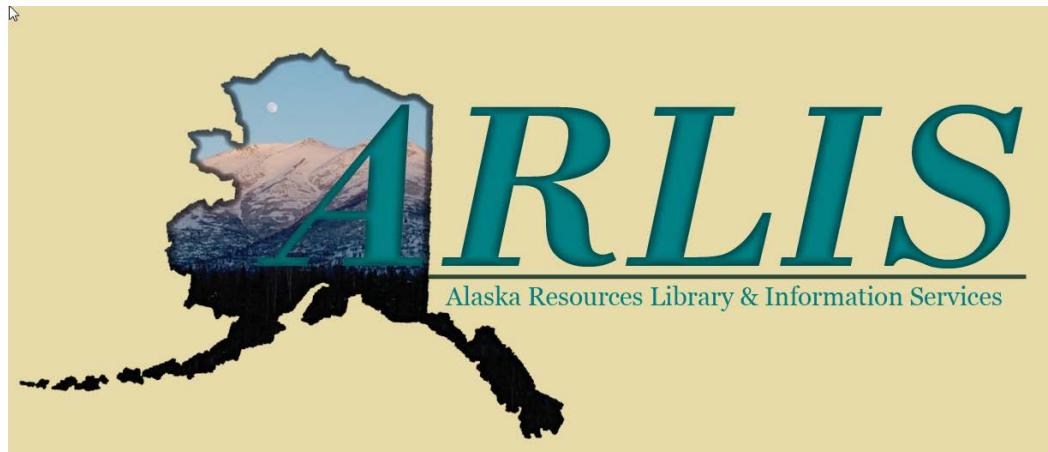


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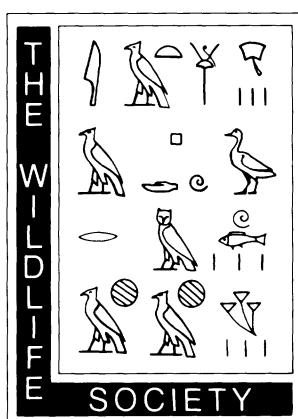


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STATISTICAL INFERENCE FOR CAPTURE-RECAPTURE EXPERIMENTS

by

KENNETH H. POLLOCK, JAMES D. NICHOLS,
CAVELL BROWNIE, AND JAMES E. HINES

NO. 107

JANUARY 1990



FRONTISPICE. This monograph is dedicated to Douglas S. Robson, formerly Professor of Biological Statistics, Cornell University, who has been our mentor and colleague for many years. (Photograph taken in the 1960's.)

STATISTICAL INFERENCE FOR CAPTURE-RECAPTURE EXPERIMENTS

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Abstract: This monograph presents a detailed, practical exposition on the design, analysis, and interpretation of capture-recapture studies. The Lincoln-Petersen model (Chapter 2) and the closed population models (Chapter 3) are presented only briefly because these models have been covered in detail elsewhere. The Jolly-Seber open population model, which is central to the monograph, is covered in detail in Chapter 4.

In Chapter 5 we consider the "enumeration" or "calendar of captures" approach, which is widely used by mammalogists and other vertebrate ecologists. We strongly recommend that it be abandoned in favor of analyses based on the Jolly-Seber model. We consider 2 restricted versions of the Jolly-Seber model. We believe the first of these, which allows losses (mortality or emigration) but not additions (births or immigration), is likely to be useful in practice. Another series of restrictive models requires the assumptions of a constant survival rate or a constant survival rate and a constant capture rate for the duration of the study. Detailed examples are given that illustrate the usefulness of these restrictions. There often can be a substantial gain in precision over Jolly-Seber estimates. In Chapter 5 we also consider 2 generalizations of the Jolly-Seber model. The temporary trap response model allows newly marked animals to have different survival and capture rates for 1 period. The other generalization is the cohort Jolly-Seber model. Ideally all animals would be marked as young, and age effects considered by using the Jolly-Seber model on each cohort separately. In Chapter 6 we present a detailed description of an age-dependent Jolly-Seber model, which can be used when 2 or more identifiable age classes are marked.

In Chapter 7 we present a detailed description of the "robust" design. Under this design each primary period contains several secondary sampling periods. We propose an estimation procedure based on closed and open population models that allows for heterogeneity and trap response of capture rates (hence the name robust design). We begin by considering just 1 age class and then extend to 2 age classes. When there are 2 age classes it is possible to distinguish immigrants and births. In Chapter 8 we give a detailed discussion of the design of capture-recapture studies. First, capture-recapture is compared to other possible sampling procedures. Next, the design of capture-recapture studies to minimize assumption violations is considered. Finally, we consider the precision of parameter estimates and present figures on proportional standard errors for a variety of initial parameter values to aid the biologist about to plan a study.

A new program, JOLLY, has been written to accompany the material on the Jolly-Seber model (Chapter 4) and its extensions (Chapter 5). Another new program, JOLLYAGE, has been written for a special case of the age-dependent model (Chapter 6) where there are only 2 age classes. In Chapter 9 a brief description of the different versions of the 2 programs is given. Chapter 10 gives a brief description of some alternative approaches that were not considered in this monograph. We believe that an excellent overall view of capture-recapture models may be obtained by reading the monograph by White et al. (1982) emphasizing closed models and then reading this monograph where we concentrate on open models. The important recent monograph by Burnham et al. (1987) could then be read if there were interest in the comparison of different populations.

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1. INTRODUCTION

A major portion of the discipline known as ecology concerns the abundance of animals and factors that affect abundance (Andrewartha and Birch 1954, Krebs 1972). An extensive and in some cases elaborate body of mathematical theory has been developed regarding animal abundance and the dynamics of animal populations (MacArthur and Wilson 1967, Fretwell 1972, Bartlett and Hiorns 1973, May 1976, Hiorns and Cooke 1981). However, in a

number of cases such theory has been characterized by a relative lack of interaction with relevant population data and thus has been constructed on weak or nonexistent empirical bases. We share Pielou's (1974: 97) belief that "... it is easier to devise hypotheses to account for population phenomena than it is to test them. To test a hypothesis entails comparing its predictions with what is actually happening in nature; and to discover what *is* happening is often extraordinarily difficult, perhaps more so in ecology than in any other nat-

ural science.” The subject of this monograph is a class of methods and models that can be used to estimate population parameters for natural animal populations. These parameter estimates can then be used to discover what is actually happening in nature and to test associated hypotheses.

When investigating dynamics of an animal population, it is naturally desirable to have estimates of abundance or population size. In addition, it is desirable to have estimates of fundamental demographic variables that affect population size, i.e., reproductive or birth rate, immigration rate, mortality rate, and emigration rate. Capture-recapture methods can be used to estimate population size, mortality + emigration rate, and birth + immigration rate (although not all models permit estimation of all 3 quantities). Capture-recapture methods have a long history of use in ecology (Le Cren 1965), and a very large literature on statistics of capture-recapture sampling models exists with important reviews given by Cormack (1968), Otis et al. (1978), Cormack (1979), Nichols et al. (1981), Pollock (1981a), Seber (1982), White et al. (1982), Seber (1986), and Burnham et al. (1987).

In capture-recapture experiments, we typically sample the population under study k times where k is usually >2 . Each time, every unmarked animal caught is uniquely marked, previously marked animals have their captures recorded, and all animals are released back into the population. In some cases animals may be injured by capture or may be needed for sacrifice in which case they will not be released and are recorded as “losses on capture.” At the end of the study, we assume that the experimenter has the complete capture history of every animal handled. Batch marks, where all animals in a particular sample cannot be distinguished, do not provide the complete capture history information and should be avoided where possible.

Statisticians have typically classified capture-recapture models into those suitable for closed or open populations. It is

important that biologists understand exactly what these terms mean, because they often are defined differently in other contexts. By open we mean that additions (births and/or immigrants) to the population and permanent deletions (deaths and/or emigrants) from the population occur during the study. A closed population is one where permanent deletions or additions do not occur, i.e., a closed population has a constant size during the entire study. (Neither type of model allows temporary additions or deletions.)

Closed population models are simpler for the statistician to study and have received much attention recently. Otis et al. (1978) presented an excellent study of these models suitable for biologists. Within the closed population framework the assumption of equal probability of capture has been relaxed in a variety of ways. A major disadvantage of closed population models is that their use is limited to short-term studies where births and deaths can be ignored. Unfortunately, even then they may not be applicable if there is significant migration in and out of the study area.

Here we will concentrate on studies where closure cannot be assumed, so that we are forced to use open population models. We shall see, however, that rigid separation of closed and open population models is rather artificial. In many studies it may be possible to use designs such that both types of models are used (Pollock 1982).

Parameters of interest to a biologist who has carried out a long-term capture-recapture study are population size, survival rate, and recruitment for each sampling period in the experiment. In populations where migration is present, recruitment includes both birth and immigration, and mortality includes both death and permanent emigration. The typical capture-recapture study provides 2 distinct types of information that can be used to estimate these parameters: (1) information from the recapture of marked animals and (2) information from comparing numbers of marked and unmarked animals captured at each sampling time. Data from (1) can

be used to estimate "survival" rates, whereas data from (1) and (2) are necessary to estimate population sizes and recruitment numbers.

In some studies, survival rate estimation is of primary concern, and the study is designed so that only information from recovery of marked animals is taken. One example is a band recovery where the animal is recovered dead, usually by a hunter or angler, and the band or tag is returned to the appropriate agency for tabulation as a recovery. There is a close relationship between band recovery models and the live recapture models discussed here. A brief description of band recovery models will be given, but for detailed study we recommend the excellent monograph by Brownie et al. (1985).

The purpose of our monograph is to present in detail the methodology to design, analyze, and interpret long-term capture-recapture experiments. The presentation is intended primarily for biologists with some understanding of statistical inference and is illustrated extensively with examples. Some of the material presented has been treated nicely in the comprehensive volume by Seber (1982). However, much of the work (including the entire chapters on the age-dependent model and the robust design, and most of the chapter on study design) presented here is either very recent or new, and no effort has previously been made to draw this material together and present it in a unified fashion.

We believe it is important that biologists who undertake capture-recapture studies become familiar with these models and use them in their work. Studying natural populations and conducting manipulative field experiments often are extremely expensive of time and effort. We believe that the data analysis associated with such field efforts deserves far greater attention than it often receives. For example, the literature of small mammal population biology contains a large number of excellent capture-recapture field efforts directed at questions about fluctuations in population size and factors that bring about such fluctuations. However, a very large proportion of these

studies employ ad hoc "estimators" that only estimate parameters of interest under very restrictive and unrealistic assumptions (Nichols and Pollock 1983). It is our hope that this monograph will make appropriate estimation methodologies more readily accessible to biologists conducting capture-recapture studies. We also have developed 2 comprehensive user-friendly computer programs (JOLLY and JOLLYAGE) to accompany this monograph. Copies of both programs are available from the authors.

To make effective use of this monograph the biologist needs to have a basic knowledge of statistical concepts. We recommend that the reader study Chapter 2 of White et al. (1982). This chapter is written clearly and uses examples related to capture-recapture models. To aid the biologist we present an overview of the models in this monograph in diagrammatic form to emphasize their relationships and interconnectedness (Fig. 1.1).

After the "robust" design in Chapter 7 we discuss the design of capture-recapture studies (Chapter 8). In Chapter 9 a brief description of program JOLLY (to accompany material in Chapters 4 and 5) and JOLLYAGE (to accompany material in Chapter 6) is given. Mainframe and mini-computer versions exist and can be obtained from the authors. Chapter 10 gives a brief discussion of some alternative approaches that are not considered in this monograph.

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The *Wildlife Monographs* reviews of L. L. McDonald and G. C. White were very

MODEL OVERVIEW

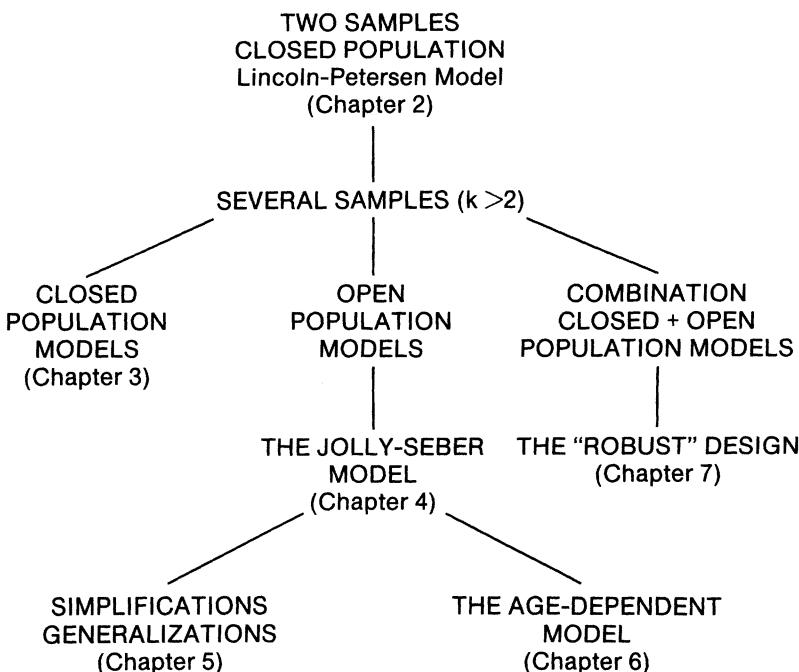


Fig. 1.1. This figure provides an overview of the models used in this monograph and their interrelationships.

detailed and informative. The editorial help of R. L. and T. J. Kirkpatrick was outstanding. Finally, we thank P. A. Sarginger whose patience, accuracy, and speed in typing the many drafts made this difficult task much more enjoyable.

2. THE LINCOLN-PETERSEN METHOD

2.1 Estimation of Population Size

This simplest form of capture–recapture experiment has a long history going back to Laplace in 1786, who used it to estimate the human population size of France (Seber 1982:104). First uses in animal population ecology were by Petersen around the turn of the century (Le Cren 1965) and Lincoln (1930). Our purpose here is to give a brief presentation that will set the stage for the more complex models that follow.

A detailed discussion of the Lincoln-Petersen method is available in Seber (1982: 59).

A sample of n_1 animals is caught, marked, and released. Later a sample of n_2 animals is captured, of which m_2 have been marked. Intuitively one can derive an estimator of the population size (N) based on the notion that the ratio of marked to total animals in the second sample should reflect the same ratio in the population so that

$$\frac{m_2}{n_2} = \frac{n_1}{N},$$

which gives the estimator

$$\hat{N} = \frac{n_1 n_2}{m_2}. \quad (2.1)$$

This estimator is sometimes called the Lincoln Index (Seber 1982:59), although this

is a misuse of the word "index," which usually refers to a measure of relative abundance (Caughley 1977:12).

