

## Estimating Population Size



### Introduction

All monitoring programs are designed to detect change in population size. Some require, in addition, estimates of population size itself. Two approaches to making such estimates, using various mark-recapture methods or removal sampling, are described in this chapter. Whatever the method, estimation of population size requires extensive data collection and analysis and is labor-intensive and time-consuming (Southwood 1978). Therefore, such estimates should be included in a project design only when the research question requires detailed knowledge of the target population.

### Mark-recapture

*MAUREEN A. DONNELLY AND CRAIG GUYER*

The mark-recapture (M-RC) method of population estimation consists of the capture and marking of animals, their release, and their subsequent recapture or resighting one or more times.

### Objectives

Mark-recapture methods are valuable in monitoring studies because they extend beyond estimation of population size to include estimation of demographic parameters (birth, death, im-

migration, emigration, and survival rates), space use patterns (home range size and utilization), and individual growth rate.

Several mathematical estimators of population size based on M-RC data are available (Caughley 1977; Southwood 1978; Begon 1979). Describing all of them is beyond the scope of this book, so we limit our treatment to four commonly used methods. For readable descriptions of M-RC techniques and models, we recommend Begon (1979) and Schemintz (1980).

### Target Organisms and Habitat

Mark-recapture techniques have been used by herpetologists since the 1920s to study many species of salamanders and frogs in a variety of habitats (Woodbury 1956). Marking methods are detailed in Appendix 2. Marking amphibian larvae is difficult, and some marking methods may have adverse effects on individuals (e.g., Travis 1981). To our knowledge, no M-RC study has ever been performed on caecilians. Although these amphibians could be captured, marked, and released, their aquatic or fossorial habits would make recapture difficult.

### Background

The mathematical estimation of animal population size was formalized by Petersen (1896) and popularized in North America by Lincoln (1930). The Petersen estimate (also referred to as the Lincoln Index and the Lincoln-Petersen Index) is relatively simple mathematically and is the basis for more-complicated estimators.

Assumptions inherent to all M-RC models are that (1) the initial sample taken is representative of the entire population (i.e., not biased by age or sex); (2) all animals taken in the initial sample are marked, and the marks are permanent and recorded correctly; (3) the marked animals are released and become distributed randomly in the

population; and (4) marking does not affect the probability of recapture or survival (i.e., marked and unmarked animals have equal catchability). These assumptions should be tested in the field or the laboratory prior to initiation of a long-term study. Activity patterns and behaviors can be influenced by age and sex, and some marking methods can affect survival, growth, and/or behavior. In some cases, marked animals are more conspicuous (to investigators and predators) than unmarked ones, thus violating assumption 4. Although few investigators have tested assumption 4, Clarke (1972) demonstrated that toe clipping adversely affected young toads, and Travis (1981) showed that staining tadpoles with neutral red dye reduced growth rate. If species exhibit age- and sex-related behavioral differences (violation of assumption 1) or if recapture rates vary with age or sex (violation of assumption 4; van Gelder and Rijdsdijk 1987), then each subgroup (i.e., age class or sex) can be analyzed separately.

The Petersen estimate of population size assumes, in addition to the above assumptions, that the population is closed (no immigration, emigration, birth, or death). If two samples are closely matched in time, the population can act as if it were closed, and the Petersen estimate is appropriate. If detailed data on population processes (immigration, emigration, birth, death, survival) are necessary, then other models must be used.

Caughley (1977), Southwood (1978), and Begon (1979) described how to test the assumptions of equal catchability, the effects of marking, and the permanence of marks. Additionally, Begon (1979) described tests of constancy of survival rate (Fisher-Ford estimator), differences between subgroups, and random sampling. Nichols (1992) recently reviewed mark-recapture models and advances in computer software for analyses of M-RC data. Table 7 summarizes some of the effects of violating the basic assumptions of M-RC models.

**Table 7. Assumptions of Mark-Recapture Models and Effects of Their Violation**

Assumption	Effects of violation
Marks permanent and noted correctly	Population size overestimated Survival rate underestimated
Probability of recapture not affected by marking	If recapture rates increase with mark: Population size underestimated Survival rate underestimated (with Manly-Parr method)
Survival not affected by marking	If marking decreases survival: Survival rate underestimated Population size overestimated in closed populations Gains overestimated <sup>a</sup> (with Jackson's Positive method)
Equal catchability	Population size underestimated

<sup>a</sup> Gains result from immigration and recruitment.

### Research Design and Field Methods

Before a M-RC study is conducted, the investigator must clearly state the goals of the research, establish a sampling protocol that will satisfy the goals, select an estimator of population size (taking underlying assumptions into account), and decide how the data will be analyzed statistically. The first step in any M-RC study is to define the target population (e.g., the reproductive amphibians at a breeding site or the number of amphibians in a 1-ha plot or along a 100-m transect). The results of the study must be interpreted specifically and only in terms of this target population (Begon 1979). The sampling protocol is dictated by the information needed (e.g., estimate of population size only, specific information on population gains and losses, annual or seasonal variation in population parameters or space use patterns). Detailed knowledge of the biology of the target organisms facilitates designing the appropriate sampling protocol and improves the accuracy of the results. The estimator and the statistical tests selected are dictated by the sampling protocol. The availability of

resources (funds, field time, personnel, and computers) must also be considered.

All M-RC techniques require that the population under study be sampled at least twice (see "Data Analysis and Interpretation," below). Animals can be sampled in plots of known size or along permanent transects. If animals are sampled within a site of known area, then density can be calculated. In the field, the study area is sampled, and individuals are captured and marked, or if they are recaptured, the mark is recorded, and they are released. In some cases, an investigator can capture all active animals in the study area; in others cases, time-constrained searches must be used to ensure equal sampling effort in all areas.

Data sheets designed for the study are a convenient way to record data in the field; data also can be recorded in a waterproof field notebook, dictated into a microcassette recorder, or entered directly into small, hand-held computers. Field notebooks are relatively small and easy to transport. For every animal captured, Donnelly (1989) recorded capture date, plot number, time (24-hr clock), location on the plot, major habitat

feature at capture point, number of individuals at each location, age (adult or juvenile, based on body size), sex, body size, mass (measured with a Pesola scale), clip code (= marking code), and variation in color pattern. R. A. Alford (pers. comm.) recorded relative humidity, air temperature, substrate temperature, water temperature, percentage of cloud cover, and rainfall, prior to each of his samples.

Many amphibians can be captured by hand or in pitfall traps, and some can be attracted with artificial habitats (see "Artificial Habitats" in Chapter 7, and Stewart and Pough 1983) or bait (Parmenter et al. 1989). If individuals are marked (e.g., with radios or fluorescent dye) such that they can be resighted without being recaptured, the effects of handling on study organisms are reduced. Analysis of capture-resight data is described briefly in a later section.

Recapture periods must be designed carefully to meet the assumption that marked animals are redistributed randomly in the population. The number of times the population is sampled with M-RC techniques depends on the question being addressed.

### Data Analysis and Interpretation

Microcomputers and database management programs allow one to store and manipulate data gathered on marked populations. The management of data is dictated by the mathematical estimator used. All M-RC studies with four or more sampling periods use an individual capture history matrix, and several software programs use these matrices to estimate abundance or survival (Nichols 1992).

If M-RC data are gathered over a long period, and if the population is sampled at least three times per interval (where intervals are weeks or months), then the data obtained may be extensive enough to allow calculation of the minimum number of individuals known to be alive (Donnelly 1989). Birth rate (or recruitment), im-

migration, loss rates, and survival rate (persistence) can be determined directly from these data. Partitioning emigration and death can be problematic. If the length of the study is short relative to the lifetime of the target organism, losses can be assumed to be the result of emigration rather than death.

Standard analytical tools (*t*-tests, ANOVAs, and nonparametric counterparts) can be used to analyze M-RC data—for example, to determine whether two populations differ in size or whether the size of one population has changed during some period. If individuals at a study site are sampled repeatedly, then observations are not independent, and the data must be analyzed with repeated-measures models (Winer 1971; Fowler 1990).

### Personnel and Materials

Mark-recapture studies can be conducted by single individuals or by teams. The materials required depend on the marking system used. Microcomputers or mainframe computers are essential for managing and analyzing large data sets.

### Population Estimators

Mark-recapture models for population estimation can be grouped according to the number of samples taken, that is, those that require two samples (Petersen, Bailey's modification of the Petersen estimate, and Chapman's modification of Petersen), those that require three (Triple Catch), and those that require several (Table 8). The models in the first group do not allow for gains or losses to the population under study and are best used when the population can be sampled only twice. The Triple Catch method estimates population size, gains (resulting from immigration and birth), and survival rates. Models in the last group (e.g., Fisher-Ford, Jolly's, Manly-Parr) estimate population size, gains, and survival rates.

