & \dfrac{b_3}{s_3^2}\left(\dfrac{b_4 a_3 - b_3 a_4}{b_4}\right) & \cdots & 0 \\[2em] \vdots & \vdots & \vdots & \ddots & \vdots \\[1em] \dfrac{b_1 a_{n-1}}{s_1 s_{n-1}} & \dfrac{b_2 a_{n-1}}{s_2 s_{n-1}} & \dfrac{b_3 a_{n-1}}{s_3 s_{n-1}} & \cdots & \dfrac{b_{n-1} a_{n-1}}{s_{n-1}^2} \end{bmatrix}$$

and then repeating this operation on the columns to give as the determinant of $[\sigma^{ij}]$

$$
D = \begin{vmatrix}
\dfrac{b_1}{s_1^2}\left(\dfrac{b_2 a_1 - b_1 a_2}{b_2}\right) & 0 & 0 & \cdots & 0 \\[2em]
0 & \dfrac{b_2}{s_2^2}\left(\dfrac{b_3 a_2 - b_2 a_3}{b_3}\right) & 0 & \cdots & 0 \\[2em]
0 & 0 & \dfrac{b_3}{s_3^2}\left(\dfrac{b_4 a_3 - b_3 a_4}{b_4}\right) & \cdots & 0 \\[1em]
\vdots & \vdots & \vdots & \ddots & \vdots \\[1em]
0 & 0 & 0 & & \dfrac{b_{n-1} a_{n-1}}{s_{n-1}^2}
\end{vmatrix}
$$

The variance $\sigma_{k,k}$ of S_k^2 is then $D_{k,k}/D$, and the cofactor D_{kk} of σ^{kk} may, likewise, be evaluated by performing these same operations on the rows and columns of D_{kk}; for example,

$$
D_{33} = \begin{vmatrix}
\dfrac{b_1}{s_1^2}\left(\dfrac{b_2 a_1 - b_1 a_2}{b_2}\right) & 0 & 0 & \cdots & 0 \\[2em]
0 & \dfrac{b_2}{s_2^2}\left(\dfrac{b_4 a_2 - b_2 a_4}{b_4}\right) & 0 & \cdots & 0 \\[2em]
0 & 0 & \dfrac{b_4}{s_4^2}\left(\dfrac{b_5 a_4 - b_4 a_5}{b_5}\right) & \cdots & 0 \\[1em]
\vdots & \vdots & \vdots & \ddots & \vdots \\[1em]
0 & 0 & 0 & \cdots & \dfrac{b_{n-1} a_{n-1}}{s_{n-1}^2}
\end{vmatrix}
$$

Thus,

$$D_{33} = \frac{\dfrac{b_4 a_2 - b_2 a_4}{b_4}}{(\dfrac{b_3 a_2 - b_2 a_3}{b_3}) \dfrac{b_3}{s_3^2} (\dfrac{b_4 a_3 - b_3 a_4}{b_4})} D$$

or, in general,

$$\sigma_{kk} = \frac{D_{kk}}{D} = s_k^2 \left[\frac{b_{k+1} a_{k-1} - b_{k-1} a_{k+1}}{(b_k a_{k-1} - b_{k-1} a_k)(b_{k+1} a_k - b_k a_{k+1})} \right]$$

$$= \frac{s_k^2}{b_k} \left[\frac{b_{k+1}}{b_{k+1} a_k - b_k a_{k+1}} + \frac{b_{k-1}}{b_k a_{k-1} - b_{k-1} a_k} \right]$$

In like manner, we find

$$\sigma_{k-j,k} = \begin{cases} 0 & \text{for } j > 1 \\[2mm] -\dfrac{s_{k-1} s_k}{b_k a_{k-1} - b_{k-1} a_k} & \text{for } j = 1 \end{cases}$$

$$\sigma_{k+j,k} = \begin{cases} -\dfrac{s_k s_{k+1}}{b_{k+1} a_k - b_k a_{k+1}} & \text{for } j = 1 \\[2mm] 0 & \text{for } j > 1 \end{cases}$$

Upon substituting for s_k, b_k and a_k their maximum likelihood estimates S_k, B_k and A_k we find

$$B_k A_{k-1} - B_{k-1} A_k = B_k \left[\frac{C_{k+1}}{B_k} (1 - \frac{B_{k-1}}{B_k}) + \cdots + \frac{C_{n+1}}{B_n} (1 - \frac{B_{k-1}}{B_n}) \right]$$

$$- B_{k-1} \left[\frac{C_{k+2}}{B_{k+1}} (1 - \frac{B_k}{B_{k+1}}) + \cdots + \frac{C_{n+1}}{B_n} (1 - \frac{B_k}{B_n}) \right]$$

$$= B_{k-1} \left[\frac{C_{k+1}}{B_k} + \cdots + \frac{C_{n+1}}{B_n} \right] (\frac{B_k}{B_{k-1}} - 1)$$

which, from (2) and (3), reduces to

$$B_k A_{k-1} - B_{k-1} A_k = R_k$$

Consequently,

$$\hat{\sigma}_{k-j,k} = \begin{cases} 0 & \text{for } j > 1 \\[2ex] -\dfrac{S_{k-1} S_k}{R_k} & \text{for } j=1 \end{cases}$$

$$\hat{\sigma}_{k+j,k} = \begin{cases} -\dfrac{S_k S_{k+1}}{R_{k+1}} & \text{for } j=1 \\[2ex] 0 & \text{for } j > 1 \end{cases}$$

and

$$\hat{\sigma}_{k,k} = S_k^2 \left[\frac{T_{k+1}}{R_{k+1}(T_{k+1} - R_{k+1})} + \frac{T_k - R_k}{R_k \, T_k} \right]$$

References

Bailey, N. J. J. 1951. On estimating the size of mobile populations from re-capture data. *Biometrika*, 38:293-306.

Darroch, J. N. 1958. The multiple-recapture census. I. Estimation of a closed population. *Biometrika*, 45:343-59.

Darroch, J. N. 1959. The multiple-recapture census. II. Estimation when there is immigration or death. *Biometrika*, 46:336-51.

Hammersley, J. M. 1953. Capture-recapture analysis. *Biometrika*, 40:137-69.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Fish Res. Bd. Canada*, Bul. 119.