A modified version with less bias was originally given by Chapman (1951) as

$$\hat{N}_c = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \quad (2.2)$$

with an approximately unbiased estimate of its variance given by

$$\begin{aligned} \text{var } \hat{N}_c \\ = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} \end{aligned} \quad (2.3)$$

from Seber (1970, 1982:60).

2.2 Model Assumptions

The Lincoln-Petersen method is based on a model with assumptions as follows:

1. The population is closed to additions (births or immigrants) and deletions (deaths or emigrants).
2. All animals are equally likely to be captured in each sample.
3. Marks are not lost and are not overlooked by the observer.

The closure assumption (1) can actually be weakened here. If additions occur, then they are always unmarked, and the Lincoln-Petersen estimator is valid for population size at the time of the second sample. If deletions occur randomly with respect to marked and unmarked animals, then the Lincoln-Petersen estimator is valid for population size at the time of the first sample. Later in this monograph we consider completely open populations (additions and deletions permitted). The Lincoln-Petersen estimator in this simple form is no longer appropriate; however, a modified version of it is central to all the open population models studied.

The second assumption, which is often called the assumption of "equal catchability" of animals, is unlikely to be true in many wild populations. It is important to distinguish 2 very different types of alternatives:

1. Heterogeneity—The probability of capture in any sample is a property of the animal and may vary over all the animals in the population. This variation in capture probability could be due to many factors such as age, sex, social status, or "territory" location in relation to trap position.

2. Trap response—The probability of capture in any sample depends on the animal's prior history of capture, i.e., marked animals may have a lower (trap-shy) or a higher (trap-happy) capture probability than unmarked animals.

The type of response will depend on the trapping method used. For example, baiting traps is likely to lead to a trap-happy response where marked animals are more likely to be captured than unmarked animals. It should be emphasized that both heterogeneity and trap response could be present in a population.

If heterogeneity is operating, then animals with high capture probabilities will be more likely captured in the first sample and recaptured in the second. This results in m_2/n_2 overestimating the true proportion marked in the population and hence in \hat{N} of eq. (2.1) being too small, i.e., \hat{N} is a negatively biased estimator. (If capture probabilities are heterogeneous in each sample but independent from sample to sample, then no bias results.) If animals are trap-happy, then m_2/n_2 will again be too large and \hat{N} too small, whereas a population with trap-shy animals will have the opposite situation. To summarize, a trap response in capture probabilities can result in either a negative bias (trap-happy animals) or a positive bias (trap-shy animals) in the population size estimator. Although the validity of the Lincoln-Petersen estimator depends on there being no heterogeneity or trap response, it is possible for capture probabilities to vary between the 2 sampling times.

Assumption (3) is clearly important. If animals lose their tags, m_2/n_2 will be too small, \hat{N} too large, and we are again in the situation of a positively biased estimator. If tag loss is likely to occur, an attempt

should be made to estimate rate of loss so that a “correction” to the number of recaptures can be made. This is commonly done in fisheries studies where tag loss can be serious. One approach is to use a double-marking scheme (Caughley 1977:139, Seber 1982:94). A detailed treatment of Petersen method assumptions, effects of deviations from these assumptions, and tests for detecting such deviations is provided by Seber (1982:70–104).

2.3 Examples

To conclude this section we present 2 examples of use of the Lincoln-Petersen method. Example 1 is taken from Skalski et al. (1983). In August 1974, a sample of 87 Nuttall's cottontail (*Sylvilagus nuttallii*) was live-trapped in central Oregon. The animals were marked with a picric acid dye on their tails and hind legs and released. On 5 September 1974, a drive count was conducted and 14 animals were counted of which 7 were marked.

This means that we have $n_1 = 87$, $n_2 = 14$, and $m_2 = 7$. The Chapman estimate (eq. 2.2) is given by

$$\begin{aligned}\hat{N}_c &= \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \\ &= \frac{88 \times 15}{8} - 1 \\ &= 164\end{aligned}$$

with its approximate variance estimate (eq. 2.3)

$$\begin{aligned}\text{var } \hat{N}_c &= \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} \\ &= \frac{88 \times 15 \times 80 \times 7}{8^2 \times 9} \\ &= 1,283.33.\end{aligned}$$

An approximate 95% confidence interval assuming normality for \hat{N}_c is given by

$$\begin{aligned}\hat{N}_c &\pm 1.96(\text{var } \hat{N}_c)^{0.5} \\ &= 164 \pm 1.96 \times (1,283.33)^{0.5} \\ &= 164 \pm 70.\end{aligned}$$

Hence we have a confidence interval rang-

ing from 94 up to 234, which is rather wide. The precision of the experiment could have been increased if the drive count had sighted more animals. Notice that 2 different sampling methods (trapping and sighting) were used in this study. Therefore, there should be little concern with trap response or heterogeneity of the capture probabilities.

Example 2 involves a bobwhite quail (*Colinus virginianus*) study at Tall Timbers Research Station, Leon County, Florida. During January 1982, 148 quail were captured over a period of 20 days in live traps baited with corn and banded with numbered aluminum leg bands. Early in February 1982 a 3-day controlled hunt was conducted, and 39 of the 82 birds that were shot were found to have leg bands.

Therefore, $n_1 = 148$, $n_2 = 82$, $m_2 = 39$, and it is possible to calculate Chapman's estimate (rounded) and its standard error as before:

$$\hat{N}_c = 308, \quad \widehat{\text{SE}}(\hat{N}_c) = 29.7.$$

An approximate 95% confidence interval is given by

$$308 \pm 1.96 \times 29.7 = 308 \pm 58.$$

Therefore, the confidence interval ranges from 250 to 366 animals, which is narrower than in the previous example. Again 2 different sampling methods have been used in this example (trapping and shooting) suggesting that we are unlikely to have serious bias due to heterogeneity or trap response of the capture probabilities. We will consider this example further in Chapter 3.

3. CLOSED POPULATION MODELS

3.1 Introduction

A brief review of a series of 8 models for closed populations will be presented here. As noted in Chapter 1, closed population models assume that no births, deaths, or migration in or out of the population occur between sampling periods. For this reason, these models generally are used for experiments covering relatively

Table 3.1. Capture-recapture models for closed populations that allow for unequal capture probabilities.

Model ^a	Source of variation in capture probability			Estimator available
	Heterogeneity	Trap response	Time	
M _o				Yes
M _h	X ^b			Yes
M _b		X		Yes
M _{bh}	X	X		Yes
M _t			X	Yes
M _{th}	X		X	No
M _{tb}		X	X	No
M _{thb}	X	X	X	No

^a This set of 8 models comes from Otis et al. (1978).

^b X's denote the sources of variation in capture probability incorporated in the models.

short periods of time (e.g., trapping every day for 5 consecutive days). Capture histories for every animal caught are the data needed for obtaining estimates under these models. These models were first considered as a set by Pollock (1974) and more fully developed by Otis et al. (1978), White et al. (1982), and Pollock and Otto (1983).

The models differ in the manner in which capture probability is modeled. Different models consider 3 sources of variation in capture probability: (1) heterogeneity (Chapter 2), (2) trap response (Chapter 2), and (3) temporal variation or variation among sampling periods (e.g., capture probability for day *i* differs from that for day *j*). A catalog of available models is presented in Table 3.1. Otis et al. (1978) provided a detailed computer program, CAPTURE, for analysis of data using the models in Table 3.1 (also see White et al. 1978). As well as providing estimators for 5 of the models, CAPTURE contains a model selection procedure that aids the biologist in choosing the most appropriate model for a particular data set, but it does not perform well when capture probabilities are low and population sizes are small (Section 3.8).

3.2 M_o: The Equal Catchability Model

Model M_o is unlikely to be realistic for natural animal populations because it as-

sumes that every animal in the population has the same probability of capture (*p*) for each sampling period in the entire study. It is mainly included for pedagogic reasons and to provide a basis for generalization.

Under this model the Maximum Likelihood Estimator (MLE) of *N*, the population size, can only be found iteratively. (This means it is not possible to give an explicit formula for the MLE.) Program CAPTURE has the capability of computing this estimator and its approximate standard error.

It should be emphasized that this estimator can be highly biased if there is unequal catchability. Heterogeneity causes a negative bias, whereas trap response can cause positive or negative bias depending on whether the animals are trap-shy or trap-happy, respectively. Otis et al. (1978) found that the estimator is reasonably robust to changes in capture probabilities over time.

3.3 M_h: The Heterogeneity Model

Model M_h allows heterogeneity but no trap response and assumes that each animal has its own unique capture probability (*p_j*, *j* = 1, . . . , *N*), which remains constant over all the sampling times. The *p_j*'s are further assumed to be a random sample of size *N* from some probability distribution *F(p)*. This model was first considered by Burnham (1972) and later by Burnham and Overton (1978, 1979). The vector of capture frequencies, which is the numbers of animals captured 1, 2, . . . , *k* times, contains all the information for estimating *N* under this model.

Difficulties exist in finding a satisfactory estimator for this model. Burnham originally tried modeling capture probabilities as coming from a 2-parameter beta distribution (Johnson and Kotz 1970:37) and using Maximum Likelihood estimation, but found it unsatisfactory.

A naive estimator of *N* is simply the number of distinct animals seen in the whole experiment and is highly biased unless capture probabilities are very high or number of samples very large. Burnham

applied the “jackknife” technique for bias reduction originally proposed by Quenouille (1956) to this estimator and came up with a series of estimators, which are given in Burnham and Overton (1978, 1979) and Otis et al. (1978:109). He also proposed an objective technique for choosing which estimator to use on a particular data set. This technique has been programmed into CAPTURE. Use of the jackknife estimator for point and interval estimation is not without difficulties (Otis et al. 1978:37). However, this jackknife estimation procedure is probably the most robust method so far proposed for Model M_h (Pollock and Otto 1983).

Calculating population-size estimates separately by identifiable categories such as age and sex to reduce heterogeneity of capture probabilities is an alternative approach that sometimes works well. Unfortunately, however, it may not be feasible in small populations.

3.4 M_b : The Trap Response Model

Model M_b allows trap response but no heterogeneity or temporal variation and makes the following assumptions:

1. Every unmarked animal in the population has the same probability of capture (p) for all samples.
2. Every marked animal in the population has the same probability of recapture (c) for all samples after it has been captured once.

Again, it is necessary to find the MLE for N numerically using program CAPTURE.

An important characteristic of this model is that animals do not contribute any information for population size estimation after first capture. Thus, this model is equivalent to the “removal” method (Zippin 1956, Seber 1982:309), except in this case an animal is not physically removed but is considered removed after initial marking.

Often a linear regression method has been used to estimate N in removal studies in the biological literature. This method has intuitive appeal and also is easy to com-

pute. However, whenever computer programs (such as CAPTURE) are available, it is probably better to use the MLE. In practice we have found that there is usually little difference between the 2 estimators.

The regression method (Seber 1982:325) is presented briefly because of its intuitive appeal and because it will be helpful when we discuss M_{bh} in Section 3.5. It is based on the expression

$$\begin{aligned} E(u_i | M_i) &= p(N - M_i) \\ &= pN - pM_i \end{aligned} \quad (3.1)$$

which can be described mathematically as follows. Given M_i (the cumulative number captured and marked before period i) the expected or “average” catch of unmarked animals on day i (u_i) is a linear function of the number of marked animals in the population. In the language of fisheries, where this technique has been applied most, we have a linear regression of catch (u_i) versus cumulative catch (M_i). The regression-based estimators of N and p are simple functions of the least squares estimators of the slope and intercept (Seber 1982:325).

3.5 M_{bh} : The Heterogeneity and Trap Response Model

Model M_{bh} allows for both heterogeneity and trap response and assumes that each animal has its own unique pair of potential capture probabilities ($p_j, c_j; j = 1, \dots, N$) with p_j and c_j referring to whether the animal is unmarked or marked, respectively. These probabilities are assumed to remain constant over all sampling times.

This model was first considered by Pollock (1974) and was developed further by Otis et al. (1978:40), who give an estimation procedure called the “generalized removal method.” Here we describe their method intuitively by generalizing the regression method described in the previous section.

If heterogeneity (as well as trap response) is operating, there is no longer a linear relationship between catch (u_i) and

cumulative catch (M_i), and thus eq. (3.1) is no longer valid. In fact we now have

$$E(u_i | M_i) = \bar{p}_i(N - M_i),$$

where \bar{p}_i is the average conditional probability of capture in the i th sample for those animals not previously captured. We would expect the \bar{p}_i 's to decrease gradually because the animals with higher first capture probabilities would tend to be caught earlier than those with lower first capture probabilities.

Otis et al. (1978) also suggest that the biggest differences between the \bar{p}_i 's will be at the beginning of the experiment. This suggests that the regression should be more nearly linear if points corresponding to earlier sampling times are excluded. An objective method of doing this is to first test if all the \bar{p}_i 's are equal. If so, we use the removal method (Section 3.4), which is a regression using all sample points. If not, we test if $\bar{p}_2 = \bar{p}_3 = \dots = \bar{p}_k$, and if this hypothesis is not rejected, we use a regression based on all points except the first. We continue sequentially removing points until the remaining \bar{p}_i 's cannot be shown to differ.

Notice that although using fewer points in the regression gives us a more general model allowing heterogeneity, it also means we are estimating N based on less information, so that standard errors for N under this model tend to be larger than under the removal model. Also a substantial negative bias on estimators of N can still exist if the heterogeneity is severe and the number of sampling times small. The problem with heterogeneity is that some animals may be essentially "invisible" because of their very small capture probabilities, and no model can deal with this extreme situation.

Pollock and Otto (1983) considered some new estimators for Model M_{bh} . They concluded that a new jackknife-type estimator may be better than the generalized removal estimator described above. It is hoped that this estimator will be included in CAPTURE soon so that biologists can use it.

3.6 M_t : The Schnabel Model (Time Variation)

Model M_t does not allow heterogeneity or trap response of the individual animal capture probabilities. The model instead assumes that every animal in the population has the same probability of capture at each sampling time, p_i ; $i = 1, 2, \dots, k$. This is the classic capture-recapture model for a closed population with a history going back to Schnabel (1938).