Table 8. Population Estimators and Their Characteristics<sup>a</sup>

Estimator	Samples required	Mark type <sup>b</sup>	Standard error	Gains	Losses	Survival rate	Assumption
Petersen <sup>c</sup>	2	D/I	+	-	-	-	Closed population
Bailey's and Chapman's modifications of Petersen	2	D/I	+	-	-	-	Closed population
Triple Catch <sup>d</sup>	3	D/I	+	+	-	+	Variable gain, variable survival
Weighted Mean	Several	D/I	+	-	-	-	Closed population
Schumacher	Several	D/I	+	-	-	-	Closed population
Jackson's Positive method <sup>e</sup>	Several	D/I	+	+	-	-	Constant gain, variable loss
Jackson's Negative method <sup>f</sup>	Several	D/I	+	+	-	+	Constant survival, variable gain
Fisher-Ford	Several	I	-	+	+	-	Constant survival
Jolly-Seber Stochastic	Several	I	+	+	+	+	Age-independent survival
Manly-Parr	Several	I	+	+	+	+	Variable survival

<sup>a</sup> In columns 4 through 7, + indicates that the method estimates the value; - indicates that the value is not estimated.

<sup>b</sup> D = date; I = individual.

<sup>c</sup> If losses (death and emigration) occur, the estimate measures population size on day 2; if gains (recruitment and immigration) occur, the method estimates population size on day 1.

<sup>d</sup> The method estimates population size on day 2, survival rate on day 1, and gains on day 2 with variable gain and survival rates. Population sizes on days 1 and 3, survival rate on day 2, and gains on day 1 assume a constant survival rate.

<sup>e</sup> This method generates little information per unit-effort.

<sup>f</sup> This method is best used when capturing and marking are relatively easy but recapturing (or mark screening) is difficult.

The Petersen estimate assumes that the population under study is closed, but it is robust when assumptions are violated (Menkens and Anderson 1988). The Triple Catch model provides considerable demographic information per unit effort. The three models that provide the most detailed information about a population are Fisher-Ford, Jolly-Seber Stochastic, and Manly-Parr. Of these, the Fisher-Ford model is best used when the sampling intensity is low, survival

rates are low and constant, and the population is small (Begon 1979). Both the Fisher-Ford and Jolly-Seber methods assume age-independent survival. The Jolly-Seber method fails when age-dependent survival is pronounced, but if separate age-classes are used, this problem can be avoided. The Manly-Parr method has the least restrictive assumptions, but it requires the most extensive data, and data management is tedious, especially if more than five samples are taken

and the study population is large. Begon (1979) described how gains and losses can be partitioned if they are estimated using these estimators.

If the design of the monitoring project is such that animals are sampled on only two occasions with M-RC methods, then the Petersen method (or the modifications of Petersen's estimate) must be used. If the animals are sampled on only three occasions, then it is best to use the Triple Catch method because it does not assume that the population is closed. If sampling is extensive (more than three samples), we recommend the Fisher-Ford or Jolly-Seber method. We describe these four methods in detail below. We follow the notation and format of Begon (1979). We use *day* to refer to sampling session, although the actual interval between "days" may be weeks, months, or some other time interval designated by the investigator.

Although we provide examples with hand calculation of some population estimators, in most cases, calculation by hand is time-consuming and tedious. Therefore, we recommend that extensive M-RC data be analyzed with a computer. A number of programs appropriate for this type of analysis are available. CAPTURE (Otis et al. 1978; White et al. 1978, 1982; Appendix 6) is a comprehensive program that has been in use for many years (Nichols 1992) and that has recently been revised (Rexstad and Burnham 1991). This program is for closed populations (no gains due to immigration or recruitment and no losses due to emigration or death). Menkens and Anderson (1988) critiqued the model selection algorithm in CAPTURE. They noted that not all goodness-of-fit tests used are independent and that the tests often have low power, especially for small populations. Recently, Pollock et al. (1990) developed two FORTRAN computer programs, JOLLY and JOLLYAGE, for open populations (Appendix 6). Pollock et al. (1990) and Nichols (1992) reviewed approaches to the estimation of population size and available computer programs.

#### PETERSEN ESTIMATE

The Petersen estimate of population size  $N$  is given by:

$$\hat{N} = \frac{rn}{m} \quad (1)$$

where

$r$  = number of animals caught, marked, and released on day 1

$n$  = total number of animals caught on day 2

$m$  = total number of marked animals caught on day 2.

For example, if on the first day 900 animals are captured, marked, and released, and 1,000 animals are caught on day 2, of which 600 had been previously marked, then using equation 1,

$$\hat{N} = \frac{900 \cdot 1,000}{600} = 1,500$$

BAILEY'S MODIFICATION. This estimator ( $\hat{N}_B$ ) derived by Bailey (1951), gives a more accurate estimate of population size when numbers of recaptures are small. It should be used when recaptures are 10 or fewer. It is calculated as follows:

$$\hat{N}_B = \frac{r(n+1)}{m+1} \quad (2)$$

For example, if 16 animals are caught, marked, and released on day 1, and 17 animals are caught on day 2, of which 9 are marked, then using equation 2,

$$\hat{N}_B = \frac{16(17+1)}{9+1} = 28.8$$

Bailey (1951) also provided a formula for calculating the standard error of  $N_B$ :



$$SE\hat{N}_B = \left[ \frac{r^2(n+1)(n-m)}{(m+1)^2(m+2)} \right]^{1/2} \tag{3}$$

Using equation 3 and the above example,

$$SE\hat{N}_B = \left[ \frac{16^2(17+1)(17-9)}{(9+1)^2(9+2)} \right]^{1/2} = 5.79$$

Given these data, the estimated population size is 28.8 individuals, and the standard error of the estimate is 5.79.

CHAPMAN'S MODIFICATION. Chapman (1951) also modified the Petersen estimate to correct for low number of recaptures (i.e.,  $m \leq 10$ ), as follows:

$$\hat{N}_C = \frac{(r+1)(n+1)}{(m+1)} - 1 \tag{4}$$

Seber (1970, 1982) provided a formula for calculating the standard error of  $\hat{N}_C$ :

$$SE\hat{N}_C = \left[ \frac{(r+1)(n+1)(r-m)(n-m)}{(m+1)^2(m+2)} \right]^{1/2} \tag{5}$$

Using the data from the previous example ( $r = 16, n = 17, m = 9$ ) and equations 4 and 5,

$$\hat{N}_C = \frac{(16+1)(17+1)}{(9+1)} - 1 = 29.6$$

and

$$SE\hat{N}_C = \left[ \frac{(16+1)(17+1)(16-9)(17-9)}{(9+1)^2(9+2)} \right]^{1/2} = 3.95$$

**TRIPLE CATCH METHOD**

This estimator requires three samples (Begon 1979) and estimates population size ( $N$ ), sur-

vival ( $\phi$ ), and gains ( $g$ ). Gains are defined as the proportion of the day ( $i + 1$ ) population added between days  $i$  and ( $i + 1$ ). Survival is defined as the proportion of the day  $i$  population that survives until day ( $i + 1$ ). The Triple Catch method allows both gain and loss rates to vary. It makes few assumptions and provides considerably more information regarding the population under study than does Petersen's estimate (and both modifications).

The following equations are corrected for bias from small sample sizes. On day 1,  $r_1$  animals are captured, marked, and released. Marks can be date- or individual-specific. On day 2,  $n_2$  animals are caught, of which  $m_{21}$  are already marked. All unmarked individuals captured on day 2 are marked (given a date-specific mark for day 2 or individual-specific marks), and all are released. On day 3,  $n_3$  animals are caught. Some are unmarked, some were marked on day 1 and were not captured on day 2 ( $m_{31}$ ); some were marked on day 2 ( $m_{32}$ ). Animals captured on both day 1 and day 2 are included in  $m_{32}$ . The number of day  $j$  marks available for capture on day  $i$  is indicated by  $M_{ij}$ ; this variable is referred to as the number of marks-at-risk. For example, on day 2 there are  $M_{21}$  marks-at-risk. This method allows the gain and survival rates to vary initially, and if the marked proportion in the sample is the same as in the population, that is

$$\frac{M_{21}}{N_2} = \frac{m_{21}}{n_2}$$

then population size on day 2 ( $N_2$ ) can be estimated with equation 6:

$$\hat{N}_2 = \frac{\hat{M}_{21}(n_2 + 1)}{(m_{21} + 1)} \tag{6}$$

The  $M_{21}$  animals are "survivors" (number of the animals marked on day 1 that survive until day 2) of  $r_1$  animals released, so the survival rate ( $\phi$ ) can be calculated as follows:

$$\hat{\phi}_1 = \frac{M_{21}}{r_1} \tag{7}$$

$$\hat{\phi}_1 = \frac{59.44}{67} = 0.89$$

To calculate  $\hat{N}_2$  (estimated population size on day 2), an estimate of  $M_{21}$  ( $\hat{M}_{21}$  = number of day 1 marks at risk on day 2) is required:

$$\hat{M}_{21} = \frac{m_{31}(r_2 + 1)}{(m_{32} + 1)} + m_{21} \tag{8}$$

Gains between day 2 and 3 ( $g_2$ ) are estimated as follows:

$$\hat{g}_2 = 1 - \frac{(m_{31} + 1)n_2}{(n_3 + 1)m_{21}} \tag{9}$$

For example, 67 animals are captured, marked, and released on day 1. Fifty-seven animals are captured on day 2; 20 animals have a day-1 mark and are given a day-2 mark, and 37 unmarked animals are given a day-2 mark. Of the 68 animals captured on day 3, 17 have a day-1 mark, 16 have a day-2 mark, and 8 have day-1 and day-2 marks.

