

THE ESTIMATION OF POPULATION SIZE, MIGRATION RATES AND SURVIVAL IN A STRATIFIED POPULATION

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INTRODUCTION

CHAPMAN and JUNG (1956, hereafter referred to as C & J) developed estimates of stratum size and migration rates for a population divided into $n \geq 2$ areas (strata) when animals were free to migrate from area to area. The method was based on data from sampling and marking observations on two occasions. The method was extended by DARROCH (1961) to allow sampling in different numbers of strata at the two sampling times, and to show how to treat some special problems that arise when using the method. These problems arise when a particular data matrix (which must be inverted) is singular or ill-conditioned. The same problems could occur with the estimates which will be given in this paper.

In order to account for deaths or losses from the areas due to permanent emigration out of the areas being sampled, it is necessary to sample on at least three occasions. I developed estimates for the three sample experiment on two areas (ARNASON 1972a) and later (ARNASON 1972b) gave asymptotic variance formulae for the estimates and suggested methods of predicting population sizes or time to extinction, using data from this experiment. The purpose of the present paper is to give the estimates for the general situation of sampling on three occasions in $n \geq 2$ areas. Modified estimates to account for losses on capture (as occur, for instance, in bird-banding studies) are also given.

DESCRIPTION OF THE EXPERIMENT AND NOTATION

n areas ($n \geq 2$) are sampled on three occasions. At the first sampling time, sampling is carried out on all n areas simultaneously (or at least close enough together in time that no migration is likely to occur within the sampling time) and all animals caught are marked and returned to the population from which they were taken. On the second and third sampling occasions this process is repeated, with all unmarked animals in the sample being marked and the capture history of all marked animals in the sample being recorded. The marks need only identify the sampling time and stratum (area) in order to form the statistics required for the estimates, but it is more usual to give each animal a distinguishing mark so that the complete capture history of every individual caught is known at the end of the experiment.

The following notation is an extension to n dimensions (areas) of the notation for two dimensions used in ARNASON (1972a).

Subscripts:

$$\left. \begin{array}{l} j=1, 2, 3 \\ i=1, \dots, (j-1) \end{array} \right\} \text{ denotes sampling time}$$

$$\left. \begin{array}{l} x \\ y \\ z \end{array} \right\} = A, B, \dots n \text{ denotes area (stratum)}$$

Observations:

- m_{ijxy} number of animals taken in sample j from area y that were last captured in sample i from area x .
- u_{jy} number of unmarked animals taken in sample j from area y .
- n_{jy} size of sample j from area y
 $= u_{jy} + \sum_i \sum_x m_{ijxy}$
- s_{jy} number of animals (all of them marked) which are returned to area y after the j^{th} sample (when there are no losses on capture or extra animals injected into the population by the experimenter, $s_{jy} = n_{jy}$).

Parameters:

- φ_{jxy} probability that an animal, alive and in area x at time j is alive and in area y at time $j+1$.
- φ_{jyx} probability that an animal, alive and in area x at time j , survives to time $j+1 = \sum_y \varphi_{jxy}$
- p_{jyx} probability that an animal, alive and in area x at the time the j^{th} sample is taken, is captured in the sample.

Unobservable Random Variables:

- M_{ijxy} the number of animals, alive and in area y at the time the j^{th} sample is taken, that were last captured at time i in area x .
- U_{jy} the number of unmarked animals alive in area y at the time of the j^{th} sample.
- N_{jy} the size of the population alive on area y at time j .

Matrix Notation:

We also require some conventions on the representation of these quantities as matrix and vector arrays, and these will be illustrated by the three dimensional case ($n=3$ areas labelled A, B, C).