A detailed treatment of this model is given by Seber (1982:130). The MLE can be found numerically using program CAPTURE. Approximations developed by Schnabel and Schumacher-Eschymeyer (Seber 1982:139) are easier to compute; however, we strongly recommend the use of program CAPTURE because of its flexibility. This model, together with M_o , does not require detailed capture history. Batch marks are sufficient to allow estimation. The Model M_t MLE, like that of Model M_o , can be highly biased if there is unequal catchability. Heterogeneity causes a negative bias, whereas trap response can cause positive or negative bias depending on whether the animals are trap-shy or trap-happy, respectively. This will be discussed further in Section 3.9 when we consider a practical example.

3.7 Other Time Dependent Models

The 3 important models M_h , M_b , and M_{bh} all require the assumption that capture probabilities do not vary over time. Their generalizations to allow for time variation are M_{th} , M_{tb} , and M_{tbb} , respectively. Although these models are conceptually very important, because they may be appropriate for a practical study, they do not permit estimation of population size without additional assumptions.

3.8 Model Selection

In Otis et al. (1978) and in program CAPTURE, an important method of choosing 1 of the 8 possible models (M_o , M_t , M_b , M_{tb} , \dots , M_{tbb}) is presented. This

model selection algorithm is based on goodness-of-fit tests and tests between models. The procedure often may need to be used, but with caution (Chapman 1980, Menkins and Anderson 1988), because the tests are not independent and often have very low power, especially for small populations (Menkins and Anderson 1988). If possible, biological information should be used to reduce the number of models considered in a study. For example, evidence may exist, based on behavior of the animal concerned, that trap response is unlikely with the trapping method used. In this case any models that allow trap response could be eliminated from consideration (M_b , M_{bh} , M_{tbh}). Menkins and Anderson (1988) suggest that, in situations where model selection is poor (i.e., low capture probabilities, small population), use of a Lincoln-Petersen estimate based on pooling of samples into an early versus late sample is often preferable to use of program CAPTURE.

3.9 Examples

For Example 1 (and elsewhere in this monograph) we use meadow vole, *Microtus pennsylvanicus*, livetrapping data collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June 1981 through January 1982. The grid contained a 10×10 matrix of trapping stations spaced at 7.6-m intervals. A single modified Fitch live trap (Rose 1973) was placed at each station. Hay and dried grass were placed in the nest box sections of the traps, and whole corn was used as bait. Traps were opened 1 evening, checked the following morning, and locked open until the evening when the procedure began again.

Here we use data from 5 consecutive trapping days in October 1981 to illustrate the output from program CAPTURE. Data include all animals of both sexes ≥ 22 g body weight. Output from the model selection procedure of CAPTURE for these data is presented in Table 3.2. In this case the heterogeneity model, M_h , is suggested.

Output corresponding to the model M_h estimates from program CAPTURE is pre-

sented in Table 3.3. The jackknife estimate of population size is 139 animals with an approximate 95% confidence interval of 117–161 animals. The average daily capture probability is 0.44, which explains the good precision of the estimate.

Example 2 is taken from O'Brien et al. (1985), and only a brief description is given here. Quail populations were studied on 2 tracts (204 and 212 ha) at Tall Timbers Research Station, Leon County, Florida. For a detailed description of habitats at Tall Timbers Research Station, Smith (1980) can be consulted. Study sites were characterized by open, annually-burned stands of loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*). The under-story was open and dominated by herbaceous plants. Some wet, hardwood hammocks also were present. Quail were captured in corn-baited live traps, banded with aluminum bands, and released (Dimmick et al. 1982). Traps were placed at an average density of approximately 1 trap/2 ha. Trapping was carried out for 15–20 days until >50% of the captured birds were banded. The capture–recapture data were used to estimate population size using program CAPTURE (Otis et al. 1978).

A systematic shooting harvest was initiated 2–3 days after trapping ended to collect a second sample of birds using a different sampling method. Harvest continued until the harvested sample equaled approximately one-half of the banded sample (approx. 3 days). A bias-corrected Lincoln-Petersen estimate (Chapman 1951) (Chapter 2) was calculated from trapping and harvest samples. Multiple captures were considered as a single trapping occasion. A second set of estimates was calculated based on trapping records alone, using the CAPTURE program (Otis et al. 1978). We ignore the fact that stopping rules for our sampling suggested inverse sampling (Seber 1982:118). In practice many stopping rules are imprecise, as in this example, and it is usually reasonable to use the estimates based on direct sampling stopping rules.

Lincoln-Petersen estimates were calculated for each of 4 years of data on the 2

Table 3.2. Model selection procedure from program CAPTURE for the meadow vole data collected by J. D. Nichols at Patuxent Wildlife Research Center, Laurel, Maryland, in October 1981.

Model Criteria	M_o	M_h	M_b	M_{bh}	M_t	M_{th}	M_{tb}	$M_{t bh}$
	0.80	1.00 ^a	0.38	0.59	0.00	0.32	0.52	0.98 ^a

^a The high values for M_h and $M_{t bh}$ suggest the appropriate model is probably M_h or $M_{t bh}$. The suggested estimate is the jackknife corresponding to M_h , the simple model. There is no estimator for $M_{t bh}$.

study areas (Tables 3.4, 3.5). Estimates also were generated (when possible) for each of the CAPTURE models and then for the most appropriate model based on the model selection procedure. Model M_{tb} has no estimators in CAPTURE, but Ken Burnham (Colo. Coop. Fish and Wildl. Res. Unit, pers. commun.) has derived an estimator that often does not perform very well and is not readily available. Models M_{th} and $M_{t bh}$ were chosen in 3 instances, and, hence, these data sets have no estimates for the most appropriate model. The Lincoln-Petersen estimate was consistently higher than CAPTURE estimates for the remaining 5 data sets.

Capture probabilities for the Lincoln-Petersen estimate averaged 0.233 (range 0.194–0.304). Average capture probabilities for the CAPTURE estimates varied from 0.10 (range 0.01–0.24) to 0.25 (range 0.12–0.42). The lowest capture probabilities for CAPTURE and the highest probabilities for the Lincoln-Petersen estimate occurred in 1982, the year that total number of birds captured was lowest (Tables 3.4, 3.5).

Comparison of the Lincoln-Petersen estimate to that of model M_t , which is equivalent to the Schnabel estimate for multiple recaptures (Schnabel 1938), showed that M_t gave an average of 0.64 ($SE = 0.003$)

as many quail on the North Tract and 0.62 ($SE = 0.0001$) as many quail on the South Tract as the Lincoln-Petersen estimate. Similarly, the ratio of the most appropriate CAPTURE model to the Lincoln-Petersen estimate was 0.67 ($SE = 0.017$) and 0.66 ($SE = 0.002$) for the North and South tracts, respectively.

In examining the differences between the Lincoln-Petersen estimates and the CAPTURE estimates, the question of how well the assumptions are being met is important. Population closure is assumed by both methods, and that assumption is probably met. Smith (1980) found that quail populations at Tall Timbers were extremely sedentary, indicating little movement between populations. Births were avoided by the timing of the trapping periods to avoid reproductive periods. Mortality during the trapping period would affect both the Lincoln-Petersen method and the CAPTURE procedures, but we believe it is negligible.

No tag loss also is assumed by both methods. This usually is not a serious problem for bird banding in general and is not considered serious in this study because the time span was so short. Smith (1980) handled a minimum of 126 double-banded birds and did not observe a single instance of lost bands.

Table 3.3. Selected statistics and parameter estimates from program CAPTURE for the meadow vole data collected at Patuxent Wildlife Research Center, Laurel, Maryland, in October 1981 by J. D. Nichols. Model M_h , the heterogeneity model, is used.

i F(i)	Frequencies of capture ^a				
	1 29	2 15	3 15	4 16	5 27
NUMBER OF ANIMALS CAPTURED 102 ^b					
AVERAGE P-HAT = 0.44					
INTERPOLATED POPULATION ESTIMATE IS 139 WITH STANDARD ERROR 10.85					
APPROXIMATE 95% CONFIDENCE INTERVAL 117 TO 161					

^a These are the numbers of animals caught from 1 to 5 times.

^b This is the number of distinct animals captured at least once.

Table 3.4. Population estimates and standard errors (SE) by year for the North Tract quail population at Tall Timbers Research Station. Included are estimates (based on trapping data) for each model in CAPTURE for which solutions exist, the model chosen by CAPTURE that fits the data best, and the Lincoln-Petersen estimate (based on trapping and harvest data).

Model	Year							
	1979		1980		1981		1982	
	\hat{N}	SE	\hat{N}	SE	\hat{N}	SE	\hat{N}	SE
M_o	325	9.9	449	9.0	339	3.7	180	8.1
M_h	429	23.3	531	16.8	332	2.6	259	21.3
M_b	336	19.3	512	29.5	341	5.1	374	166.2
M_{bh}	361	67.2	403	2.9	328	0.3	175	13.9
M_t	323	9.5	446	8.7	338	3.5	178	7.7
M_{tb}^a	357	53.5	462	27.0	331	2.3	247	102.8
Model chosen	M_{tb}^b		M_{tbh}^b		M_t		M_{tb}	
Petersen	488	36.1	571	31.2	625	26.0	308	29.7

^a Estimates for this model from K. P. Burnham (Colo. Coop. Fish. & Wildl. Res. Unit, pers. commun.).

^b There are no estimates available for these models chosen by the model selection procedure in program CAPTURE.

The equal catchability assumption is unlikely to be true for either the Lincoln-Petersen or CAPTURE method. We cannot be sure that all animals in a population have the same probability of capture. In fact, this assumption is probably false. For the Lincoln-Petersen estimate, however, we can be sure that no trap response is occurring because different sampling methods were used. Also, there is likely no relationship between the probability of capture in the first sample and probability of capture in the second sample, which suggests that heterogeneity should not be a problem (Seber 1982:85). Therefore, al-

though we cannot be sure without shooting every quail, we believe the Lincoln-Petersen estimate is approximately unbiased.

The CAPTURE estimates are almost uniformly lower than the Lincoln-Petersen estimates, suggesting a negative bias. This bias may arise from several sources. First, a trap-happy response could be occurring due to trap baiting with grain, causing probability of recapture to be higher than probability of first capture. Second, a heterogeneity in capture probabilities of individual birds due to fixed trap placement also may cause negative bias. Model choices (Tables 3.4, 3.5) sug-

Table 3.5. Population estimates and standard errors (SE) by year for the South Tract quail population at Tall Timbers Research Station. Included are estimates (based on trapping data) for each model in CAPTURE for which solutions exist, the model chosen by CAPTURE that fits the data best, and the Lincoln-Petersen estimate (based on trapping and harvest data).

Model	Year							
	1979		1980		1981		1982	
	\hat{N}	SE	\hat{N}	SE	\hat{N}	SE	\hat{N}	SE
M_o	301	7.3	310	9.2	216	3.2	141	13.8
M_h	405	20.8	373	16.2	210	1.9	195	21.6
M_b	373	34.3	409	50.5	241	11.9	not estimated ^a	
M_{bh}	280	6.2	270	4.0	208	0.2	not estimated ^a	
M_t	298	6.8	307	8.4	215	3.0	134	12.4
M_{tb}^b	307	18.2	364	75.0	212	3.0	102	9.2
Model chosen	M_{tbh}^c		M_{tb}		M_{tb}		M_t	
Petersen	488	37.0	489	41.1	353	13.7	207	23.5

^a For models M_b and M_{bh} in 1982 the data were such that nonsensical estimates resulted.

^b Estimates for this model from K. P. Burnham (Colo. Coop. Fish. & Wildl. Res. Unit, pers. commun.).

^c There is no estimate available for the model (M_{tbh}) chosen by the model selection procedure in program CAPTURE.

gest that trap response and/or heterogeneity factors are involved in most of the data. All of the models also indicate variability in capture probabilities over time. Unfortunately, models M_{tb} , M_{th} , and M_{tth} are models for which it is hard to find estimates.

Trap-happy response can be avoided by changing the trapping technique used in subsequent captures, but this usually is not possible in multiple recapture studies. Heterogeneity in capture probabilities often arises because animals have different encounter probabilities with traps due to trap locations outside of home ranges or in habitat that is not visited often. A solution to this problem is to rerandomize trap locations for each capture period, but this also may be impractical. Heterogeneity could be reduced, but not eliminated, by decreasing the distance between traps. This would have the effect of decreasing heterogeneity in encounter probabilities among different coveys of quail.

For bobwhite quail, social organization may generate a lack of independence in captures because quail are usually caught in groups rather than as individuals. This can cause problems in estimating variance because it is not clear whether the unit being captured is a single bird, a covey, or some fraction of a covey. We know that because birds are associated to some degree, the variance estimates will be biased low.

Finally, the model selection procedure in CAPTURE is subject to error. Notice that different models are selected in different years and on different sites. Biologically, 1 model is probably appropriate for the 2 study sites over most of the years. Unfortunately, this model is most likely M_{tth} , which does not have an estimator associated with it.

In conclusion, we believe that severe negative bias exists in CAPTURE estimates of quail population size due to a combination of heterogeneity in capture probabilities and trap-happy response to capture. Heterogeneity could be reduced by close trap placement. Other methods of reducing bias will be difficult to imple-

ment in a multiple capture study. Social organization of quail (and other animals that move in groups) presents a problem in estimating the variance associated with an estimate.

4. THE JOLLY-SEBER MODEL

4.1 Introduction

In many capture-recapture studies it is not possible to assume the population is closed to additions and permanent deletions. The basic open population model suitable for this situation is the Jolly-Seber model (Jolly 1965, Seber 1965), and it is crucial that the reader study this chapter carefully as a building block for the later ones. Cormack (1973) gave a brief intuitive description of this model and its estimators, and Seber (1982:196) gave the best detailed presentation. Comprehensive computer programs are available to help with analyses under this model (e.g., PO-PAN-3, Arnason and Schwarz 1987; SURGE, Lebreton and Clobert 1986). Also, a program JOLLY has been written to accompany the material in this chapter and the next and is described briefly in Chapter 9.

The Jolly-Seber model allows estimation of population size at each sampling time as well as survival rates and birth numbers between sampling times. However, as mentioned earlier, migration cannot be separated from the birth and death processes without additional information.

4.2 Assumptions and Notation

This model makes the following assumptions:

1. Every animal present in the population at the time of the i th sample ($i = 1, 2, \dots, k$) has the same probability of capture (p_i).
2. Every marked animal present in the population immediately after the i th sample has the same probability of survival (ϕ_i) until the $(i + 1)$ th sampling time ($i = 1, 2, \dots, k - 1$).
3. Marks are not lost or overlooked.

Table 4.1. Notation for the Jolly-Seber model described in detail in Chapter 4 of this monograph.