$r_1 = 67$	$m_{21} = 20$	$n_1 = 67$
$r_2 = 57$	$m_{31} = 17$	$n_2 = 57$
$r_3 = 68$	$m_{32} = 24$	$n_3 = 68$

Using equations 6 through 9,

$$\hat{M}_{21} = \frac{17 \cdot 58}{25} + 20 = 59.44$$

$$\hat{N}_2 = \frac{59.44 \cdot 58}{20 + 1} = 164.17$$

$$\hat{g}_2 = 1 - \left[ \frac{18 \cdot 57}{69 \cdot 20} \right] = 0.26$$

If we assume that gain rates and survival rates are constant, and if the interval between sample periods is the same, then  $\hat{\phi}_2 = \hat{\phi}_1$  and  $\hat{g}_1 = \hat{g}_2$ . If these assumptions are made, then population sizes on day 1 and day 3 can be estimated using the equations:

$$\hat{N}_1 = \frac{(1 - \hat{g}_1) \hat{N}_2}{\hat{\phi}_1} \tag{10}$$

$$\hat{N}_3 = \frac{\hat{N}_2 \hat{\phi}_2}{1 - \hat{g}_2} \tag{11}$$

Continuing with our example,  $\phi_2 = \phi_1 = 0.89$ ,  $\hat{g}_1 = \hat{g}_2 = 0.26$ , and using equations 10 and 11, estimated population sizes on days 1 and 3 are as follows:

$$\hat{N}_1 = \frac{(1 - 0.26)164.17}{0.89} = 136.50$$

$$\hat{N}_3 = \frac{164.17 \cdot 0.89}{(1 - 0.26)} = 197.45$$

The Triple Catch method includes standard error estimates for population size on day 2 ( $N_2$ ) and survival rate ( $\phi_1$ ) on day 1 as follows:

$$SE_{\hat{N}_2} = \left\{ \hat{N}_2 (\hat{N}_2 - n_2) \left[ \frac{\hat{M}_{21} - m_{21} + r_2}{\hat{M}_{21}} \left( \frac{1}{m_{32}} - \frac{1}{r_2} \right) + \frac{1}{m_{21}} - \frac{1}{n_2} \right] \right\}^{1/2} \tag{12}$$

$$SE_{\hat{\phi}_1} = \left\{ (\hat{\phi}_1)^2 \frac{(\hat{M}_{21} - m_{21})(\hat{M}_{21} - m_{21} + r_2)}{(\hat{M}_{21})^2} \left( \frac{1}{m_{32}} - \frac{1}{r_2} \right) + \frac{1}{\hat{M}_{21}} - \frac{1}{r_1} \right\}^{1/2} \tag{13}$$



Applying equations 12 and 13 to our sample data yields

$$SE_{\hat{N}_2} = \left\{ 164.17(164.17 - 57) \left[ \frac{59.44 - 20 + 57}{59.44} \left( \frac{1}{24} - \frac{1}{57} \right) + \frac{1}{20} - \frac{1}{57} \right] \right\}^{1/2} = 35.54$$

and

$$SE_{\hat{\phi}_1} = \left\{ 0.89^2 \frac{(59.44 - 20)(59.44 - 20 + 57)}{59.44^2} \left( \frac{1}{24} - \frac{1}{57} \right) + \frac{1}{59.44} - \frac{1}{67} \right\}^{1/2} = 0.15$$

**FISHER-FORD ESTIMATOR**

The Fisher-Ford estimator of population size is a modification of the Petersen estimate that assumes that the ratio of marks to the total number of animals captured in the day *i* sample is the same as the ratio of total marks to the total population. It requires that animals be marked and recaptured on several occasions and assumes a constant survival rate that is obtained by "trial and error." The estimate of population size on day *i* is given by the equation:

$$\hat{N}_i = \frac{(n_i + 1)}{(m_i + 1)} (M_i) \tag{14}$$

where

- $\hat{N}_i$  = estimated population size on day *i*
- $n_i$  = total number captured on day *i*
- $m_i$  = number of marked animals captured on day *i*
- $M_i$  = number of marks at risk (number of marks available for recapture) on day *i*.

The number of marks-at-risk ( $M_i$ ) has to be estimated by a complicated and indirect process. The total number of marks caught on day *i* is given by the equation

$$m_i = \sum_j m_{ij}$$

where

- $m_i$  = number of marked animals captured on day *i*
- $m_{ij}$  = individuals caught on day *i* with a day-*j* mark
- $j$  = day mark was given (or last seen), ranging from 1 to (*i* - 1)
- $\sum_j$  = summation for all *j* values.

Each mark is (*i* - *j*) days old, and the total age of all marks (the number of days survived by marks caught on day *i*) is

$$\sum_j m_{ij} (i - j) \tag{15}$$

The total days survived by marks (TDS) during the study is given by the equation

$$TDS = \sum_i \sum_j m_{ij} (i - j) \tag{16}$$

To calculate TDS, the M-RC data are arranged in a table in which the rows indicate the day of the study and the columns indicate the day of the marks. To construct the table, the capture history for every individual must be tabulated. In Table 9 we illustrate this procedure with data from Dowdeswell et al. (1940). Examination of these data shows that on some days (3, 7, 10, 11),

**Table 9. Mark-Recapture Data for Sample Calculations of Population Estimates<sup>a,b</sup>**

<i>i</i>	<i>n<sub>i</sub></i>	<i>r<sub>i</sub></i>	Date of mark																	
			1	2	4	5	6	8	9	12	13									
1	43	40	—																	
2	43	40	5																	
3	0	0																		
4	13	12	0	3																
5	52	50	3	8	5															
6	56	51	6	12	6	15														
7	0	0																		
8	52	52	4	10	3	16	14													
9	50	50	4	5	1	11	5	14												
10	0	0																		
11	0	0																		
12	15	15	1	1	1	3	1	5	5											
13	20	20	1	1	2	3	2	7	8	6										
14	20	—	0	0	0	2	2	4	1	0	4									

<sup>a</sup> Data are from Dowdeswell et al. 1940.

<sup>b</sup> *i* = day; *n<sub>i</sub>* = total number of animals captured each day; *r<sub>i</sub>* = total number released.

no animals were captured. On some days (1, 2, 4, 5, 6) not all animals were marked and released (i.e., some died during handling or were collected as vouchers). On day 8 of the study, 52 animals were caught; 47 were already marked, and the remaining 5 were marked at that time; all 52 were released. Of the 47 marked animals captured on day 8, 14 had day-6 marks, 16 had day-5 marks, 3 had day-4 marks, 10 had day-2 marks, and 4 had day-1 marks.

Once the data are arranged in the table, another table is constructed to calculate the observed TDS (see Table 10). It has three columns: *i* (day); *m<sub>i</sub>* (the number of marked animals caught on day *i*); and  $\sum_j m_{ij} (i - j)$  [the total age of all marks on day *i*]. The value *m<sub>i</sub>* (Table 10) is

obtained by summing row values for day *i* (Table 9). For example, on day 6,

$$m_6 = (15 + 6 + 12 + 6) = 39$$

and

$$\begin{aligned} \sum_j m_{6j}(6 - j) &= m_{65}(6 - 5) + m_{64}(6 - 4) + m_{63}(6 - 3) \\ &\quad + m_{62}(6 - 2) + m_{61}(6 - 1) \\ &= 15(1) + 6(2) + 0(3) + 12(4) + 6(5) \\ &= 105 \end{aligned}$$

Total days survived by marks (TDS) is the sum of column 3 in Table 10. In this example, TDS = (0 + 5 + 0 + 6 + . . . + 67) = 788.