Let square brackets denote an array. If the symbol within the brackets has two subscripts replaced by dots, the array is an $n \times n$ matrix with rows and columns indicated by the dots:

$$\text{e. g. } [m_{12. .}] = \begin{bmatrix} m_{12AA} & m_{12AB} & m_{12AC} \\ m_{12BA} & m_{12BB} & m_{12BC} \\ m_{12CA} & m_{12CB} & m_{12CC} \end{bmatrix}$$

If the symbol within the brackets has a single dot in the subscript list, the array is a $1 \times n$ (row) vector

$$\text{e. g. } [N_{2.}] = [N_{2A} \ N_{2B} \ N_{2C}]$$

If the symbol within the brackets is D with the name of a vector as subscript, then the array is the $n \times n$ diagonal matrix with the vector elements along the diagonal and zeros elsewhere.

$$\text{e. g. } [Dn_{1.}] = \begin{bmatrix} n_{1A} & 0 & 0 \\ 0 & n_{1B} & 0 \\ 0 & 0 & n_{1C} \end{bmatrix}$$

The inverse of a matrix will be indicated in the usual way by a superscript -1 . For diagonal matrices note that

$$[Dn_{1.}]^{-1} = \begin{bmatrix} 1/n_{1A} & 0 & 0 \\ 0 & 1/n_{1B} & 0 \\ 0 & 0 & 1/n_{1C} \end{bmatrix} \text{ etc.}$$

The assumptions used to derive the estimates are identical to those given in ARNASON (1972a) for the unrestricted model. These require that all animals behave independently with respect to capture, survival and migration and that all animals together in one stratum at any time have the same probability of being subject to these events (regardless of age, size, capture history, etc.) although these probabilities may differ among areas and sampling times. Animals may migrate freely among areas between sampling times but if they emigrate beyond the n areas, they do so permanently. It is assumed that no births or new entries occur. For the moment, we assume that there are no losses on capture.

The "conditional likelihood" for this model can be formed as a straightforward extension of the model given in ARNASON (1972a, Appendix A), but its form—the product of multinomial distributions and convolutions of multinomials—is too complex to allow for derivation of "maximum likelihood" estimates after the fashion of JOLLY (1965). As before, we must resort to moment estimates.

DERIVATION OF ESTIMATES

The following moment equations follow from the properties of the model. The expectation signs have been omitted from the left hand side of the equations. Each equation represents n or n^2 equations by letting x, y assume all possible values (A, B, ... n).

$$n_{1x} = N_{1x} p_{1x} \tag{1.1}$$

$$N_{2y} = \sum_x N_{1x} \varphi_{1xy} \tag{1.2}$$

$$\begin{aligned} n_{2y} &= N_{2y} p_{2y} \\ &= \sum_x N_{1x} \varphi_{1xy} p_{2y} \end{aligned} \tag{1.3}$$

$$m_{12xy} = n_{1x} \varphi_{1xy} \hat{p}_{2y} \quad (1.4)$$

$$N_{3y} = \sum_x N_{2x} \varphi_{2xy} \quad (1.5)$$

$$\begin{aligned} n_{3y} &= N_{3y} \hat{p}_{3y} \\ &= \sum_x N_{2x} \varphi_{2xy} \hat{p}_{3y} \end{aligned} \quad (1.6)$$

$$m_{23xy} = n_{2x} \varphi_{2xy} \hat{p}_{3y} \quad (1.7)$$

$$m_{13xy} = \sum_z n_{1x} \varphi_{1xz} (1 - \hat{p}_{2z}) \varphi_{2zy} \hat{p}_{3y} \quad (1.8)$$

Using 1.4, substitute $\varphi_{1xy} \hat{p}_{2y} = m_{12xy}/n_{1x}$ into 1.3 to give n equations in the n unknowns N_{1A}, \dots, N_{1n} . The solution of these n equations is given below. Similarly, using 1.7 to substitute for $\varphi_{2xy} \hat{p}_{3y}$ in 1.6 gives the solution for N_{2A}, \dots, N_{2n} . Using 1.4 to give $\varphi_{1xz} \hat{p}_{2z}$ and 1.7 to give $\varphi_{2zy} \hat{p}_{3y}$, substitute for these quantities in 1.8 to give

$$m_{13xy} = \sum_z n_{1x} \varphi_{1xz} m_{23zy} / n_{2z} - \sum_z m_{12xz} m_{23zy} / n_{2z}$$