PARAMETERS

- M_i = the number of marked animals in the population at the time the i th sample is taken ($i = 1, \dots, k$;
 $M_1 \equiv 0$).
 N_i = the total number of animals in the population at the time the i th sample is taken ($i = 1, \dots, k$).
 B_i = the total number of new animals entering the population between the i th and ($i + 1$)th sample and
still in the population at the time ($i + 1$)th sample is taken ($i = 1, \dots, k - 1$).
 ϕ_i = the survival probability for all animals between the i th and ($i + 1$)th sample ($i = 1, \dots, k - 1$).
 p_i = the capture probability for all animals in the i th sample ($i = 1, \dots, k$).

STATISTICS

- m_i = the number of marked animals captured in the i th sample ($i = 1, \dots, k$).
 u_i = the number of unmarked animals captured in the i th sample ($i = 1, \dots, k$).
 $n_i = m_i + u_i$, the total number of animals captured in the i th sample ($i = 1, \dots, k$).
 R_i = the number of the n_i that are released after the i th sample ($i = 1, \dots, k - 1$). This may not be all of
the n_i due to losses on capture as discussed in the text.
 r_i = the number of the R_i animals released at i that are captured again ($i = 1, \dots, k - 1$).
 z_i = the number of animals captured before i , not captured at i , and captured again later ($i = 2, \dots,$
 $k - 1$).

4. All samples are instantaneous and each release is made immediately after the sample.

Assumptions (1), (3), and (4) were required under the Lincoln-Petersen model. Because only marked animals are used to estimate survival rates, we do not need to assume that marked and unmarked animals have equal survival rates. However, in practice, biologists will want to use the survival estimates to refer to the whole population rather than just the marked component. The Jolly-Seber model allows for “losses on capture,” i.e., some animals may not be returned to the population after capture. Implicit from the above assumptions is that all emigration from the population is permanent.

The following notation (Table 4.1) is used in this chapter and is based on Seber (1982:196). The statistics defined in Table 4.1 ($m_i, u_i, n_i, R_i, r_i, z_i$) are summary statistics that we need to calculate from the complete capture-history information for each animal captured at least once in the study. Capture-history information is usually represented by series of zero’s and one’s that represent not captured or captured, respectively, in a particular sample. Let us illustrate by showing some typical capture histories for animals in a 5-sample capture–recapture study (Table 4.2). In Table 4.2, animal 1 was captured in the first sam-

ple, recaptured in the second sample, and never seen again. Animal 2 was captured in the first sample and never seen again. Animal 3 was captured in the first sample, and then recaptured in the fourth sample. Animal 4 was first captured in sample 2 and then recaptured in samples 3, 4, and 5. We advise biologists to record this information on every animal, as well as whether it was lost on capture and not released back into the population.

The User Guide for Program Jolly (Hines, Brownie, Nichols, and Pollock; in preparation) describes how the capture-history information should be formatted. POPAN-3 (Arnason and Schwarz 1987) also allows complete capture-history information to be input. We strongly advise this form of input rather than summary statistics. It allows more alternative analyses to be carried out (Chapter 5) and also allows more detailed goodness-of-fit tests to be run (Section 4.5).

Table 4.2. Hypothetical example to illustrate that capture-history information can be summarized by a series of zeros and ones for each animal.

Animal	Capture period				
	1	2	3	4	5
1	1	1	0	0	0
2	1	0	0	0	0
3	1	0	0	1	0
4	0	1	1	1	1

4.3 Parameter Estimation

Here an intuitive discussion of parameter estimation will be given. First imagine that M_i , the number of marked animals in the population just before the i th sample, is known for all values $i = 2, \dots, k$ (there are no marked animals at the time of the first sample so that $M_1 = 0$). Later we will discuss how to estimate the M_i , which are always unknown in an open population.

An intuitive estimator of N_i , the population size in sample i , is the Lincoln-Petersen estimator discussed in Chapter 2. If the model assumptions are valid, then the proportion of marked animals in the sample should equal that in the population,

$$\frac{m_i}{n_i} \approx \frac{M_i}{N_i}.$$

This yields the following estimator for N_i :

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i}, \quad (4.1)$$

where m_i and n_i are the marked and total numbers of animals captured in the i th sample, respectively.

The survival rate estimator is obtained by first considering the number of marked animals in the population immediately after sample i , which is given by $(M_i - m_i + R_i)$. The $(M_i - m_i)$ in this expression represents the marked animals not caught in i , whereas the R_i denotes the number of animals caught in i and released, with marks, back into the population. We then simply consider the number of animals in this group that are still alive and in the population just before the $(i+1)$ th sample, M_{i+1} . A natural survival rate estimator is then the ratio of these 2 quantities:

$$\phi_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}. \quad (4.2)$$

An obvious estimator of the recruitment between i and $(i+1)$ is

$$\hat{B}_i = \hat{N}_{i+1} - \phi_i(\hat{N}_i - n_i + R_i). \quad (4.3)$$

This is simply the estimated difference between population size at sample $(i+1)$ (which is \hat{N}_{i+1}) and the expected number

of survivors from i to $i+1$ (which is $\phi_i [N_i - n_i + R_i]$).

Capture probability, p_i , can be estimated as the proportion of marked or total (marked + unmarked) animals alive at i that are captured in i :

$$\hat{p}_i = \frac{m_i}{\hat{M}_i} = \frac{n_i}{\hat{N}_i}. \quad (4.4)$$

To complete this intuitive outline, we need an estimator of the M_i because they are obviously unknown in an open population. This can be obtained by equating the 2 ratios

$$\frac{z_i}{M_i - m_i} \approx \frac{r_i}{R_i},$$

which are the future recovery rates of the 2 distinct groups of marked animals in the population at sampling period i : (1) $(M_i - m_i)$ are the marked animals not seen at i and (2) R_i are the animals seen at i , marked, and then released for possible recapture. Note that z_i and r_i are the members of $(M_i - m_i)$ and R_i , respectively, which are captured again at least once. Therefore the estimator of M_i is given by

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i}, \quad (4.5)$$

and is defined only for $i = 2, \dots, k-1$ because we need animals seen before and after each i . It follows that N_i in eq. (4.1) is defined for $i = 2, \dots, k-1$; ϕ_i in eq. (4.2) for $i = 1, \dots, k-2$; \hat{B}_i in eq. (4.3) for $i = 2, \dots, k-2$; and \hat{p}_i in eq. (4.4) for $i = 2, \dots, k-1$.

Two of the above estimators (ϕ_i , \hat{p}_i) are maximum likelihood estimators and all 5 (ϕ_i , \hat{p}_i , \hat{N}_i , \hat{B}_i , \hat{M}_i) are intuitively reasonable. These estimators are biased, however, and the following approximately unbiased estimators (denoted by \sim) were recommended by Seber (1982:204; for ϕ_i , \hat{N}_i , \hat{B}_i , \hat{M}_i) and Jolly (1982:304; for \hat{p}_i):

$$\tilde{M}_i = m_i + \frac{(R_i + 1)z_i}{r_i + 1}, \quad (4.6)$$

$$\tilde{N}_i = \frac{(n_i + 1)\tilde{M}_i}{m_i + 1}, \quad (4.7)$$

$$\tilde{\phi}_i = \frac{\tilde{M}_{i+1}}{\hat{M}_i - m_i + R_i}, \quad (4.8)$$

$$\tilde{B}_i = \tilde{N}_{i+1} - \tilde{\phi}_i(\tilde{N}_i - n_i + R_i), \quad (4.9)$$

and

$$\tilde{p}_i = \frac{m_i}{\hat{M}_i}. \quad (4.10)$$

Seber (1982:204) recommended that m_i and r_i should be >10 for satisfactory performance of these bias-adjusted estimators.

4.4 Approximate Variances and Covariances

We now give asymptotic (or large sample) variances and covariances of estimators presented in Section 4.3. These variances include the variability due to estimation (i.e., only the variation resulting from the fact that capture probabilities are not equal to 1). Therefore, we use the notation $\text{var}(\hat{\theta}_i | \theta_i)$ to distinguish from $\text{var}(\hat{\theta}_i)$ used by Seber (1982:202), which includes both sampling variation and nonsampling variation associated with the stochasticity of the birth and death processes. The expression $E(\cdot)$ refers to the expected or average value of that particular random variable. These variances are as follows:

$$\begin{aligned} \text{var}(\hat{M}_i | M_i) &= [M_i - E(m_i)][M_i - E(m_i) + R_i] \\ &\quad \cdot \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right], \end{aligned} \quad (4.11)$$

$$\begin{aligned} \text{var}(\hat{N}_i | N_i) &= N_i[N_i - E(n_i)] \\ &\quad \cdot \left\{ \frac{M_i - E(m_i) + R_i}{M_i} \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right] \right. \\ &\quad \left. + \frac{(N_i - M_i)}{N_i E(m_i)} \right\}, \end{aligned} \quad (4.12)$$

$$\begin{aligned} \text{var}(\hat{\phi}_i | \phi_i) &= \phi_i^2 \left\{ \frac{[M_{i+1} - E(m_{i+1})]}{M_{i+1}^2} \right. \\ &\quad \left. \cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right] \right\}, \end{aligned}$$

$$\begin{aligned} &\cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right] \\ &+ \frac{[M_i - E(m_i)]}{[M_i - E(m_i) + R_i]} \\ &\cdot \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right] \}, \end{aligned} \quad (4.13)$$

$$\text{var}(\hat{B}_i | B_i)$$

$$\begin{aligned} &= \frac{B_i^2[M_{i+1} - E(m_{i+1})]}{[M_{i+1} - E(m_{i+1}) + R_{i+1}]^2} \\ &\cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right] \\ &+ \frac{[M_i - E(m_i)]}{[M_i - E(m_i) + R_i]} \\ &\cdot \frac{[\phi_i R_i(N_i - M_i)]^2}{M_i^2} \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right] \\ &+ \frac{[N_i - E(n_i)][N_{i+1} - B_i]}{N_i[M_i - E(m_i) + R_i]} \\ &+ \frac{\cdot (N_i - M_i)(1 - \phi_i)}{N_i[M_i - E(m_i) + R_i]} \\ &+ \frac{N_{i+1}[N_{i+1} - E(n_{i+1})][N_{i+1} - M_{i+1}]}{N_{i+1}E(m_{i+1})} \\ &+ \frac{\phi_i^2 N_i[N_i - E(n_i)][N_i - M_i]}{N_i E(m_i)}, \end{aligned} \quad (4.14)$$

$$\text{var}(\hat{p}_i | p_i)$$

$$= p_i^2(1 - p_i)^2 \cdot \left[\frac{1}{E(r_i)} - \frac{1}{R_i} + \frac{1}{E(m_i)} + \frac{1}{E(z_i)} \right], \quad (4.15)$$

$$\text{cov}(\hat{\phi}_i, \hat{\phi}_{i+1})$$

$$= -\phi_i(\phi_{i+1}) \frac{[M_{i+1} - E(m_{i+1})]}{M_{i+1}} \cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right], \quad (4.16)$$

and

$$\begin{aligned} \text{cov}(\hat{B}_i, \hat{B}_{i+1}) \\ = -\phi_{i+1} \frac{[N_{i+1} - E(n_{i+1})](N_{i+1} - M_{i+1})}{N_{i+1}} \\ \cdot \left\{ \frac{B_i R_{i+1}}{M_{i+1}} \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right] + \frac{N_{i+1}}{E(m_{i+1})} \right\}. \end{aligned} \quad (4.17)$$

All other covariance terms are zero.

The full variance of $\hat{\phi}_i$ is

$$\begin{aligned} \text{var}(\hat{\phi}_i) &= \text{var}(\hat{\phi}_i | \phi_i) \\ &+ \frac{\phi_i(1-\phi_i)}{M_i - E(m_i) + R_i}. \end{aligned} \quad (4.18)$$

N_i , M_i , and B_i are all random variables, and we believe that biologists generally will be interested only in the variance associated with their estimation ($\text{var} \hat{\theta}_i | \theta_i$). With respect to $\hat{\phi}_i$, however, we suspect that biologists will be interested in the underlying survival probability (ϕ_i) itself, and that variance estimates containing both sampling and nonsampling variation will be of interest. The full variance of $\hat{\phi}_i$ ($\text{var}[\hat{\phi}_i]$) can be obtained by adding the binomial variance term to eq. (4.13), which is how we arrived at eq. (4.18).

In practice, approximate variance estimates are obtained by replacing the parameters and unobservable variables in eq. (4.11)–eq. (4.18) by their estimates and all expected values of the other random variables by the actual observed quantities. The performance of the resulting variance estimators has been studied empirically via computer simulation by Manly (1971) and Roff (1973). Manly (1971) found that for small sample sizes, the Jolly variance estimates tend to be positively correlated with the estimates of the corresponding parameter (e.g., $\text{var}[\hat{N}_i | N_i]$ tends to be correlated with \hat{N}_i). Thus, underestimates will appear to be more accurate than they really are, whereas estimated variances will tend to be conservative in the case of overestimates.

Performance of the Jolly variance estimators when sample sizes are small has led

to several suggestions of different methods for estimating confidence intervals and variances. Manly (1977) used the generalized jackknife method of Gray and Shucany (1972) to obtain confidence intervals for Jolly-Seber estimates. Buckland (1980) used a Monte Carlo simulation approach to estimate both confidence intervals and variances. Both approaches produced confidence intervals that compared well with those based on the Jolly variance estimators. Manly (1984) pointed out that both of these approaches require iterative computations on an electronic computer, but this is not necessarily an important limitation.

The problem of correlation between estimates and their estimated variances "... arises because the variance formulae involve the unknown population parameters. An obvious way to overcome it is therefore to transform estimates in such a way that transformed values have variances that are not directly dependent upon these parameters. Logarithmic and reciprocal transformations of population size and survival probability estimates have been investigated in the past with this in mind. It has been found that they do improve confidence intervals somewhat, but not enough to be relied upon in general (Manly 1971). However, this is not surprising because it is clear from the form of Jolly's variance formulae that these are not the best transformations" (Manly 1984:749). Manly (1984) goes on to suggest transformations based on eq. (4.12) and eq. (4.18) for population size and survival probability, respectively. Simulation studies led him to conclude that confidence intervals based on these transformations performed very well. There is, however, still some element of arbitrariness in these transformations, which gives them an "ad hoc" appearance to us.