The next step is to estimate TDS based on the average age of marks with a survival rate se-

**Table 10. Calculation of Observed TDS Using the Fisher-Ford Method of Population Estimation<sup>a,b</sup>**

<i>i</i>	<i>m<sub>i</sub></i>	$\sum_j m_{ij} (i - j)$
1	0	0
2	5	5
3	0	0
4	3	6
5	16	41
6	39	105
7	0	0
8	47	176
9	40	145
10	0	0
11	0	0
12	17	91
13	30	152
14	13	67
		788

Observed TDS =  $\sum_i \sum_j m_{ij} (i - j)$

<sup>a</sup> Based on data from Table 9. See text for explanation. TDS = total days survived by marks.

<sup>b</sup> *i* = day; *m<sub>i</sub>* = total number of marked animals caught on day *i*;  $\sum_j m_{ij} (i - j)$  = total age of all marks on day *i*.

lected by the investigator. The goal of this step is to find a survival rate that results in an estimated TDS that equals the observed TDS (calculated in Table 10). The average age of marks on day *i* is denoted as *A<sub>i</sub>*, and before day *i* there are *M<sub>i</sub>* marks-at-risk. On day *i*, some marked animals are captured, and unmarked animals are marked and released (*r<sub>i</sub>*). After the day *i* sample, there are (*M<sub>i</sub>* + *r<sub>i</sub>*) marks-at-risk, the *M<sub>i</sub>* marks are *A<sub>i</sub>* days old, and the *r<sub>i</sub>* marks are zero days old. On day (*i* + 1), the marks are 1 day older:

$$A_{i+1} = \frac{A_i M_i}{M_i + r_i} + 1 \tag{17}$$

All values of *r<sub>i</sub>* are known, and *M<sub>i</sub>* values are calculated using an arbitrarily selected survival rate ( $\phi$ ). This survival rate has to be adjusted iteratively so that the estimated TDS ( $\sum_i A_i m_i$ ) equals the observed TDS. If the *M<sub>i</sub>* values are known, then the mean age of marks on day 2 = 1, and *A<sub>3</sub>* can be calculated with equation 17.

On day (*i* + 1), there are (*M<sub>i</sub>* + *r<sub>i</sub>*) marks-at-risk, but only some survive ( $\phi$  = daily survival rate, which is assumed to be constant). The number that survive to day (*i* + 1) is expressed as

$$M_{i+1} = \phi (M_i + r_i) \tag{18}$$

All *r<sub>i</sub>* values are known, and  $\phi$  is selected by the investigator; the number of marks-at-risk on day 1 (*M<sub>1</sub>*) = zero. The number of marks-at-risk on day 2 (*M<sub>2</sub>*) is equal to the survival rate ( $\phi$ ) multiplied by the number of marked animals released on day 1 ( $\phi r_1$ ), because *M<sub>1</sub>* = zero (equation 18). Because *r<sub>2</sub>*,  $\phi$ , and *M<sub>2</sub>* are known, *M<sub>3</sub>* and all other values can be calculated.

To obtain a reasonably accurate estimated TDS (i.e., one that equals the observed TDS), an iterative procedure is used wherein the value of  $\phi$  is varied. Equations 17 and 18 are used with the selected value  $\phi$  (given that *M<sub>1</sub>* = 0, *M<sub>2</sub>* = ( $\phi r_1$ ), and *A<sub>2</sub>* = 1). In Table 11, the daily survival rate is 0.8, *M<sub>2</sub>* = 0.8 · 40 = 32, *M<sub>3</sub>* = 0.8(32 + 40) = 57.6, and no animals were captured on day 3, so *M<sub>4</sub>* =  $\phi M_3$  = 0.8 · 57.6 = 46.1. Similarly, *A<sub>2</sub>* = 1, so

$$A_3 = \frac{1 \cdot 32}{32 + 40} + 1 = 1.44 \approx 1.4$$

and because there were no captures on day 3, *A<sub>4</sub>* = *A<sub>3</sub>* + 1 = 1.4 + 1 = 2.4. Examination of Table 11 shows that by using  $\phi$  = 0.8, the estimated TDS of 755.67 is less than the observed TDS of 788. The

**Table 11. TDS Estimated Using the Fisher-Ford Method and a Survivorship Value ( $\phi$ ) of 0.8<sup>a,b</sup>**

<i>i</i>	<i>r<sub>i</sub></i>	<i>M<sub>i</sub></i>	<i>A<sub>i</sub></i>	<i>m<sub>i</sub></i>	<i>A<sub>i</sub>m<sub>i</sub></i>
1	40	0	—	0	0
2	40	32.0	1.00	5	5
3	0	57.6	1.44	0	0
4	12	46.1	2.44	3	7.33
5	50	46.5	2.94	16	47.04
6	51	77.2	2.42	39	94.38
7	0	102.6	2.46	0	0
8	52	82.0	3.46	47	162.62
9	50	107.2	3.12	40	124.80
10	0	125.8	3.12	0	0
11	0	100.6	4.12	0	0
12	15	80.5	5.12	17	87.04
13	20	76.4	5.32	30	159.60
14	—	77.1	5.22	13	67.86
Estimated TDS =					755.67

<sup>a</sup> Values for *r<sub>i</sub>* are from Table 9; values for *m<sub>i</sub>* are from Table 10. TDS = total days survived by marks.

<sup>b</sup> *i* = day; *r<sub>i</sub>* = total number of animals released on day *i*; *M<sub>i</sub>* = number of marks at risk on day *i*; *A<sub>i</sub>* = average age of marks on day *i*; *m<sub>i</sub>* = total number of marked animals caught on day *i*; *A<sub>i</sub>m<sub>i</sub>* = estimated days survived by marks caught on day *i*.

estimated TDS is recalculated in Table 12 using a daily survival rate of 0.9, yielding a TDS of 873.35.

At least one additional table (similar to Tables 11 and 12) with  $\phi$  varying must be constructed so that a survival rate can be obtained graphically; the goal is to get an estimated TDS equal to the observed TDS. In our example,  $\phi = 0.8$  gives an estimated TDS that is too low, and  $\phi = 0.9$  gives one that is too high. By varying  $\phi$  two or three times, the obtained TDS values can be plotted against these selected survival rates, and  $\phi$  can be determined by interpolation (Fig. 27). With  $\phi = 0.75$ , the estimated TDS = 698.04, and if

**Table 12. TDS Estimated Using the Fisher-Ford Method and a Survivorship Value ( $\phi$ ) of 0.9<sup>a,b</sup>**

<i>i</i>	<i>r<sub>i</sub></i>	<i>M<sub>i</sub></i>	<i>A<sub>i</sub></i>	<i>m<sub>i</sub></i>	<i>A<sub>i</sub>m<sub>i</sub></i>
1	40	0	—	0	0
2	40	36.0	1.00	5	5
3	0	68.4	1.47	0	0
4	12	61.6	2.47	3	7.41
5	50	66.2	3.07	16	49.12
6	51	104.6	2.75	39	107.25
7	0	140.0	2.85	0	0
8	52	126.0	3.85	47	180.95
9	50	160.2	3.73	40	149.20
10	0	189.2	3.84	0	0
11	0	170.3	4.84	0	0
12	15	153.3	5.84	17	99.28
13	20	151.5	6.32	30	189.60
14	—	154.4	6.58	13	85.54
Estimated TDS =					873.35

<sup>a</sup> Values for *r<sub>i</sub>* are from Table 9; values for *m<sub>i</sub>* are from Table 10. TDS = total days survived by marks.

<sup>b</sup> *i* = day; *r<sub>i</sub>* = total number of animals released on day *i*; *M<sub>i</sub>* = number of marks at risk on day *i*; *A<sub>i</sub>* = average age of marks on day *i*; *m<sub>i</sub>* = total number of marked animals caught on day *i*; *A<sub>i</sub>m<sub>i</sub>* = estimated days survived by marks caught on day *i*.

$\phi = 0.85$ , the estimated TDS = 813.62. From Figure 27, the  $\phi$  that gives an estimated TDS of 788 is 0.828. Table 13 estimates TDS with  $\phi = 0.828$ .