This system of n^2 equations involves the n^2 unknowns φ_{1xy} $x, y = A, B, \dots, n$. Straight-forward matrix manipulation then gives the desired estimates:

$$[\hat{N}_1.] = [n_2.] [m_{12..}]^{-1} [Dn_1.] \quad (1.9)$$

$$[\hat{N}_2.] = [n_3.] [m_{23..}]^{-1} [Dn_2.] \quad (1.10)$$

$$[\hat{\varphi}_{1..}] = [Dn_1.]^{-1} \{ [m_{13..}] [m_{23..}]^{-1} [Dn_2.] + [m_{12..}] \} \quad (1.11)$$

It is interesting to note that this last equation can be rearranged to give

$$[Dn_1.] [\hat{\varphi}_{1..}] - [m_{12..}] = [m_{13..}] [m_{23..}]^{-1} [Dn_2.]$$

or

$$[\hat{M}_{12..}] - [m_{12..}] = [m_{13..}] [m_{23..}]^{-1} [Dn_2.]$$

In the 1-dimensional case this reduces to the following result (in the notation of JOLLY (1965)):

$$\hat{M}_2 - m_2 = z_2 R_2^{-1} n_2 = n_2 z_2 / R_2$$

which is identical to JOLLY's estimate for M_2 in the case of no losses on capture ($n_2 = s_2$).

Estimates of survival are formed from the row sums of $[\hat{\varphi}_{1..}]$. For example $\hat{\varphi}_{1A}$ is given by summing the elements in the first row of $[\hat{\varphi}_{1..}]$. Estimates of the φ_{2xy} are not available from this experiment, nor are estimates for N_{3x} . Estimates for \hat{p}_{1x} or \hat{p}_{2x} can be derived using the relations:

$$\hat{p}_{1x} = n_{1x} / \hat{N}_{1x}$$

$$\hat{p}_{2x} = n_{2x} / \hat{N}_{2x}$$

COMMENTS AND AN EXAMPLE

It should be noted that the estimates involve the inverses of two data matrices: $[m_{12..}]$, and $[m_{23..}]$. These inverses cannot be formed if the matrix is singular; this will arise if a row or column is all zeros, or if one row (or column) is a linear combination of the others (for example, if two rows are identical, or one row is the sum of two others, etc.). In such a case, one could pool the two (or more) offending strata together to give a matrix of reduced dimensions. DARROCH (1961) gives some

guidance on this. Even though a data matrix is not singular, it may be ill conditioned. This arises when linear dependencies among the rows or columns "almost" occur. This will be reflected by the determinant of the matrix being close to zero (in practice if the determinant is less than about 10, the estimates are unreliable). If the matrix is ill conditioned, most numerical inversion formulae can be quite inaccurate (though this can always be checked by multiplying the matrix and its inverse together and ensuring that the result is the identity matrix), but more important, it indicates that the experiment was uninformative about some of the parameters and some (or all) of the estimates may be unreliable. Always check the determinants of $[m_{12.}]$ and $[m_{23.}]$ first. If they are close to zero, pooling of strata may again be necessary.

The estimates of the N_{1x} can be shown to be identical to those given in C & J for the two sample experiment. This is as we would expect, since their estimates are a generalized Lincoln Index and it is well known that the estimate of initial population size is unaffected by deaths. The estimates given here for N_{2x} , of course, are different from those of C & J. These authors gave a variance formula for $\hat{N}_1 = \sum_x \hat{N}_{1x}$ and stated that the formula was basically unchanged if deaths occurred. The dominant term in their formula for the estimated asymptotic variance is (in the notation of this paper)

$$\text{as. var. } (\hat{N}_1) = \sum_x \sum_y m_{12xy} \left(\frac{\hat{N}_{1x} \hat{N}_{2y}}{n_{1x} n_{2y}} \right)^2 \quad (1.12)$$

(from equations 20 and 21 of C & J). Note that in their development, they assume that only the m_{12xy} are random variables, whereas the n_{ix} are assumed to be fixed (hypergeometric distribution for sampling as opposed to the binomial model used in ARNASON 1972a). This tends to reduce the size of the variances of the estimates, but the above formula was nevertheless found to give satisfactory results. C & J give formulae for \hat{N}_{2x} and $\hat{T}_{1xy} = \hat{N}_{1x} \hat{\phi}_{1xy}$ (the net number of transfers from x to y) and their variances but these formulae are not applicable if deaths occur (unless the number of deaths and losses is known or can be sampled). They also suggest a number of tests for the assumptions of the model. I am currently developing variance formulae and testing procedures along these lines for the triple catch experiment, and the results of these studies will be given at a later date.