4.5 Goodness-of-fit Tests

Seber (1982:223) suggested a traditional chi-square goodness-of-fit test based on comparing observed and expected values for numbers of animals captured with each

possible capture history. He emphasized, however, that often many cells will need to be pooled because of their small expected values. Seber (1982:224) also suggested an indirect ad hoc test based on work of Leslie et al. (1953). Jolly (1982) also has proposed an overall test. To avoid the large scale pooling necessary for Seber's chi-square test, he suggested comparing observed and expected values of the triangular array of animals caught in sample i that were last previously caught in sample j using a chi-square goodness-of-fit test. The disadvantage of the Jolly (1982) test is that we believe it eliminates too much capture-history information by over pooling (Pollock et al. 1985).

Specific tests for individual assumptions also have been proposed. Carothers (1971) has suggested a specific test for heterogeneity of capture probabilities that extends earlier work of Leslie (1958). Robson (1969), Pollock (1975), and Brownie and Robson (1983) have suggested tests for survival and capture probabilities being influenced by marking for a temporary period. Balser (1981) provided a test for temporary emigration (animals moving out of and then back into the population) in the Jolly-Seber model. His test is based on conditioning on sufficient statistics and turns out to be asymptotically equivalent to the Jolly (1982) overall test mentioned above.

Pollock et al. (1985) developed 2 contingency table chi-square tests of the Jolly-Seber model based on use of minimal sufficient statistics and examined their power against a variety of types of alternatives by conducting a detailed simulation study. These tests have a simple intuitive structure, and we present the second test (which has been implemented in program JOLLY).

The test has 2 components, the first of which includes $k - 2$ contingency tables. The columns of these general tables correspond to the different previous capture histories of animals captured in period i ($i = 2, \dots, k - 1$). For the simpler version implemented in JOLLY, we pool all animals captured both at i and some previous

	First captured before i	First captured in i
Captured in i and recaptured	*	*
Captured in i and not recaptured	*	*

Fig. 4.1. A typical 2×2 table illustrating the first component of the goodness-of-fit test of the Jolly-Seber model presented in this monograph.

period ($< i$) to form 1 column and use animals captured for the first time at i to form the other column. The 2 rows of these tables correspond to animals that are and are not captured again at some period $> i$, and these, of course, require no pooling. Note that with these pooling rules, this first component of the test reduces to the test for short-term mortality due to marking given by Robson (1969) and Brownie and Robson (1983). A typical 2×2 table for sample i ($i = 2, \dots, k - 1$) with *'s representing where the cell entries would appear is shown in Figure 4.1.

The second component of the test includes $k - 3$ contingency tables. The columns of the general tables correspond to the different previous capture histories of animals captured at or before sample $i - 1$ (i.e., $\leq i - 1$ for $i = 2, \dots, k - 2$) and at some later period ($> i - 1$). For the simpler version implemented in JOLLY, we pool all of these animals that were captured at some period $< i - 1$ to form 1 column and use all animals captured for the first time at $i - 1$ to form a second column. The 2 rows of these tables correspond to animals next recaptured at i and to animals next recaptured at some later period ($> i$). A typical 2×2 table for sample i ($i = 3, \dots, k - 1$) with *'s representing where the cell entries would appear is shown in Figure 4.2.

The version of the test described here is easy to interpret and has been implemented in program JOLLY. Much initial pooling already has been done over the general version described in Pollock et al. (1985). However, even with this initial pooling, expected cell values sometimes will be small. Our approach is to omit a 2×2 contingency table from the test, if any of its 4 cells has an expected value < 2.0 .

	First captured before $i - 1$	First captured in $i - 1$
Recaptured in i	*	*
Recaptured after i but not in i	*	*

Fig. 4.2. A typical 2×2 table illustrating the second component of the goodness-of-fit test of the Jolly-Seber model presented in this monograph.

On the other hand, if capture probabilities are high our initial pooling may be too extreme. There is an option in program JOLLY that produces more extensive tables for the second test component.

Our simulation results (Pollock et al. 1985) showed that the 2 test components were not equally sensitive to specific assumption failures, with the first component being most sensitive to some failures and the second component to others. For example, for heterogeneous capture probabilities, both test components performed equally well; whereas for heterogeneous survival probabilities, component 2 was much more powerful. We also did a small comparison of the 2 tests when both capture and survival probabilities were heterogeneous. We found that the overall test performed better when there was a positive relationship between the capture and survival probabilities. However, in terms of the 2 components, the first component performed better for the inverse relationship whereas the second performed better for the direct relationship.

Finally, we note that a nonsignificant goodness-of-fit test statistic certainly does not guarantee that all model assumptions have been met by the data. The test can have low power, especially for small populations, with low capture probabilities and survival rates. In addition, this test cannot detect all types of failures of assumptions. Permanent trap response of capture probabilities cannot be detected. Also a permanent lowering of survival due to marking, an important problem in fisheries, cannot be detected. However it is possible to detect short-term influences on survival or capture probabilities (Robson 1969, Pollock 1975, Brownie and Robson 1983). Finally we also mention that if mark loss is

a function of time since marking, the test may have some power to detect it. We present a detailed discussion of model assumptions and the effects of their failure on model estimates in the next section.

4.6 Assumptions and Model Robustness

The effects of heterogeneity of capture probability on Jolly-Seber estimators have been well studied. If certain individuals are more likely to be caught than others and if these different capture probabilities persist throughout the capture-recapture experiment, then the marked individuals in the population will tend to be those with the higher capture probabilities. Because of this difference in average capture probabilities between marked and unmarked animals, the proportion of marked animals in any sample (m_i/n_i) will tend to overestimate the true proportion of marked animals in the population (M_i/N_i). This leads to a negative bias in \hat{N}_i (eq. 4.1). In addition, we have noted that the estimator \hat{M}_i (eq. 4.5) is derived intuitively by equating the proportions of 2 groups of marked animals in the population just after period i (those seen at i , R_i ; and those not seen at i , $M_i - m_i$) that are captured at some subsequent period ($>i$). Heterogeneity can result in a somewhat larger average capture probability for those animals caught at i (R_i) than for marked animals not caught then ($M_i - m_i$). This results in a relatively small negative bias in \hat{M}_i (Carothers 1973). Biased \hat{M}_i contribute not only to the bias of \hat{N}_i , but also result in biased ϕ_i (eq. 4.2). A more detailed intuitive discussion of the effects of heterogeneity on Jolly-Seber estimates is provided by Cormack (1972).

Carothers (1973) and Gilbert (1973) used computer simulation and analytic expressions to approximate the bias in Jolly-Seber estimators resulting from heterogeneous capture probabilities. These authors studied both \hat{N}_i and its bias-adjusted counterpart, \hat{N}'_i (eq. 4.7). Biases in both population size estimators resulting from heterogeneity tended to be negative and often were severe. Magnitude of the biases was found

to depend largely on the average capture probability and the degree of variation in capture probability among individuals (e.g., as indicated by the coefficient of variation of the capture probability distribution, Carothers 1973). Heterogeneous capture probabilities are relatively unimportant when average capture probability is high, leading Gilbert (1973:524) to suggest that “an experimenter need not attempt to design an experiment so that all animals have the *same* probability of capture, but only that the distribution be shifted nearer one so that nearly all animals have probabilities of capture say ≥ 0.50 .” Of course this suggestion has limited practicality. Carothers (1973) also approximated the bias of ϕ_i and $\hat{\phi}_i$ and found them to exhibit only small relative bias in response to heterogeneous capture probabilities. In an interesting example, Carothers (1979) found strong evidence of heterogeneous sighting probabilities in a capture-resighting study of fulmars (*Fulmarus glacialis*). Through computer simulation he was able to approximate the degree of heterogeneity reflected by his test statistic. He then approximated the relative bias in his survival rate estimate and found it to be negligible (<0.01) for most years (Carothers 1979). This example illustrates well the robustness of the Jolly-Seber survival rate estimator to heterogeneous capture probabilities. Finally, we note that the bias in survival rate estimators resulting from heterogeneity of p_i is generally negative, but can sometimes be positive (Nichols and Pollock 1983).

Temporary trap response in capture probability refers to the situation in which an animal exhibits a different capture probability for 1 or more periods after initial capture. Pollock (1975) developed a test of this phenomenon, as well as a set of models and appropriate estimators for this situation (Chapter 5). Permanent trap response in capture probability refers to a situation in which the change in capture probability with initial capture persists for the remainder of the capture-recapture experiment. It is important to consider effects of permanent trap response on Jolly-

Seber estimators because it is difficult to detect and because there are no models available that incorporate this form of trap response. The Jolly-Seber estimator, \hat{M}_i , depends only on marked animals (eq. 4.5) and is hence unaffected on permanent trap response. The survival rate estimator, $\hat{\phi}_i$, is based also on marked animals (see eq. 4.2) and remains unaffected by permanent trap response. The precision of the survival estimator is affected, however, and a trap-happy response increases precision whereas a trap-shy response decreases precision. The population size estimator (eq. 4.1), however, includes the proportion of marked animals in the sample, m_i/n_i , which is assumed to estimate the true proportion marked in the population, M_i/N_i . Under a trap-happy response, animals exhibit higher capture probabilities after initial capture and m_i/n_i will overestimate M_i/N_i resulting in a negative biased \hat{N}_i (Nichols et al. 1984a). Under a trap-shy response, animals exhibit lower capture probabilities after initial capture. This results in m_i/n_i underestimating the true M_i/N_i , thus producing a positive bias in \hat{N}_i . Approximations of the magnitudes of the resulting biases are provided by Nichols et al. (1984a). Relative biases are most severe when the population exhibits substantial turnover (low survival and high recruitment) and also when the marked ratio in the population is small. Also we note that a trap-happy response increases precision of the population size estimate whereas a trap-shy response decreases precision.

If marking decreases the animal's survival rate, serious negative bias can occur to the survival rate estimators. Some methods of marking fish suffer severely from this problem (Ricker 1958). Population size estimators are still unbiased. Temporary reductions in survival rate associated with initial marking can be detected and then estimated using the models and associated tests and estimators of Robson (1969), Pollock (1975), and Brownie and Robson (1983) (Chapter 5).

Heterogeneity of survival probabilities sometimes can be detected using the good-

ness-of-fit test of Pollock et al. (1985). However, models (and associated estimators) that incorporate such heterogeneity are not available. Therefore, effects of heterogeneous survival on Jolly-Seber estimators are of interest. Cormack (1972: 340) considered this problem intuitively and stated, "Since the parameter ϕ_i to be estimated is an average survival probability, variation of survival between individuals will not affect the Jolly-Seber estimates provided that the variation is not correlated with marking, either directly or indirectly through age or otherwise." We find that this is true only if an animal's survival probability in 1 period is independent of its survival probability in another period and if its survival probability is independent of its capture probability (Pollock and Raveling 1982). The nature of the bias on survival estimators has been studied by Pollock and Raveling (1982) and Nichols et al. (1982) in the band recovery model context, which has its own special problems. In the capture-recapture situation, no one has yet done a detailed study. A common case is likely to be heterogeneous survival rates, which are positively related for the same animal (i.e., if survival is high for an animal in 1 year, it is likely to be high also in the next year) but which are independent of capture probability. In this case there is a positive bias on survival rate estimators and also on population size estimators. It is not known how large these biases are likely to be in natural populations, but we suspect that they will be small.

Age-specific differences in survival probabilities can be thought of as a special kind of heterogeneity. Manly (1970) studied effects of age-specific differences in survival probability on Jolly-Seber estimators and examined several different patterns of age-specificity. For example, when survival probabilities are lower for young animals (a common situation in natural populations), resulting Jolly-Seber \hat{N}_i and ϕ_i were found to exhibit positive bias (Manly 1970:17). In situations where age of an animal can be ascertained at time of marking, the model of Pollock (1981b)

can be used to test for age-specific differences in survival and capture probabilities and to estimate age-specific parameters when such differences are detected (also see Stokes 1984 and Chapter 6). However, age determination is not always possible (e.g., for many passerine birds banded during winter), and the results of Manly (1970) are of special interest in such situations. Manly (1970:18) concluded, "The results suggest that this method (Jolly-Seber) can reasonably be used whenever mortality rates are not strongly affected by age."

The assumption of no tag loss also is very important, because if animals lose their marks the number of recaptures will be too low. The result is underestimation of survival rates but no influence on population size estimates (Arnason and Mills 1981). Seber (1982:94–96) gives a method to estimate and adjust for tag loss using a double-marking scheme. It is important to realize that tag loss will cause a decrease in precision of estimators even when it can be estimated and the estimators adjusted (Pollock 1981b).

An implied assumption is that any emigration from the study area is permanent. Balser (1981) derived a test for temporary emigration, which was discussed in Section 4.5. He also stated that population size and survival rate estimators are always positively biased (which we believe to be in error), but he did not attempt to quantify the degree of bias and thus it is difficult to assess how important this violation is likely to be in practice. Temporary emigration is likely to occur in a number of practical field situations, and our opinion is that the bias induced could be serious.

4.7 Examples

In Example 1 we analyze data from a 2-year study on gray squirrels (*Sciurus carolinensis*) carried out in a mature oak woodland at Alice Holt Forest Research Station, Surrey, England, by A. Duboeck. Squirrels were captured at approximately monthly intervals from November 1972 until September 1974. Multiple capture traps baited with grain were located

Table 4.3. Capture-recapture statistics for a gray squirrel population at Alice Holt Forest Research Station, Surrey, England, November 1972–September 1974.

Period	Date	n_t^a	m_t	R_t	r_t	z_t
1	Nov 1972	46		46	43	
2	Dec 1972	46	42	46	44	1
3	Jan 1973	48	42	48	48	3
4	Feb 1973	46	42	46	45	9
5	Mar 1973	51	46	50	46	8
6	Apr 1973	37	37	37	35	17
7	May 1973	41	41	41	40	11
8	May-Jun 1973	42	39	42	37	12
9	Jun 1973	47	43	47	40	6
10	Jul 1973	31	26	31	26	20
11	Aug 1973	8	7	8	8	39
12	Sep 1973	2	2	2	2	45
13	Oct 1973	1	0	1	1	47
14	Nov 1973	4	3	4	3	45
15	Dec 1973	9	8	9	8	40
16	Jan 1974	19	17	18	17	31
17	Feb 1974	19	14	19	18	34
18	Mar 1974	27	20	27	24	32
19	Apr 1974	36	36	36	32	20
20	May 1974	45	34	44	33	18
21	Jul 1974	74	46	73	15	5
22	Aug 1974	22	20	22	2	0
23	Sep 1974	3	2	2		

^a Notation is explained in Table 4.1.

throughout the area on the ground and disguised by leaves. The squirrels were uniquely marked using a toe clipping method.

Basic statistics required for Jolly-Seber estimates are given in Table 4.3, and the parameter estimates and approximate standard errors are given in Table 4.4. Notice that no estimates are presented for periods 12–14 because we believed they would be misleading because of the small numbers of captures (2, 1, and 4). Notice also that survival estimates are sometimes >1 and have been recorded as 1. Similarly some birth number estimates are negative and have been recorded as zero.