Now that we have a sequence of *M<sub>i</sub>* values, we can estimate population size (*N*) using equation 14 (*n<sub>i</sub>* values are from Table 9, *M<sub>i</sub>* and *m<sub>i</sub>* values are from Table 13). For example, on day 12:

$$\hat{N}_{12} = \frac{(15 + 1)}{(17 + 1)} (96.4) = 85.7 \approx 86$$

The estimated number of losses (*L<sub>i</sub>*) between day *i* and (*i* + 1) is given by the equation:

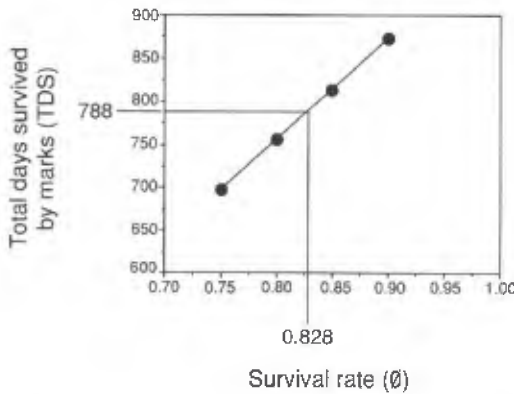


Figure 27. Graphical estimation of the total days survived by marks (TDS). The investigator selects three (or four) survival rates, calculates an estimated TDS, and plots the result. The survival rate that yields a TDS equal to the observed TDS is determined by interpolation. In this example, a survival rate of 0.828 gives a TDS equal to the observed TDS of 788.

$$\hat{L}_i = (1 - \phi)\hat{N}_i \tag{19}$$

The estimated number of gains ( $g_i$ ) between day  $i$  and day  $(i + 1)$  is given by:

$$\hat{g}_i = \hat{N}_{i+1} - \phi\hat{N}_i \tag{20}$$

For day 12,

$$\hat{L}_{12} = (1 - 0.828)86 = 14.8 \approx 15$$

$$\hat{g}_{12} = 63 - 0.828 \cdot 86 = -8.2 \approx -8$$

The estimates in Table 14 are rounded up to reflect biological reality—tenths of organisms do not exist. Although losses can be estimated for each day of the study, gains can be calculated only for days on which animals were captured. Negative gains are a mathematical artifact; gains on days 5 and 12 (Table 14) are, in reality, equal to zero. Negative losses would also be interpreted as zeros.

Based on the values in Table 14, the size of the population is estimated to have decreased from

Table 13. TDS Estimated Using the Fisher-Ford Method and a Survivorship Value ( $\phi$ ) of 0.828<sup>a,b</sup>

$i$	$r_i$	$M_i$	$A_i$	$m_i$	$A_i m_i$
1	40	0	—	0	0
2	40	33.1	1.00	5	5
3	0	60.5	1.45	0	0
4	12	50.1	2.45	3	7.35
5	50	51.4	2.98	16	47.68
6	51	84.0	2.51	39	97.89
7	0	112.0	2.56	0	0
8	52	92.7	3.56	47	167.32
9	50	119.8	3.28	40	131.20
10	0	140.6	3.31	0	0
11	0	116.4	4.31	0	0
12	15	96.4	5.31	17	90.27
13	20	92.2	5.60	30	168.00
14	—	93.0	5.60	13	72.80
Estimated TDS =					787.51
					≈788

<sup>a</sup> Values for  $r_i$  are from Table 9; values for  $m_i$  are from Table 10. TDS = total days survived by marks.

<sup>b</sup>  $i$  = day;  $r_i$  = total number of animals released on day  $i$ ;  $M_i$  = number of marks at risk on day  $i$ ;  $A_i$  = average age of marks on day  $i$ ;  $m_i$  = total number of marked animals caught on day  $i$ ;  $A_i m_i$  = estimated days survived by marks caught on day  $i$ .

237 at the beginning of the study to 53 on the last day of the study.

**JOLLY-SEBER STOCHASTIC METHOD**

The advantage of the Jolly-Seber Stochastic method over the Fisher-Ford estimator is that the Jolly-Seber model allows survival rates to vary and is, therefore, more realistic biologically. This method estimates population size ( $N_i$ ), survival rates ( $\phi_i$ ), and gains ( $g_i$ ). Each estimate has an associated formula for the calculation of the standard error (not available with Fisher-Ford). The Jolly-Seber estimator of population size re-

**Table 14. Population Size ( $\hat{N}_i$ ), Losses ( $\hat{L}_i$ ), and Gains ( $\hat{g}_i$ ) Estimated Using the Fisher-Ford Method and Assuming a Constant Survivorship ( $\phi$ ) of 0.828<sup>a</sup>**

<i>i</i>	$n_i$	$m_i$	$M_i$	$\hat{N}_i$	$\hat{L}_i$	$\hat{g}_i$
1	43	0	0	—	—	—
2	43	5	33.1	237.0	41	—
3	0	0	60.5	60.5	10	—
4	13	3	50.1	175.0	30	15
5	52	16	51.4	160.0	28	-12
6	56	39	84.0	120.0	21	—
7	0	0	112.0	112.0	19	—
8	52	47	92.7	85.0	15	79
9	50	40	119.8	149.0	26	—
10	0	0	140.6	140.6	24	—
11	0	0	116.4	116.4	20	—
12	15	17	96.4	86.0	15	-8
13	20	30	92.2	63.0	11	1
14	20	13	93.0	53.0	9	—

<sup>a</sup> *i* = day;  $n_i$  = the total number of animals captured on day *i*;  $m_i$  = the total number of marked animals caught on day *i*;  $M_i$  = the number of marks at risk on day *i*;  $\hat{N}_i$  = estimated population size on day *i*;  $\hat{L}_i$  = estimated number of losses (from death and emigration) on day *i*;  $\hat{g}_i$  = estimated number of gains (from birth and immigration) on day *i*.

quires several sampling periods, but only the most recent mark (= most recent recapture) is considered in calculations. Detailed capture histories are required for all individuals, and these data are arranged in a table (see Table 15). For this example, we use M-RC data from Jolly (1965) as modified by Begon (1979). To construct the table, the animals recaptured on any day ( $m_{ij}$ ) are tallied according to the most recent date of recapture. On day 7 of the sample data set, 250 animals were captured, 112 of which were already marked. Of those, 56 were last captured on day 6, 34 on day 5, 10 on day 4, 5 on day 3, 6 on day 2, and 1 on day 1.

The number of marked individuals at risk on day *i* ( $M_i$ ) has to be estimated so that population size ( $N_i$ ) can be estimated. The estimation of the number of marked individuals at risk is given by the equation

$$\hat{M}_i = m_i + \frac{z_i r_i}{y_i} \tag{21}$$

The number of marked animals released on day *i* ( $r_i$ ) is known;  $m_i$ ,  $y_i$ , and  $z_i$  are obtained from the table (Table 15). The number of marked animals ( $m_i$ ) caught on day *i* is the sum of  $m_{ij}$  values in row *i* of the table. For example, on day 7,

$$m_7 = 1 + 6 + 5 + 10 + 34 + 56 = 112$$

The number of animals marked and released on day *i* and caught after day *i* is  $y_i$ , or the sum of  $m_{ij}$  values for column *j* of the table. For animals released on day 7,

$$y_7 = 46 + 28 + 17 + 8 + 7 + 2 = 108$$

The calculation of  $z_i$ —the number of animals marked before day *i* that are not caught on day *i* but are caught after day *i*—is more complicated. The sum of  $m_{ij}$  in columns to the left of column *j* (i.e., *j* values less than  $j_i$  values) and in rows below row *i* (i.e., row numbers greater than *i*) equals  $z_i$  (see Table 15; for day 7, these values are enclosed by dashed lines). For example, on day 7,

$$\begin{aligned} z_7 &= 0 + 4 + 0 + 3 + 14 + 19 \\ &\quad + 0 + 2 + 4 + 2 + 11 + 12 \\ &\quad \quad \quad + \dots \\ &\quad + 0 + 1 + 0 + 2 + 3 + 3 \\ &= 110 \end{aligned}$$

The estimated  $M_i$  values (using equation 21) based on data in Table 15 are presented in Table 16. Given that there are no marked indi-



**Table 15. Mark-Recapture Data for Sample Calculations of Population Size Using the Jolly-Seber Method<sup>a,b</sup>**

<i>i</i>	<i>n<sub>i</sub></i>	<i>r<sub>i</sub></i>	Day of mark ( <i>j</i> )													
			1	2	3	4	5	6	7	8	9	10	11	12		
			Recaptured marks ( <i>m<sub>ij</sub></i> )													
1	54	54														
2	146	143	10													
3	169	164	3	34												
4	209	202	5	18	33											
5	220	214	2	8	13	30										
6	209	207	2	4	8	20	43									
7	250	243	1	6	5	10	34	56								
8	176	175	0	4	0	3	14	19	46							
9	172	169	0	2	4	2	11	12	28	51						
10	127	126	0	0	1	2	3	5	17	22	34					
11	123	120	1	2	3	1	0	4	8	12	16	30				
12	120	120	0	1	3	1	1	2	7	4	11	16	26			
13	142	—	0	1	0	2	3	3	2	10	9	12	18	35		

<sup>a</sup> Mark-recapture data are from Jolly (1965) as modified by Begon (1979).