The following numerical example is a reworking of the data in Appendix B of ARNASON (1972a) using the matrix notation used here (for a 2-dimensional model). The data are as follows:

$$\begin{aligned} [n_{1.}] &= [n_{1A} \ n_{1B}] = [193 \ 228] \\ [n_{2.}] &= [85 \ 176] \quad [n_{3.}] = [84 \ 144] \\ [m_{12.}] &= \begin{bmatrix} m_{12AA} & m_{12AB} \\ m_{12BA} & m_{12BB} \end{bmatrix} = \begin{bmatrix} 31 & 8 \\ 7 & 64 \end{bmatrix} \\ [m_{23.}] &= \begin{bmatrix} 18 & 9 \\ 11 & 42 \end{bmatrix} \quad [m_{13.}] = \begin{bmatrix} 9 & 9 \\ 12 & 33 \end{bmatrix} \end{aligned}$$

The determinant of $[m_{12..}]$ is $(31)(64) - (7)(8) = 1928$ and of $[m_{23..}]$ is 657 so no problems of ill conditioning arise. Thus, using equation 1.9

$$\begin{aligned} [\hat{N}_1.] &= [\hat{N}_{1A} \ \hat{N}_{1B}] \\ &= [85 \ 176] \begin{bmatrix} .0332 & -.004149 \\ -.003631 & .01608 \end{bmatrix} \begin{bmatrix} 193 & 0 \\ 0 & 228 \end{bmatrix} \\ &= [421.2 \ 564.8] \end{aligned}$$

The inverse of $[m_{12..}]$ can easily be calculated by hand for a 2×2 matrix. For larger matrices an iterative method, such as the GAUSS elimination method, should be used on a computer (see, for example, GRAYBILL 1969 chapter 11). The calculation of $[\hat{N}_2.]$ using equation 1.10 is similar. To calculate $[\hat{\varphi}_{1..}]$, use equation 1.11

$$\begin{aligned} [\hat{\varphi}_{1..}] &= \begin{bmatrix} \hat{\varphi}_{1AA} & \hat{\varphi}_{1AB} \\ \hat{\varphi}_{1BA} & \hat{\varphi}_{1BB} \end{bmatrix} \\ &= \begin{bmatrix} 1/193 & 0 \\ 0 & 1/228 \end{bmatrix} \left\{ \begin{bmatrix} 9 & 9 \\ 12 & 33 \end{bmatrix} \begin{bmatrix} .063927 & -.013699 \\ -.016743 & .027397 \end{bmatrix} \begin{bmatrix} 85 & 0 \\ 0 & 176 \end{bmatrix} + \begin{bmatrix} 31 & 8 \\ 7 & 64 \end{bmatrix} \right\} \\ &= \begin{bmatrix} .005181 & 0 \\ 0 & .004386 \end{bmatrix} \left\{ \begin{bmatrix} 36.1 & 21.7 \\ 18.24 & 130.2 \end{bmatrix} + \begin{bmatrix} 31 & 8 \\ 7 & 64 \end{bmatrix} \right\} \\ &= \begin{bmatrix} .3476 & .1539 \\ .1107 & .8517 \end{bmatrix} \end{aligned}$$

Hence

$$[\hat{\varphi}_1.] = [\hat{\varphi}_{1A} \ \hat{\varphi}_{1B}] = [.5015 \ .9624]$$

Also $\hat{N}_1 = \hat{N}_{1A} + \hat{N}_{1B} = 421.2 + 564.8 = 986$

Using the approximate asymptotic variance formula (equation 1.12) gives

$$\begin{aligned} \text{as. var}(\hat{N}_1) &\approx 4449.78 \\ \text{as. s.d.}(\hat{N}_1) &\approx 66.7 \end{aligned}$$