This is a precise study, overall, with relatively small standard errors for most sampling periods. The precision results from the high capture and survival probabilities. Once a squirrel is marked it stays in the population a long time and provides information every time it is captured. Also the precision of estimates does vary considerably. This is mainly due to changes

Table 4.4. Jolly-Seber estimates and approximate standard errors^a for a gray squirrel population at Alice Holt Forest Research Station, Surrey, England, November 1972–September 1974.

Period	Date	\hat{N}_t^b	\hat{SE}	$\hat{\phi}_t$	\hat{SE}	\hat{B}_t	\hat{SE}
1	Nov 1972			0.94	0.037		
2	Dec 1972	47.1	0.39	0.96	0.030	6.3	0.77
3	Jan 1973	51.3	0.70	1.00	0.004	4.5	1.27
4	Feb 1973	56.0	1.19	0.99	0.023	5.1	1.53
5	Mar 1973	60.5	1.51	0.94	0.041	0.0	1.06
6	Apr 1973	54.9	1.23	0.95	0.038	0.0	0.00
7	May 1973	52.3	0.60	1.00	0.030	3.9	1.22
8	May-Jun 1973	56.5	2.06	0.90	0.052	3.7	1.45
9	Jun 1973	54.6	1.57	0.92	0.067	8.7	3.30
10	Jul 1973	58.9	4.59	0.84	0.066	2.2	6.60
11	Aug 1973	51.8	5.99	1.00	0.000	0.0	5.99
12	Sep 1973						
13	Oct 1973						
14	Nov 1973						
15	Dec 1973	58.3	9.20	0.93	0.115	1.0	6.57
16	Jan 1974	55.3	4.30	0.98	0.068	13.1	8.25
17	Feb 1974	66.4	8.14	1.00	0.071	6.8	10.14
18	Mar 1974	74.5	7.91	0.93	0.067	0.0	6.28
19	Apr 1974	58.4	2.13	0.99	0.071	18.2	4.22
20	May 1974	76.0	6.12	1.00	0.168	33.9	8.86
21	Jul 1974	110.3	18.10	0.21	0.048	0.0	2.23
22	Aug 1974	21.9	0.00				
23	Sep 1974						

^a $\hat{SE}(\hat{N}_t)$ and $\hat{SE}(\hat{B}_t)$ include only sampling variation or “error of estimation”; $\hat{SE}(\hat{\phi}_t)$ was obtained using the full variance estimator of Jolly (1965).

^b Notation explained in Table 4.1.

in capture probabilities. It should be emphasized, however, that even in studies where the capture probabilities are constant the precision will not be constant and the sampling periods towards the middle of the study will yield more precise estimates. The marked population gradually builds up and there are still plenty of sampling periods to get recaptures because the random variable r_i needs to be large for good precision.

In terms of validity of the estimates, there are many factors to consider. The biologist believed that migration was negligible and therefore interpreted survival and birth estimates as being representative of true survival and birth rates. There is likely to be heterogeneity of capture probabilities due to age, sex, and other factors and also a trap-happy response of capture probabilities. Both departures tend to cause underestimation of population size and, to a lesser extent, underestimation of survival rates. Note that the goodness-of-fit test of Section 4.5 could not be computed because actual capture-history data were not available to us.

Young animals should have been joining the catchable population in April and May. This shows up in high estimates of the birth numbers of 1974 but not in 1973. The biologist had predicted this because 1973 was a very bad year for squirrel reproduction. After all the young animals joined the population in May 1974, there was a large drop in the survival estimate and the population size estimate. Unfortunately this occurred right at the end of the study, and there were so few captures in September 1974 that the estimates are very imprecise.

Example 2 is a study on the domestic pigeon or rock dove (*Columba livia*) carried out by Kautz (1985) in upstate New York. He studied 4 local populations using capture-resighting methods during 1980–83. Here we consider data from a single population in Dryden, New York, sampled on 6 occasions from March through October 1981.

In late March 1981, 152 birds were captured in barns using a spotlight and noose pole. All birds were marked using num-

bered patagial wing tags and released. In August and September, 2 and 3 additional birds were captured and marked in the same way. Each month from June through October, birds were observed through a spotting scope. By reading tag numbers, capture histories were obtained on the marked birds. This enables us to estimate the marked population size each month and hence the survival rate from month to month. At the same time Kautz also obtained numbers of marked and unmarked birds. This information enables us to estimate population sizes and hence birth numbers. With these sampling methods, unmarked birds were counted but were not “released” into the population with marks or tags as in the standard capture-recapture situation. This results in a large difference between the numbers seen (n_i) and released (R_i), with the latter group being composed almost entirely of birds marked at the beginning of the study. In the usual capture-recapture context, the difference, $n_i - R_i$, reflects trap or handling mortalities (eqs. 4.3, 4.9), which are appropriately subtracted from N_i in the estimation of B_i . However, in the pigeon study, this difference ($n_i - R_i$) does not represent any sort of mortality. In estimating B_i for this study, we therefore modified eq. (4.9) as follows: $\hat{B}_i = \tilde{N}_{i+1} - \tilde{\phi}_i \tilde{N}_i$ (Kautz 1985).

Summary statistics for this experiment are presented in Table 4.5 and estimates and standard errors in Table 4.6. Notice that typically around 300 birds were counted each month using a spotting scope. This is approximately three-fourths of the estimated population, and the resighting rates of marked birds were extremely high. This shows up in high precision of estimates in Table 4.6. Notice that the population size appears to be approximately constant during the study and that survival rates are high. The estimates of birth numbers (\hat{B}_i) are interesting. None of them is significantly different from zero, but they do show an increase from nearly 10 to nearly 50. This suggests that young birds may be entering the sampled population in increasing numbers as the study pro-

Table 4.5. Capture-recapture statistics for a rock dove population sampled at Dryden, New York, in 1981 (Kautz 1985).

Period	Date	n_i^a	m_i	R_i	r_i	z_i
1	Late Mar			152	101	
2	Jun	268	66	66	57	35
3	Jul	283	68	68	66	24
4	Aug	280	65	67	56	25
5	Sep	330	69	72	49	12
6	Oct	301	61			

^a Notation is explained in Table 4.1.

gresses. Finally, we note that detailed capture-history data were not available for this example; therefore we were not able to conduct the goodness-of-fit test of Pollock et al. (1985). However, we did find that Jolly's test of the Jolly-Seber model (Jolly 1982) (Section 4.5) showed a significant lack of fit; therefore the estimates should be considered with caution despite their high precision.

In Example 3 we return to the live-trapping study on *Microtus pennsylvanicus* conducted at Patuxent Wildlife Research Center (Section 3.9) (Example 1). To illustrate the use of the Jolly-Seber model and the proposed goodness-of-fit test, we selected data from 6 consecutive monthly trapping periods extending from June through December 1981. Each monthly period included 5 consecutive days of trapping, but here we just use the information of whether an animal was captured at least once (i.e., we pool the 5 days together). More detailed descriptions of the field methods are presented in Section 3.9 and in Nichols et al. (1984b). The data are summarized in Table 4.7.

The bias-adjusted estimates of survival rate, population size, and number of new animals are presented with associated standard error estimates in Table 4.8. The estimated mean capture probability for this study was 0.91 and the resulting estimates are very precise.

In Table 4.9 we present the complete set of contingency tables for the goodness-of-fit test formulation of Section 4.5. Notice that for $i = 2$ and the second test component, there are zeros in the first column because it is not possible for an animal to be captured before period 1. The other

Table 4.6. Population estimates and approximate standard errors^a for a Dryden, New York, rock dove population, in 1981 (Kautz 1985).

Period	i	\hat{N}_i^b	$\hat{S}E$	$\hat{\phi}_i$	$\hat{S}E$	\hat{B}_i	$\hat{S}E$
Late Mar	1			0.70	0.043		
Jun	2	427.3	30.62	0.87	0.043	9.4	32.98
Jul	3	381.6	20.87	1.00	0.029	13.4	32.12
Aug	4	403.7	27.16	0.89	0.053	48.4	30.24
Sep	5	409.1	24.25				
Oct	6						

^a $\hat{S}E(\hat{N}_i)$ and $\hat{S}E(\hat{B}_i)$ include only sampling variation or "error of estimation"; $\hat{S}E(\hat{\phi}_i)$ was obtained using the full variance estimator of Jolly (1965).

^b Notation is explained in Table 4.1.

contingency tables where no chi-squared tests have been computed are due to expected values being <2 .

In this case we found there was a highly significant result for each component and the overall test. This is not surprising because looking at our simulations (Pollock et al. 1985) and doing some rough interpolation, we found that with $k = 6$ and $N = 120$ we would expect high power against heterogeneity of capture and survival probabilities. This is because average capture probability is very high ($E[p] \cong 0.9$) and average survival is reasonably high ($E[\phi] \cong 0.7$). Despite this evidence of heterogeneity, the results of Carothers (1973, 1979) lead us to believe that our survival probability estimates probably are not badly biased. Indeed, the high capture probabilities caused us to suspect that even population size estimates probably are not biased severely (Carothers 1973, Gilbert 1973). In Chapter 7 we will compare the Jolly-Seber \hat{N}_i of Table 4.8 with closed model \hat{N}_i based on the heterogeneity mod-

Table 4.7. Capture-recapture statistics for meadow voles trapped by J. D. Nichols at Patuxent Wildlife Research Center, Laurel, Maryland, 1981.

Period	Date	n_i^a	m_i	R_i	r_i	z_i
1	27 Jun–1 Jul	108		105	87	
2	1 Aug–5 Aug	127	84	121	76	5
3	29 Aug–2 Sep	102	73	101	68	8
4	3 Oct–7 Oct	103	73	102	63	3
5	31 Oct–4 Nov	102	61	100	84	5
6	4 Dec–8 Dec	149	89	148		

^a Notation is explained in Table 4.1.

Table 4.8. Jolly-Seber estimates and approximate standard errors^a of survival rates, population sizes, and numbers of new animals for meadow voles trapped by J. D. Nichols at Patuxent Wildlife Research Center, Laurel, Maryland, 1981.

Period	Date	\hat{N}_t^b	\hat{SE}	$\hat{\phi}_t$	\hat{SE}	\hat{B}_t	\hat{SE}
1	27 Jun–1 Jul			0.88	0.039		
2	1 Aug–5 Aug	138.4	4.14	0.66	0.048	30.9	3.50
3	29 Aug–2 Sep	118.1	4.41	0.69	0.049	28.6	2.84
4	3 Oct–7 Oct	109.4	2.93	0.63	0.049	43.3	2.98
5	31 Oct–4 Nov	111.2	3.13				
6	4 Dec–8 Dec						

^a $\hat{SE}(\hat{N}_t)$ and $\hat{SE}(\hat{B}_t)$ include only sampling variation or "error of estimation"; $\hat{SE}(\hat{\phi}_t)$ was obtained using the full variance estimator of Jolly (1965).

^b Notation is explained in Table 4.1.

el, Model M_h (Section 3.3), and these comparisons suggest that the bias in the \tilde{N}_t is small as expected.

5. OTHER METHODS FOR OPEN POPULATIONS

5.1 Introduction

The Jolly-Seber model for open populations described in Chapter 4 is a probabilistic model; estimators are derived using statistical theory and have optimal statistical properties. This is in contrast to methods employed by many vertebrate biologists, which use recaptures or resightings only as a means of establishing that a marked individual was alive in some previous sampling period when it was not caught or seen. This approach has been labeled the "enumeration method" by mammalogists, and we retain that terminology here, recognizing that all groups using the approach do not refer to it by that name. Shortcomings of the enumeration method are discussed before we describe other models for open populations.

Under the Jolly-Seber model, survival rates, capture rates, birth rates, and population sizes are assumed to be time-specific, making this a fairly general model. As a consequence, the number of parameters to be estimated is large, and except in data sets with many recaptures, precision of estimators is poor. When stronger assumptions can be made and the number of parameters reduced, estimators have better precision. We describe several special cases of the Jolly-Seber model, each with a reduced number of parameters.

We also consider situations where the Jolly-Seber assumptions are too restrictive and more general models are needed. One other general model allowing age-dependence of survival and capture probabilities is postponed to Chapter 6 because of its importance. To aid the reader, we present a diagram (Fig. 5.1) that gives an overview of the open population models covered in this monograph. Our treatment is obviously centered on the Jolly-Seber model covered in Chapter 4.

5.2 The Enumeration Method

As noted earlier, we use the term enumeration method to refer to methods that use recaptures or resightings only as a means of establishing that a marked animal was alive in some previous sampling period. Animals that are caught or seen in a particular sampled period, i , and never seen again are assumed to have died or emigrated between i and $i + 1$. Enumeration estimators, which also are known in the mammalogy literature as "minimum number known alive" and "calendar of catches" estimators (Newson and Chitty 1962, Krebs 1966, Krebs et al. 1969), are widely used in small mammal capture-recapture studies. However, they also see wide use in ornithological (see discussion in Loery and Nichols 1985) and herpetological (see Woodward et al. 1987) capture-recapture (or capture-resighting) studies, particularly with respect to survival rate estimation. We believe that estimators based on the Jolly-Seber and related probabilistic models are preferable

Table 4.9. Contingency tables of goodness-of-fit test implemented in program Jolly described in Section 4.5 and Pollock et al. (1985). The capture–recapture data are for meadow voles trapped by J. D. Nichols at Patuxent Wildlife Research Center, Laurel, Maryland, 1981.