<sup>b</sup> Dashed lines enclose *m<sub>ij</sub>* values that are included in the calculation of *z<sub>7</sub>* (see text for explanation); *i* = day; *n<sub>i</sub>* = total number of animals captured on day *i*; *r<sub>i</sub>* = total number of animals released on day *i*; *j* = day the animal was captured (or last seen); *m<sub>ij</sub>* = number of animals captured on day *i* with a day-*j* mark.

viduals at risk on day 1, *M*<sub>1</sub> = zero. For example, on day 7:

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{(\hat{M}_i - m_i + r_i)} \tag{23}$$

$$\hat{M}_7 = 112 + \frac{110 \cdot 243}{108} = 359.50$$

Gains (*g<sub>i</sub>*) between day *i* and day (*i* + 1) are estimated as follows:

Once Table 16 is constructed, population size can be estimated as follows:

$$\hat{g}_i = \hat{N}_{i+1} - \hat{\phi}_i \hat{N}_i \tag{24}$$

$$\hat{N}_i = \frac{\hat{M}_i (n_i + 1)}{(m_i + 1)} \tag{22}$$

For example, on day 6,

$$\hat{N}_6 = \frac{\hat{M}_6(n_6 + 1)}{(m_6 + 1)} = \frac{324.99(209 + 1)}{(77 + 1)} = 874.97 \approx 875$$

On day (*i* + 1), there are (*M<sub>i</sub>* - *m<sub>i</sub>* + *r<sub>i</sub>*) marked individuals in the population. Of these marked individuals, *M<sub>i+1</sub>* survive until day (*i* + 1). The survival rate ( $\hat{\phi}$ ) is estimated as follows:

$$\hat{\phi}_6 = \frac{M_7}{\hat{M}_6 - m_6 + r_6} = \frac{359.50}{324.99 - 77 + 207} = 0.79$$

$$\hat{g}_6 = \hat{N}_7 - (\hat{\phi}_6 \hat{N}_6) = 799 - 0.79 \cdot 875 = 107.8 \approx 108$$

**Table 16. Calculated Values Required for Estimating Population Size Using the Jolly-Seber Method<sup>a,b</sup>**

<i>i</i>	<i>r<sub>i</sub></i>	<i>m<sub>i</sub></i>	<i>y<sub>i</sub></i>	<i>z<sub>i</sub></i>	$\hat{M}_i$
1	54	—	24	—	0
2	143	10	80	14	35.03
3	164	37	70	57	170.54
4	202	56	71	71	258.00
5	214	53	109	89	227.73
6	207	77	101	121	324.99
7	243	112	108	110	359.50
8	175	86	99	132	319.33
9	169	110	70	121	402.13
10	126	84	58	107	316.45
11	120	77	44	88	317.00
12	120	72	35	60	277.71
13	—	95	—	—	—

<sup>a</sup> Calculations based on data from Table 15.

<sup>b</sup> *i* = day; *r<sub>i</sub>* = total number of animals released on day *i*; *m<sub>i</sub>* = number of marked animals caught on day *i*; *y<sub>i</sub>* = number of individuals marked and released on day *i* and caught after day *i*; *z<sub>i</sub>* = number of animals caught before and after, but not on, day *i*;  $\hat{M}_i$  = estimated number of marks at risk on day *i*, calculated with equation 21.

**Table 17. Estimates of Population Size ( $\hat{N}_i$ ), Population Gain ( $\hat{g}_i$ ), and Survival Rate ( $\hat{\phi}_i$ ) and Their Standard Errors, Calculated Using the Jolly-Seber Method<sup>a</sup>**

<i>i</i>	Estimate			Standard error		
	$\hat{N}_i$	$\hat{g}_i$	$\hat{\phi}_i$	SE $\hat{N}_i$	SE $\hat{g}_i$	SE $\hat{\phi}_i$
1	—	—	—	—	—	—
2	468	288	1.015	136	168	0.11
3	763	289	0.867	126	136	0.10
4	951	396	0.564	138	120	0.06
5	932	96	0.836	118	110	0.07
6	875	108	0.790	94	75	0.07
7	799	130	0.651	72	55	0.06
8	650	-13	0.985	59	53	0.09
9	627	47	0.686	59	35	0.08
10	477	82	0.884	49	40	0.12
11	504	71	0.771	65	40	0.13
12	460	—	—	69	—	—

<sup>a</sup> Survival rate = chance of an individual in the day-*i* population surviving until day (*i* + 1); population gain = number of births plus number of immigrants; *i* = day.

All population parameters estimated with the Jolly-Seber method have standard errors (equations 25–27) associated with them as follows:

$$SE_{\hat{N}_i} = \left\{ \hat{N}_i (\hat{N}_i - n_i) \left[ \frac{\hat{M}_i - m_i + r_i \left( \frac{1}{y_i} - \frac{1}{r_i} \right) + \frac{1}{m_i} - \frac{1}{n_i}}{\hat{M}_i} \right] \right\}^{1/2} \tag{25}$$

$$SE_{\hat{\phi}_i} = \hat{\phi}_i \left\{ \left( \frac{(\hat{M}_{i+1} - m_{i+1}) (\hat{M}_{i+1} - m_{i+1} + r_{i+1})}{(\hat{M}_{i+1})^2} \right) \left( \frac{1}{y_{i+1}} - \frac{1}{r_{i+1}} \right) + \left( \frac{\hat{M}_i - m_i}{\hat{M}_i - m_i + r_i} \right) \left( \frac{1}{y_i} - \frac{1}{r_i} \right) \right\}^{1/2} \tag{26}$$

The following equation (27) for the standard error of gains is from Jolly (1965). Equations in Southwood (1978), Begon (1979), and Davis and Winstead (1980) are different.

$$SE_{\hat{g}_i} = \left[ \frac{(\hat{g}_i)^2 (\hat{M}_{i+1} - m_{i+1})(\hat{M}_{i+1} - m_{i+1} + r_{i+1}) \left( \frac{1}{y_{i+1}} - \frac{1}{r_{i+1}} \right)}{(\hat{M}_{i+1})^2} + \frac{\hat{M}_i - m_i}{\hat{M}_i - m_i + r_i} \left( \frac{\hat{\phi}_i r_i \left( 1 - \frac{m_i}{n_i} \right)}{\frac{m_i}{n_i}} \right) \left( \frac{1}{y_i} - \frac{1}{r_i} \right) + \frac{(\hat{N}_i - n_i)(\hat{N}_{i+1} - \hat{g}_i) \left( 1 - \frac{m_i}{n_i} \right) (1 - \hat{\phi}_i)}{\hat{M}_i - m_i + r_i} + \hat{N}_{i+1}(\hat{N}_{i+1} - n_i) \left( \frac{1 - \frac{m_{i+1}}{n_{i+1}}}{m_{i+1}} \right) + (\hat{\phi}_i)^2 \hat{N}_i (\hat{N}_i - n_i) \left( \frac{1 - \frac{m_i}{n_i}}{m_i} \right) \right]^{1/2} \quad (27)$$

Estimates of population size ( $\hat{N}$ ), survival rate ( $\phi$ ), and gains ( $g$ ) for the data in Table 15 are presented in Table 17. Values needed to calculate standard errors of these estimates are given in Tables 15, 17, and 18. If values are calculated

and summarized as in Table 18, then hand calculation of the standard errors is relatively easy. The following are calculations of the standard errors given in Table 17 for day 9 of our example:

$$SE_{\hat{N}_9} = \left[ 627 \cdot 455 \cdot \frac{461.13}{402.13} \cdot \left( \frac{1}{70} - \frac{1}{169} \right) + \frac{1}{110} - \frac{1}{172} \right]^{1/2} = [285,285[1.147(0.008) + 0.009 - 0.006]]^{1/2} = 58.9 \approx 59$$

$$SE_{\hat{\phi}_9} = 0.686 \left[ \frac{232.45 \cdot 358.45}{316.45^2} \cdot \left( \frac{1}{58} - \frac{1}{126} \right) + \frac{292.13}{461.13} \cdot \left( \frac{1}{70} - \frac{1}{169} \right) \right]^{1/2} = 0.686[0.832(0.009) + 0.634(0.008)]^{1/2} = 0.078 \approx 0.08$$

$$SE_{\hat{g}_9} = \left[ \frac{47^2 \cdot 232.45 \cdot 358.45}{316.45^2} \cdot 0.009 + 0.6335 \left( \frac{115.93 \cdot 0.360}{0.640} \right)^2 \cdot 0.008 + \frac{455(477 - 47) \cdot 0.360 \cdot 0.314}{461.13} + 477 \cdot 350 \cdot \left( \frac{0.339}{84} \right) + 0.471 \cdot 627 \cdot 455 \left( \frac{0.360}{110} \right) \right]^{1/2} = 34.63 \approx 35$$