Using the exact asymptotic variance formulae for the two dimensional model given in ARNASON (1972b) it can be shown that

$$\text{as. s.d.}(\hat{N}_1) = 63.7$$

ESTIMATES WHEN LOSSES ON CAPTURE OCCUR

Suppose animals may be lost on capture. That is, they may die due to handling, or part of the captured population may be removed for laboratory study, or the method of capture, as in bird banding studies, may involve the killing of animals. In the latter case, all animals are lost on capture, and marked animals are added to the population by an independent capture and/or releasing program. The quantities s_{ix} include all marked animals released into the population at time i , whether or not they were a member of the u_i , some previous n_j ($j=1 \dots i-1$; e.g. animals retained in the laboratory for one or more sampling intervals), or are new stocks released into the population. The only restriction on the s_{ix} is that they must behave the same (with respect to survival, migration and capture) as the animals in stratum x at time i , and they must be marked as having been last seen in stratum x . JOLLY

(1965 page 240) gives some guidance on this. There is no need to treat losses on capture as stochastic, as JOLLY does. Treating the number lost as a fixed known quantity does not affect the estimates, and prevents the variances of the estimates from being artificially inflated. The moment equations corresponding to equations 1.1 to 1.8 are:

$$n_{1x} = N_{1x} p_{1x} \quad (2.1)$$

$$N_{2y} = \sum_x (N_{1x} - n_{1x} + s_{1x}) \varphi_{1xy} \quad (2.2)$$

$$n_{2y} = N_{2y} p_{2y} = \sum_x (N_{1x} - n_{1x} + s_{1x}) \varphi_{1xy} p_{2y} \quad (2.3)$$

$$m_{12xy} = s_{1x} \varphi_{1xy} p_{2y} \quad (2.4)$$

$$N_{3y} = \sum_x (N_{2x} - n_{2x} + s_{2x}) \varphi_{2xy} \quad (2.5)$$

$$n_{3y} = N_{3y} p_{3y} \quad (2.6)$$

$$m_{23xy} = s_{2x} \varphi_{2xy} p_{3y} \quad (2.7)$$

$$m_{13xy} = \sum_x s_{1x} \varphi_{1xz} (1 - p_{2z}) \varphi_{2zy} p_{3y} \quad (2.8)$$

Matrix manipulation of these equations in an analagous fashion gives the estimates.

$$[\hat{N}_{1.} - n_{1.} + s_{1.}] = [n_{2.}] [m_{12.}]^{-1} [Ds_{1.}]$$

That is:

$$[\hat{N}_{1.}] = \{[n_{2.}] [m_{12.}]^{-1} [Ds_{1.}]\} + [n_{1.}] - [s_{1.}]$$

Similarly:

$$[\hat{N}_{2.}] = \{[n_{3.}] [m_{23.}]^{-1} [Ds_{2.}]\} + [n_{2.}] - [s_{2.}]$$

And

$$[\hat{\varphi}_{1.}] = [Ds_{1.}]^{-1} \{[m_{13.}] [m_{23.}]^{-1} [Ds_{2.}] + [m_{12.}]\}$$

SUMMARY

Estimates of survival, migration rates, and population size are developed for a triple catch marking experiment on n ($n \geq 2$) areas with migration among all areas and death in all areas occurring, but no recruitment (birth). This represents the extension to three sampling times of the method of CHAPMAN and JUNG (1956) for estimates in a stratified population. The method is further extended to allow for 'losses on capture'.

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層別された個体群における個体数,
移動率および生存率の推定

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2つ以上の場所にまたがって存在しその各場所間で個体の移動が起きている個体群に対して3回捕獲の標識再捕実験を行なった場合の生存率, 移動率および個体数の推定法を提示した。これは層別された個体群を対象とした CHAPMAN and JUNGLE (1956) の方法を拡張したものである。さらに捕獲に伴なうロス(死亡あるいは除去)があっても適用できるような形への拡張もあわせ行なった。