	First capture before <i>i</i>	First capture in <i>i</i>		First capture before <i>i</i> – 1	First capture in <i>i</i> – 1
<i>i</i> = 2					
Capture in <i>i</i> and recaptured	47.00	29.00	Capture in <i>i</i>	0.00	84.00
Expected value	48.99	27.01	Expected value	0.00	84.00
Capture in <i>i</i> and not recaptured	31.00	14.00	Capture after <i>i</i> , not in <i>i</i>	0.00	5.00
Expected value	29.01	15.99	Expected value	0.00	5.00
$\chi^2 = 0.6127$, 1 df, $P = 0.4338$			$\chi^2 = 0.0000$, 0 df, $P = 1.0000$		
<i>i</i> = 3					
Capture in <i>i</i> and recaptured	55.00	13.00	Capture in <i>i</i>	50.00	23.00
Expected value	49.15	18.85	Expected value	46.86	26.14
Capture in <i>i</i> and not recaptured	18.00	15.00	Capture after <i>i</i> , not in <i>i</i>	2.00	6.00
Expected value	23.85	9.15	Expected value	5.14	2.86
$\chi^2 = 7.6912$, 1 df, $P = 0.0055$			$\chi^2 = 5.9339$, 1 df, $P = 0.0149$		
<i>i</i> = 4					
Capture in <i>i</i> and recaptured	53.00	10.00	Capture in <i>i</i>	60.00	13.00
Expected value	44.47	18.53	Expected value	60.51	12.49
Capture in <i>i</i> and not recaptured	19.00	20.00	Capture after <i>i</i> , not in <i>i</i>	3.00	0.00
Expected value	27.53	11.47	Expected value	2.49	0.51 ^a
$\chi^2 = 14.5472$, 1 df, $P = 0.0001$			$\chi^2 = 0.0000$, 0 df, $P = 1.0000$		
<i>i</i> = 5					
Capture in <i>i</i> and recaptured	52.00	32.00	Capture in <i>i</i>	52.00	9.00
Expected value	49.56	34.44	Expected value	51.76	9.24
Capture in <i>i</i> and not recaptured	7.00	9.00	Capture after <i>i</i> , not in <i>i</i>	4.00	1.00
Expected value	9.44	6.56	Expected value	4.24	0.76 ^a
$\chi^2 = 1.8312$, 1 df, $P = 0.1760$			$\chi^2 = 0.0000$, 0 df, $P = 1.0000$		
Column $\chi^2 = 24.6823$, 4 df, $P = 0.0001$			Column $\chi^2 = 5.9339$, 1 df, $P = 0.0149$		
Overall $\chi^2 = 30.6162$, 5 df, $P = 0.0000$					

^a These 2 tables had expected values for a cell <2 so that using our pooling rule the chi-square statistics were not computed.

to enumeration estimators and should be adopted in capture–recapture (or capture–resighting) studies of vertebrate populations. Nichols and Pollock (1983) is the source of most of the material in this section.

The enumeration estimator for survival rate (called “return rate” in the ornithological literature) between time *i* and (*i* + 1) is given by

$$\hat{\phi}_i^E = r_i \div R_i, \quad (5.1)$$

where R_i is the number of animals released after the *i*th sample and r_i is the number of those R_i captured again later. The expected value of this estimator can be written as

$$E(\hat{\phi}_i^E) = 1 - \chi_i \\ = \phi_i(1 - q_{i+1} \chi_{i+1}), \quad (5.2)$$

where $q_{i+1} = 1 - p_{i+1}$, and χ_i is the probability of never capturing an animal after time *i*, given that the animal is alive and in the population at the time of release in period *i*. Thus the estimator, $\hat{\phi}_i^E$, can be shown to estimate a complicated function involving every survival and capture probability subsequent to period *i* and is only unbiased in the unlikely event that every capture probability is 1.

The enumeration estimator for population size at time *i* is given by

$$\hat{N}_i^E = n_i + z_i, \quad (5.3)$$

where n_i is the number of animals captured in the *i*th sample and z_i is the number of animals caught before and after the *i*th sample but not in the *i*th sample. The expected value of this estimator can be written as

OPEN MODEL OVERVIEW

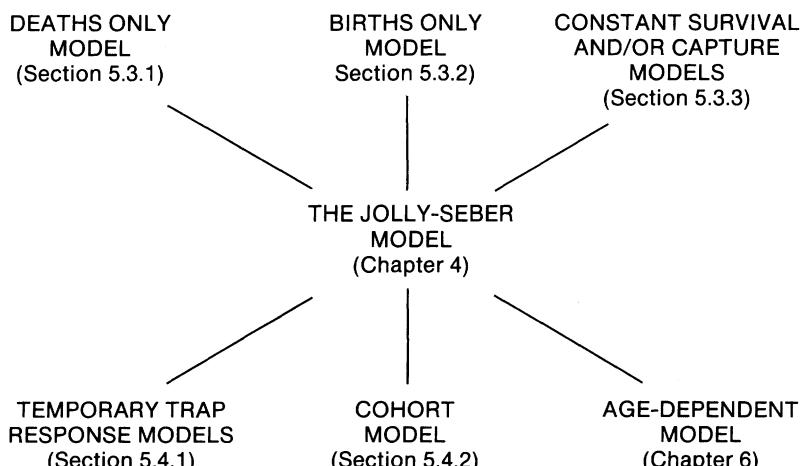


Fig. 5.1. This figure provides an overview of the different open capture-recapture models and their interrelationships.

$$E(\hat{N}_i^E) = N_i p_i + M_i q_i (1 - \chi_i). \quad (5.4)$$

Because of the χ_i term, this expected value is seen to involve all of the capture probabilities and survival probabilities occurring subsequent to period i . In addition, M_i is itself a function of all capture probabilities occurring before time i . Therefore, \hat{N}_i^E also estimates a complicated function involving a large number of parameters and again is only unbiased in the unlikely event that every capture probability is 1. Another way of considering this is that the unmarked portion of the population is always estimated as zero (from eqs. [5.3] and [5.4]).

The reason provided most frequently for preferring enumeration to Jolly-Seber estimators is that capture probabilities, p_i , often are not the same for all individuals in the population (or in the stratum of interest) for a given time period. We can think of unequal capture probabilities as resulting either from heterogeneity or trap response, and we have discussed these concepts in detail in earlier chapters of this monograph. In Section 4.6 we showed that heterogeneity and trap response result in biases in Jolly-Seber estimates; however, we do not believe that this should result in

the preference of enumeration estimators. Enumeration estimators are always biased when capture probabilities are < 1 . The situation (high average capture probability) for which the bias of enumeration estimators is said to be acceptably small (Hilborn et al. 1976) is the same situation for which the Jolly-Seber estimates have small bias (Section 4.6). In the case of negative bias due to heterogeneity or trap-happy response, Nichols and Pollock (1983) also show that the absolute value of the bias of the Jolly-Seber estimates is either equal to or smaller than the absolute value of the bias of the enumeration estimates. Therefore, the Jolly-Seber estimates perform better than the enumeration estimates even in the case of heterogeneity and trap-happy response, the 2 sources of unequal capture probability most likely to occur in small mammal studies. Finally, we note that trap response lasting for 1 period has been explicitly incorporated in the general probabilistic models of Robson (1969), Pollock (1975), and Brownie and Robson (1983), which are described later in this chapter (Section 5.4.1). Despite the fact that trap response occurs commonly in small mammal capture-recapture studies (Tanaka 1980), we are not aware of any

uses of these general models in small mammal literature.

The inability of the Jolly-Seber model to handle more than 1 age class perhaps limits its utility for some vertebrate studies; however, a more general model permitting different capture and survival probabilities for different age classes has recently been developed (Pollock 1981b) and is discussed in Chapter 6 of this monograph. This negates another common criticism of the use of probabilistic models.

The actual values of estimates of demographic parameters may not be as important as comparisons of such estimates (e.g., between populations or time periods). Therefore, if the enumeration estimators provided relative estimates that could be used in such comparisons, an argument could be made for their use. However, if we wish to use comparisons of different estimates to draw inferences about differences between underlying parameters, we must be willing to assume that the biases are equal for the estimates being compared. Because these biases are always functions of survival and capture probabilities and also population sizes for the population size estimate, it is unlikely that this assumption will ever be met. Even in the situation of equal population sizes, survival rates, and capture probabilities for all time periods, the negative bias of the enumeration survival and population size estimates will be larger at the end of the study, and temporal comparisons will not be appropriate. Temporal changes in capture probability also can cause problems in comparing enumeration estimates. Enumeration survival estimates may be lowest during the period of the year in which capture probabilities are lowest. Although such results generally would be interpreted by biologists as evidence of low survival rates during the period of interest, they also would be expected to occur simply as a result of the low capture probabilities.

Finally, the argument that the Jolly-Seber estimates are difficult to compute is no longer valid. Several powerful, flexible program packages, including programs JOLLY, JOLLYAGE, POPAN-3 (Arnason

Table 5.1. Parameter^a values for the experiments depicted in Fig. 5.2A–E.

Experiment ^b	<i>N</i>	ϕ	p_{1-5}	p_{6-9}	p_{10-12}
1	200	0.75	0.70	0.30	0.07
2	200	0.75	0.70	0.30	0.70
			(0.60) ^c	(0.20) ^c	(0.60) ^c
3 Group 1 ^d	100	0.75	0.80	0.40	0.80
Group 2 ^d	100	0.75	0.60	0.20	0.60

^a *N* denotes population size (assumed constant for all periods), ϕ is survival rate (constant for all periods), and p_{i-j} denotes capture probability for periods *i* through *j*.

^b Experiment 1 corresponds to the Jolly-Seber model (equal capture probability for all individuals within each capture period), experiment 2 to a model incorporating positive trap response (trap-happy), and experiment 3 to a model incorporating heterogeneity of capture probability (different capture probabilities for individuals in each of 2 groups).

^c Capture probability for unmarked individuals is written in parentheses under the capture probability for marked individuals.

^d Groups 1 and 2 refer to groups of animals having different capture probabilities in experiment 3; group 1 animals are inherently more catchable than group 2 animals.

and Schwarz 1987), and SURGE (Lebreton and Clobert 1986) are now available (Chapter 9). The data required for the programs are each individual's complete capture history together with any attribute data such as age or sex. It is easy to obtain analyses stratified by age or sex or any other coded attribute data.

In order to illustrate some of the points made above, we computed approximate expectations of Jolly-Seber and enumeration estimators under 3 hypothetical capture-recapture experiments. All experiments included 12 trapping periods (e.g., these could represent monthly trapping for a period of 1 year) and assumed constant expected total population size of $E(N_i) = N = 200$ animals (Table 5.1). We assumed constant survival rates of $\phi_i = \phi = 0.75$ and, because of the assumption of $E(N_i) = N$, we implicitly assumed a constant expected number of new animals entering the population, $E(B_i) = B = (1 - \phi)N = 50$ animals.

The 3 experiments differed in their assumptions about capture probability. Experiment 1 corresponded to the Jolly-Seber model and assumed equal capture probability within each trapping period for all individuals in the population. Capture probability was 0.70 for periods 1–5 and 10–12 and 0.30 for periods 6–9 (Table 5.1). This time-specific variation in capture probability was intended to represent sea-

sonal variation in capture probability characteristic of many small mammal studies (e.g., Smith et al. 1975:33–34, Krebs et al. 1976, Boonstra and Krebs 1977). Although the assumed range in capture probability was large, we believe that such variation may be typical in small mammal studies (Nichols and Conley 1982, Nichols and Hines 1982, Nichols and Pollock 1983). Experiment 2 corresponded to a model with permanent trap response. Capture probability for unmarked animals was assumed to be 0.60 for periods 1–5 and 10–12 and 0.20 for periods 6–9. Capture probability for marked individuals was 0.70 for periods 1–5 and 10–12 and 0.30 for periods 6–9 (Table 5.1). Experiment 3 corresponded to a model with heterogeneous capture probability. The total population consisted of 1 group of 100 animals with capture probability of 0.80 for periods 1–5 and 10–12 and 0.40 for periods 6–9, and another group of 100 animals with capture probability of 0.60 for periods 1–5 and 10–12 and 0.20 for periods 6–9 (Table 5.1).

Our expectations of the Jolly-Seber and enumeration estimators were computed using large sample approximations similar to those used by Carothers (1973) to study effects of heterogeneity on Jolly-Seber model estimates. We first expressed the expectations of the necessary summary statistics in terms of model parameters and then evaluated these expectations using the 3 sets of parameter values in Table 5.1. Finally, we used these expected values to approximate the expectations of the Jolly-Seber and enumeration estimates of population size and survival rate. Monte Carlo simulation experiments conducted by Carothers (1973) and us indicate that these approximations generally perform well for the range of parameter values in Table 5.1.

In experiment 1, where the Jolly-Seber model assumptions were exactly met, the Jolly-Seber estimates of population size naturally performed well (Fig. 5.2A). Enumeration estimates of population size were negatively biased, with the worst biases occurring in the first and last trapping periods and during the periods of low p_i (periods 6–9, Fig. 5.2A). In experiment 2, with

positive trap response, the Jolly-Seber population size estimates exhibited negative bias, which was worst during periods (6–9) of low capture probability (Fig. 5.2B). The enumeration population size estimates exhibited substantial negative bias, which varied considerably among capture periods (Fig. 5.2B). In experiment 3, with heterogeneous capture probability, the Jolly-Seber population size estimates exhibited slight negative biases, whereas enumeration biases again were much larger and varied considerably over time (Fig. 5.2C).

Both the enumeration and Jolly-Seber estimates of survival rate depend only on marked animals, and expectations of estimates were thus unaffected by permanent trap response. For this reason, expectations in Fig. 5.2D correspond to both experiments 1 and 2. The enumeration estimates exhibited substantial negative bias, which was worst during periods of low capture probability and at the end of the experiment (Fig. 5.2D). In experiment 3, with heterogeneous capture probability, the Jolly-Seber estimator was quite robust to heterogeneity, whereas the enumeration estimates again showed substantial negative bias (Fig. 5.2E).

5.3 Special Cases of the Jolly-Seber Model

5.3.1 Deaths Only Model.—For some populations where births and immigration are known to be negligible, a model that allows for losses (deaths and emigration) is reasonable. Because the birth numbers B_1, B_2, \dots, B_{k-1} no longer have to be estimated, there is a gain in precision for the remaining parameter estimators. This model was originally developed for the special case of no losses on capture by Darroch (1959). Jolly (1965) discusses it as a special case of his general model (the Jolly-Seber model). Seber (1982:217) also discusses this model. Program JOLLY can be used to carry out the estimation and test procedures described below.