**Table 18. Sample Calculated Values Required for Determining Standard Error for Population Estimators Derived Using the Jolly-Seber Method<sup>a</sup>**

<i>i</i>	$\hat{M}_i - m_i$	$\hat{M}_i - m_i + r_i$	$\hat{M}_i$	$m_i$	$\frac{1}{y_i} - \frac{1}{r_i}$	$\frac{\hat{M}_i - m_i}{\hat{M}_i - m_i + r_i}$	$\hat{\phi}_i r_i$	$1 - \frac{m_i}{n_i}$	$\frac{m_i}{n_i}$	$\hat{N}_i - n_i$	$1 - \hat{\phi}_i$	$(\hat{\phi}_i)^2$
1	—	—	0	—	—	—	—	—	—	—	—	—
2	25.03	168.03	35.03	10	0.006	0.1490	145.15	0.931	0.069	322	-0.015	1.030
3	133.54	297.54	170.54	37	0.008	0.4488	142.19	0.781	0.219	594	0.133	0.752
4	202.00	404.00	258.00	56	0.009	0.5000	113.93	0.732	0.268	742	0.436	0.318
5	174.73	388.73	227.73	53	0.005	0.4495	178.90	0.759	0.241	712	0.164	0.699
6	247.99	454.99	324.99	77	0.005	0.5450	163.53	0.632	0.368	666	0.210	0.624
7	247.50	490.50	359.50	112	0.005	0.5046	158.19	0.552	0.448	549	0.349	0.424
8	233.33	408.33	319.33	86	0.004	0.5714	172.38	0.511	0.489	474	0.015	0.970
9	292.13	461.13	402.13	110	0.008	0.6335	115.93	0.360	0.640	455	0.314	0.471
10	232.45	358.45	316.45	84	0.009	0.6485	113.38	0.339	0.661	350	0.116	0.782
11	240.00	360.00	317.00	77	0.014	0.6667	92.52	0.374	0.626	381	0.229	0.594
12	205.71	325.71	277.71	72	0.020	0.6316	—	0.400	0.600	340	—	—

<sup>a</sup> *i* = day;  $\hat{M}_i$  = estimated number of marks at risk on day *i*;  $m_i$  = number of marked animals caught on day *i*;  $r_i$  = number of animals released on day *i*;  $y_i$  = number of animals marked and released on day *i* and caught after day *i*;  $\hat{\phi}_i$  = estimated survival rate on day *i*;  $n_i$  = total number of animals captured on day *i*;  $\hat{N}_i$  = estimated population size on day *i*.

**Capture-Resight**

Minta and Mangel (1989) developed an estimator of population size using capture-resight data. It is important to note that this method works only in conjunction with a technique (such as radio telemetry) that allows an investigator to estimate the number of marked animals never seen that are still alive. Minta and Mangel's method employs a Monte Carlo simulation that gives a full probability distribution for the population. From this distribution, the maximum likelihood estimate and likelihood interval on the population can be computed. The likelihood interval allows asymmetric interval estimates, rather than the symmetric interval estimates of Petersen's variance equations. A paper describing this method and the BASIC program (for IBM compatible computers) used to calculate the estimator are available from S. Minta (see "Computer Programs" in Appendix 6).

**Bayesian Approach to Mark-Recapture Data**

Gazey and Staley (1986) provided a sequential Bayes algorithm (= equation) for estimating population size. This approach can be used when populations are small and recapture frequencies are low. The Bayesian approach is an attractive alternative to Petersen's estimate (and all methods based upon it), which underestimates population size at low densities. The advantages of the Bayesian approach include estimation of the population distribution from Bayes's theory rather than from an assumed normal distribution (Kempthorne and Folks 1971); estimation of population size free from effects of sample size or sampling procedure; assessment of the degree of population closure; and description of the magnitude of difference between two or more populations, not just the presence of a difference.

CONTRIBUTORS: J. ERIC JUTERBOCK AND ROSS A. ALFORD

## Removal sampling

LEE-ANN C. HAYEK

Removal sampling is a means of estimating the size of a population, usually from a certain area; it may or may not provide information on the entire population. Animals are physically removed from a designated area (locality, plot, or quadrat) for a short interval. At the end of the study, they are released as near to their original capture point as possible. Removal sampling is an important means of investigating long-term population stability. Age, size, breeding condition, and sex can also be obtained from the animals held in captivity.

### Target Organisms and Habitats

This technique is most useful for species with low mobility or limited home ranges and for aquatic larvae (see Chapter 6), because a high proportion of the population is available for capture at any given time. It is inappropriate for secretive species, fossorial species, and highly mobile species, including frogs and salamanders that disperse widely from breeding ponds. Hairston (1981, 1986, 1987) used removal methods as a tool for estimating population density in species of *Plethodon* and *Desmognathus*. Harris et al. (1988) used this technique to evaluate the effectiveness of enclosure sampling methods for the broken-striped newt, *Notophthalmus viridescens dorsalis*.

### Background

The most widely used removal sampling methods are based on analytical models that assume a closed population and a constant sampling effort. Open-population models are much less common, and more general models relax the second assumption (below) to varied degrees. Several important conditions should be met in

most applications of removal-sampling methods:

1. There should be a reasonable chance that the target population is closed, or at least stationary, during the sampling period. This assumption usually requires that time intervals between successive sampling periods be short. Some models, such as certain catch-per-unit-effort (CE) models (e.g., Dupont 1983), are applicable if the population does not remain closed during sampling.
2. It should be possible, at least in theory, to remove all animals in the study area (White et al. 1982). At least two samples are needed for estimation of population size (Seber 1982), but three to five are usual. White et al. (1982) recommended three or more samples unless the capture probability is 0.8 or more on each pass.
3. Each individual within any single sample should be equally catchable, and any individual's probability of being caught should be independent of that for any other individual. This condition is relaxed with the heterogeneity and trap response model (model  $M_{bh}$  in the 1991 version of CAPTURE). Harris et al. (1988) pointed out that taxa differ in their catchability and described the assumptions and calculations that can be used to determine whether this condition is met. In some situations, stratified sampling may be required. Hayne (1949) suggested a plot of number of individuals caught in each sample versus the total of all previously collected specimens from the same stratum or group to detect problems with this assumption. Zippin (1958) used regression estimates to evaluate equal catchability.
4. Catchability of individuals should be equal over sampling periods. Meeting this condition may be a problem for comparative studies, especially over seasons or when



individuals of more than one species are removed. Some models (e.g.,  $M_{th}$  in the 1991 version of CAPTURE) can handle temporal variation, but comparison of results across studies is problematic. Changes in the structure of vegetation or the size of a study plot (e.g., drying of pond), and fluctuations in temperature or rainfall between samples can affect catchability. Some models can deal with such change.

5. The sampling proficiency of the investigator should remain constant. This condition is a special case of condition 4 because learning and/or fatigue can produce variation over sampling periods. This problem can be minimized by providing equivalent training for all personnel.
6. Time and intensity of effort devoted to collection and removal should remain constant over samples. This condition is another special case of condition 4 and is a potential source of temporal variation. For example, in successive larval removal samples, the decrease of both larvae and vegetative growth may contribute to a change in sampling effort. Temporal variation can be handled by some models (e.g., some CE models in the 1991 version of CAPTURE).

If the number of traps remains constant and the amount of observer time is equal over the course of the study, a generalized removal model ( $M_{th}$ ) can be used (Rexstad and Burnham 1991). The catch-per-unit-effort is then equal to the number of animals caught, and this model allows for unequal catchability due to behavioral or other changes.

### Research Design and Field Methods

Animals can be removed physically or by marking (from the unmarked population). Thus, mark-recapture methods (see previous section in this chapter) and removal methods (described

here) can be equivalent for use in population estimation when the assumption of a closed population is met. In general, models based on removal are special kinds of capture-recapture models; the latter were developed for the many situations to which removal models do not apply (see, e.g., Pollock et al. 1990).

In designing removal studies, the investigator must consider plot size and location, sampling interval, number of samples, and capture method. Removal methods are suitable for short-term studies with temporary plots and for long-term monitoring at sites where permanent plots can be established. For long-term studies the location of the plot must be recorded with precision. Plots should be large enough to ensure that a representative target population is available for sampling. However, they must be small enough to allow the investigator to capture a major proportion of the target population over the duration of the study. Study plots should be located so as to minimize short-term migration in and out of the plot and movement of animals into areas vacated by previous samples. In some cases, temporary fencing of plots may be desirable. The time between samples must be such that the population can reasonably be considered to be closed. For pond larvae or populations of explosively breeding species in which most of the adults are available and relatively easily captured, the time interval should be quite short. Zippin (1956) provided methods useful for ascertaining if assumptions hold during the removal period. He demonstrated how a suspected violation of a design assumption often can be verified by increasing the number of removal samples. In addition, the 1991 version of CAPTURE includes formal statistical goodness-of-fit and between-model tests specifically designed for testing assumptions.

Removal sampling requires hand capture, netting, or trapping of animals. The animals are placed in plastic bags that are labeled with a waterproof felt-tip pen. The animals are im-



mediately brought to the laboratory and held in suitable containers until the end of the study. For short-term studies a container such as a Styrofoam ice chest may be used as a holding area at the site. When sampling is complete, all animals are returned to the original study plot.

Removal methods have appeal for practical reasons as well as scientific ones. In particular, they allow in certain cases for collection of data by persons other than the primary investigator (e.g., volunteers or students; see "Group Activities and Field Trips," Chapter 7) with minimal threat to the animals, minimal disruption of the study plot, and reduced individual effort and cost.

### Data Analysis and Interpretation

Data include simple counts of captures (removals) for each sample; from these, abundance and density may be estimated. Hairston (1981) provided a clear example of the calculations; Harris et al. (1988) discussed use of the counts and of their associated environmental and morphological data.

Estimation of population size by removal methods is based on the assumption that the size of the available population is reduced by a large proportion on each sampling occasion. Zippin (1958:87) reported the proportion of the total population that would have to be trapped to obtain a specified level of precision for the sampling. For example, for a true population composed of 200 individuals, 55% would have to be captured over the entire sampling period to have a two-thirds chance that an estimate of size would be correct to within 30%.

Three types of population estimation methods are described below. The 1991 version of the program CAPTURE (see Appendix 6) performs the calculations required in most of the standard removal models.

### CATCH-PER-UNIT-EFFORT ESTIMATORS

Catch-per-unit-effort is a general regression estimation method based on the relationship between the expected decrease in catch per unit of effort expended over repeated samples and the total catch. Effort expended can be constant (standard removal models— $M_b$ ,  $M_{bh}$ , and  $M_{tb}$  in CAPTURE) or variable (regression estimators—Pollock et al. 1984). An expected catch of zero is the logical presumed end of the study and the point at which all of the specimens have been removed. In practice, tactical problems are involved in any attempt to remove 100% of the individuals, so that this zero point is predicted from a linear regression equation. It is not the usual least-squares equation, because both the catch-per-unit-effort (the  $y$ -variable) and the summed removals (the  $x$ -variable) in most cases depend upon the same removals. This procedure has been used under varied conditions with a variety of taxa, and its properties have been widely discussed (Leslie and Davis 1939; Chapman 1954; Overton 1969; Seber 1982).

Assumptions of this method include the following: a closed population, except for removals (for standard models); equal probability of capture per unit effort over the duration of the study; all removals known; linear decline in catch per unit effort with time or with decrease in number of remaining animals, when removal is intense; and actual capture of a large proportion of the population.

The method also has several limitations. Equal probability of capture per unit effort may be difficult to obtain, but it can be evaluated by an examination of the regression line (over time) itself. If the regression trend is nonlinear, the assumption is violated, and the procedure should not be used (Caughley 1977). Another limitation is that a negative population estimate (which is the  $x$ -intercept) can be obtained when the regression slope is positive (Overton 1969). Also, estimates of population size are unrealistic if the

slope is negative (as it should be) and close to zero. This situation can occur if the removal proportions are not sufficiently large (i. e., under approximately 75%).

#### CHANGE-IN-RATIO ESTIMATORS

In the change-in-ratio type of estimation procedure, simultaneous algebraic equations are used to relate population sizes before and after sample removal. The desired estimates are the solutions to these equations. The Petersen-type estimators discussed previously in this chapter are a special case. Krebs (1989) pointed out that large samples are usually required for this class of estimator, and the sampling program must be carefully planned with the model assumptions in mind.

This method requires that the population, in addition to being closed, include only two classes (called *x*-type and *y*-type) of animals. This requirement is minor because the amphibians in the target population can be designated as adult and larva or male and female. The method estimates population size based on changes in the proportions of the two classes between the first and second removals. The first sample provides the initial estimate of the proportion of the two types, and an additional proportion estimate is obtained from the second sample. Under an assumption of preremoval and postremoval estimate independence, Seber (1982) derived variance estimates for total population size as well as for the number of animals of each type in the preremoval population. He also derived a solution for the special case of the removal of only one of the two types.

This method assumes that observed proportions of both classes of animals are unbiased estimates of the true proportions in the population; this assumption can be evaluated when equal catchability of the two classes can be reasonably assumed. The method further assumes a closed study population, except for removals, and a known number of removals of both classes. The latter should be true for amphibian

studies. The methods of Paulik and Robson (1969) provide for estimation of removals when the number is unknown.

Several limitations apply to this method. The method cannot be used if the proportion of *x*-types (and therefore *y*-types) is the same before and after removal. The reason for this limitation is not biological but algebraic. The difference between the two proportions (the change in ratio, or  $\Delta P$ ) forms the denominator in the equation for the total population size estimate. If  $\Delta P$  is zero, no mathematical calculations can be made. A second limitation is that the interrelationships of the preremoval estimate,  $\Delta P$ , and the total sample size (number of animals removed) directly affect both the accuracy and the precision of these estimates (Paulik and Robson 1969; Seber 1982), as is shown by a review of the algebraic equations for the method. Also, negative population estimates can occur if  $\Delta P$  is near zero.

#### TWO-STAGE-CHANGE-IN-RATIO ESTIMATORS

The two-stage-change-in-ratio method is similar to the change-in-ratio procedure described above, but the former requires that the proportions of the animal classes be estimated in at least three removal periods ( $t_1, t_2, t_3$ ), and it does not assume equal catchability. Between each pair of removal periods, two additional samples are taken, in which only one type or class of animal is removed and counted. These interim values are used to estimate relative observability. Variances for both the type proportions and the relative observability estimates are available with this procedure (Pollock et al. 1985). Pollock et al. (1985) provided a detailed description of the method, with illustrative examples.

This method assumes a closed population; two classes of animals (*x*-types and *y*-types), as in the single stage procedure; and constant observability or catchability only within the study period from  $t_1$  to  $t_3$ .

The procedure has several limitations. The assumption of equal catchability is difficult to meet because it requires constant conditions during the period of study. An estimate of catchability can be obtained, however, from formulas in Pollock et al. (1985). Another limitation is that, generally, as the proportions of animals decrease, the accuracy and precision of the estimates decrease (Pollock et al. 1985).

Additional refinements of change-in-ratio methods are described by Udevitz and Pollock (1991).

#### OTHER METHODS

Eberhardt (1982) described a catch-per-unit-effort method in which the number of points upon which the regression is based is reduced. This decrease appears to make predictions based on the regression less reliable, and I do not recommend this method for amphibian studies. Dupont (1983) provided an estimation method useful for open populations.

#### Special Considerations

When the target population consists of easily observable individuals, a counting method that uses quadrat, patch, or transect sampling is preferable to either mark-recapture or removal sampling. However, many amphibians are not readily observable, and capture methods must be employed for population estimation. Removal

methods are less expensive than M-RC methods and require less time and personnel. However, the M-RC methods may yield more-precise estimates per unit of effort expended. Other advantages of removal methods include elimination of changes in capture probability after first capture, easier handling of animals (no tagging required), and reduced field time because numbers of animals caught usually decline after the first sample. However, removal methods are inappropriate for endangered, rare, or highly mobile species, and temporary removal methods require good temporary holding facilities.

The degree to which the assumptions of the removal method are met determines its reliability as a method of population estimation (Carle and Strub 1978), although, under certain limited conditions, unequal probability of capture across individuals may have negligible effect on certain estimation procedures (Seber and Whale 1970; Carle and Strub 1978). Other threats to validity are not easily detectable, but they can affect the final results and must be considered. If a violation of assumptions is not correctable, I advise use of alternative methods of estimation.

I recommend that the investigator record morphological and environmental data while the animals are being held (e.g., see Harris et al. 1988). Other parameters relevant to population studies (e.g., age structure) can be estimated from these data.