The population size estimators now take the form

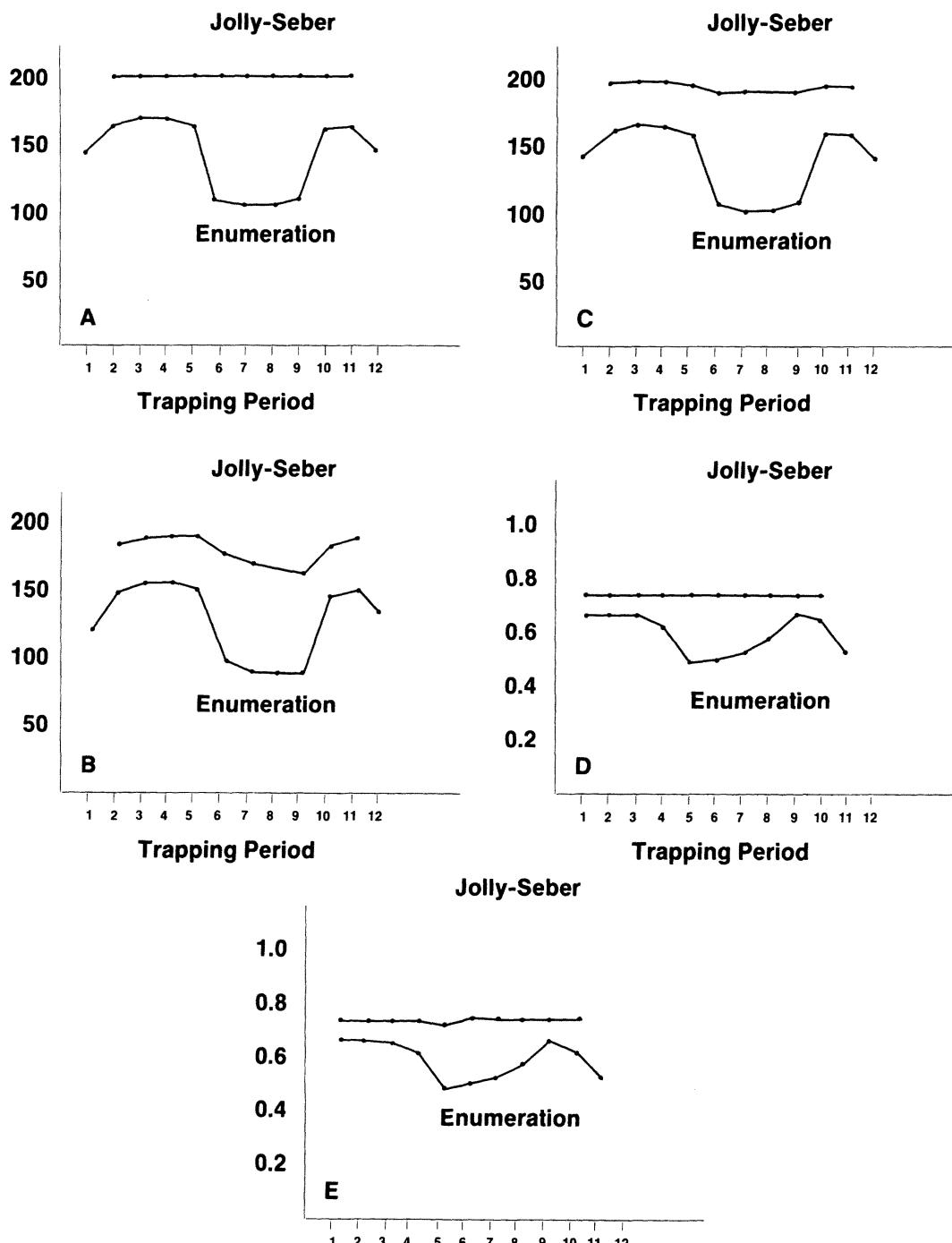


Fig. 5.2. Approximate expectations of the Jolly-Seber and enumeration estimates of N for (A) experiment 1, (B) experiment 2, and (C) experiment 3. Approximate expectations of the Jolly-Seber and enumeration estimates of ϕ , for (D) experiments 1 and 2, and (E) experiment 3.

$$\hat{N}_i = n_i + \frac{R_i z'_i}{r_i} \quad (5.5)$$

and are defined for $i = 1, 2, \dots, k - 1$, unlike for the Jolly-Seber model where N_1 cannot be estimated. This estimator can be derived intuitively using the following argument. There are 2 distinct groups of animals in the population at sampling period i that should have the same probability of recapture if the model assumptions are true. These are all the animals not seen at i ($N_i - n_i$) and all the animals seen and released at i (R_i) that have z'_i and r_i recaptures, respectively. Therefore

$$\frac{z'_i}{N_i - n_i} = \frac{r_i}{R_i},$$

which on solution for N_i gives eq. (5.5). Note that z'_i is the number of animals not seen at i that are seen later and that

$$z'_i = z_i + \sum_{j=i+1}^k u_j.$$

The survival estimators are simply obtained from the ratio of 2 consecutive population size estimators adjusted for losses on capture

$$\hat{\phi}_i = \frac{\hat{N}_{i+1}}{\hat{N}_i - n_i + R_i} \quad (5.6)$$

and are defined for $i = 1, 2, \dots, k - 2$. Note that bias adjusted estimators can be obtained in a similar way to that described in Section 4.3.

The approximate variance and covariance formulae now simplify to

$$\begin{aligned} \text{var}(\hat{N}_i | N_i) &= [N_i - E(n_i)][N_i - E(n_i) + R_i] \\ &\cdot \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right], \end{aligned} \quad (5.7)$$

$\text{var}(\hat{\phi}_i | \phi_i)$

$$\begin{aligned} &= \phi_i^2 \left\{ \frac{[N_{i+1} - E(n_{i+1})]}{[N_{i+1} - E(n_{i+1}) + R_{i+1}]} \right. \\ &\quad \left. \cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right] \right\}, \end{aligned}$$

$$\begin{aligned} &+ \frac{[N_i - E(n_i)]}{[N_i - E(n_i) + R_i]} \\ &\cdot \left[\frac{1}{E(r_i)} - \frac{1}{R_i} \right] \}, \end{aligned} \quad (5.8)$$

$\text{var}(\hat{\phi}_i)$

$$= \text{var}(\hat{\phi}_i | \phi_i) + \frac{\phi_i(1 - \phi_i)}{N_i - n_i + R_i}, \quad (5.9)$$

and

$$\begin{aligned} \text{covar}(\hat{\phi}_i, \hat{\phi}_{i+1}) &= -\phi_i(\phi_{i+1}) \frac{[N_{i+1} - E(n_{i+1})]}{N_{i+1}} \\ &\cdot \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}} \right]. \end{aligned} \quad (5.10)$$

All other covariance terms are equal to zero.

An analogous goodness-of-fit test to that of the Jolly-Seber model, which was presented in Section 4.5, can be derived. The only change is that in the second test component we need to include an additional column for unmarked animals in the population before i that were captured after $i - 1$. This additional information can be included because no new animals are allowed to move into the population. Hence, we know that any unmarked animals must have survived from the beginning of the study. This goodness-of-fit test will be illustrated in the following example.

In this example we demonstrate the utility of the Deaths Only model with data on juvenile wood ducks (*Aix sponsa*) collected by G. M. Haramis (Haramis and Thompson 1984) at Montezuma Wildlife Refuge, New York, in the summer of 1974. There were 3 sampling periods, each of which used a different trapping procedure. In the first period (mid-May–early Jul), young wood ducks were captured just before leaving their nest boxes and marked with web tags. In the second period (mid-Jul–mid-Aug), the fledged young, which were flightless, were captured using bait traps on the impoundment surrounding the nest boxes. Marked animals were recorded, and unmarked animals received a leg band. In

Table 5.2. Capture–recapture summary statistics for a juvenile wood duck population banded by G. M. Haramis at Montezuma Wildlife Refuge, New York, in 1974.

Period	n_i	m_i	R_i	r_i	z_i	z'_i ^a
1	364		364	113		209
2	196	60	194	50	53	126
3	176	103	176			

^a The notation used here is presented in Table 4.1 except for z'_i . In Section 5.3.1 for the Deaths Only model we defined $z'_i = z_i + \sum_{j=i+1}^k u_j$.

the third period (late Jul–mid-Sep) the young, which were now flying, were captured from an airboat using a long-handled net.

This is an unusual study in that young animals are being sampled, and therefore no recruitment into the population after the first period is possible. It thus forms a good example for the model where only losses to the initial population are possible. The study also is unusual in having 3 distinct capture techniques. Thus independence of samples should reduce the chance of bias due to heterogeneity of capture probabilities. One disadvantage is that each capture period is spread over several weeks resulting in survival rates having to be viewed as pertaining to the interval from the midpoint of 1 period to the midpoint of the next period.

In Table 5.2 the capture–recapture summary statistics are presented for this study. This is followed by the population size and survival estimates for both the Deaths Only model and the Jolly–Seber model in Table 5.3. Let us first consider the population size estimates. Notice as expected that there is a considerable decrease in standard errors (or a gain in precision) when we use the

model allowing no births. Also notice that we can estimate the first population size (N_1) under this model. The survival rate estimates are quite similar under the 2 models and again there is a reduction in the standard error for the model allowing no births.

In Table 5.4 the goodness-of-fit test is presented. In this case the overall test is not significant ($P = 0.09$), but it is in the region where some doubt is cast on the model assumptions. Also notice that the second test component does show significance. We believed that this was a good example to illustrate the Deaths Only model, but, as is often the case, our goodness-of-fit tests suggest the results should be treated with some caution despite the high precision of the estimates.

5.3.2 Births Only Model.—On rare occasions one may have the situation where there are no deaths or emigration for a population. Therefore, the only changes in population size are due to recruitment (births or immigration). In this model the marked population sizes (M_i , $i = 2, \dots, k$) are known quantities, and the survival parameters ($\phi_1, \phi_2, \dots, \phi_{k-1}$) are assumed to be 1. The estimators of population size are the usual Lincoln–Petersen estimators, i.e.,

$$\hat{N}_i = \frac{n_i M_i}{m_i}, \quad (5.11)$$

and are now defined for $i = 2, \dots, k$. The birth number estimators are

$$\hat{B}_i = \hat{N}_{i+1} - (\hat{N}_i - n_i + R_i) \quad (5.12)$$

allowing for losses on capture ($n_i - R_i$) and

Table 5.3. Population and survival estimates^a and approximate standard errors for a juvenile wood duck population banded by G. M. Haramis at Montezuma Wildlife Refuge, New York, in 1974. Both the Deaths Only and the Jolly–Seber models are used.

Period	Deaths Only model				Jolly–Seber model			
	\hat{N}_i	\hat{SE}	$\hat{\phi}_i$	\hat{SE}	\hat{N}_i	\hat{SE}	$\hat{\phi}_i$	\hat{SE}
1	1,033.17	64.95 ^b	0.65	0.080 ^c				
2	677.76	71.18			848.22	137.00	0.72	0.100
3								

^a Bias adjusted estimates are presented.

^b Notice that for the Deaths Only model it is possible to estimate N_1 . This is not true for the more general Jolly–Seber model, which allows Births.

^c \hat{SE} includes binomial variance and uses eq. (5.9).

Table 5.4. Goodness-of-fit test for the Death Only model with the juvenile wood duck data.

	First capture before i	First capture in i		First capture before $i - 1$	First capture in $i - 1$	First capture after $i - 1$
$i = 2$						
Capture in i , released & recaptured	17.00	33.00	Capture in i	0.00	60.00	136.00
Expected value	15.31	34.69	Expected value	0.00	68.78	127.22
Capture in i , released & not recaptured	43.00	103.00	Capture after i , not in i	0.00	53.00	73.00
Expected value	44.69	101.31	Expected value	0.00	44.22	81.78
$\chi^2 = 0.36$, 1 df, $P = 0.70$			$\chi^2 = 4.41$, 1 df, $P = 0.04$			
Overall $\chi^2 = 4.77$, 2 df, $P = 0.09$						

the estimators are defined for $i = 2, \dots, k - 1$.

The approximate variance and covariance formulae now simplify to

$$\text{var}(\hat{N}_i | N_i) = N_i [N_i - E(n_i)] \left[\frac{(N_i - M_i)}{N_i E(m_i)} \right], \quad (5.13)$$

$$\text{var}(\hat{B}_i | B_i) = \text{var}(\hat{N}_{i+1} | N_{i+1}) + \text{var}(\hat{N}_i | N_i), \quad (5.14)$$

and

$$\begin{aligned} \text{cov}(\hat{B}_i, \hat{B}_{i+1}) &= -N_{i+1} [N_{i+1} - E(n_{i+1})] \\ &\cdot \left[\frac{(N_{i+1} - M_{i+1})}{N_{i+1} E(m_{i+1})} \right]. \end{aligned} \quad (5.15)$$

All other covariance terms are equal to zero.

This model was first considered for the special case of no losses on capture by Darroch (1959). Jolly (1965) briefly presents it as a special case of his general model (the Jolly-Seber model). Seber (1982:219) also discusses this model.

5.3.3 Constant Survival and Capture Models.—Jolly (1982) introduced 3 restricted versions of his original model, which seem likely to be of great practical value. These models are appropriate in situations where births and deaths may occur, and where it may be reasonable to assume that survival and/or capture probabilities are constant over the whole experiment. The 3 models, with the Jolly-Seber model included for comparison, can be summarized as follows:

(1) Model A—the Jolly-Seber model, which allows capture and survival probabilities to vary over sampling periods,

(2) Model B—the Constant Survival model, which assumes that the survival probabilities are constant over the whole experiment ($\phi_1 = \phi_2 = \dots = \phi_{k-1}$),

(3) Model C—the Constant Capture model, which assumes that the capture probabilities are constant over the whole experiment ($p_1 = p_2 = p_3 = \dots = p_k$), and

(4) Model D—the Constant Survival and Capture model, which assumes both the survival and capture probabilities are constant over the whole experiment.

Jolly (1982) showed that where the restricted models are reasonable, there can be a large gain in precision of the estimators. Unfortunately, for Models B, C, and D, Maximum Likelihood estimation requires iterative numerical techniques for which a computer program is necessary. Jolly and Dickson (1980) describe such a program (see also POPAN-3, Arnason and Schwarz 1986), and program JOLLY will carry out analyses for all but Model C. Both these programs allow for a variable period between sampling dates, by assuming survival constant per unit of time in Models B and D.

Note that Models D, B, and A form a nested series of increasingly general models, as do D, C, and A. Comparisons between models in either sequence are of

Table 5.5. Capture-recapture summary statistics for roseate tern data collected by Spendelow (1982) on Falkner Island, Connecticut, from 1978 to 1984.

Period	Date	n_t	m_t	R_t	r_t	z_t
1	1978	92		92	34	
2	1979	143	17	143	47	17
3	1980	100	23	100	52	44
4	1981	213	58	212	72	35
5	1982	137	70	137	41	37
6	1983	78	48	78	24	30
7	1984	143	54	143		

interest to determine the model that has fewest parameters and yet adequately describes the data. Program JOLLY provides goodness-of-fit tests to Models D, B, and A, and tests to compare these models. These tests developed by Brownie et al. (1986) are different from those described by Jolly (1982), in that they utilize the data in a more complete manner. The tests of fit in Jolly (1982) do not utilize individual capture-history information and the tests between models do not make proper use of information in the m_i 's and z_i 's (Brownie

et al. 1986). The following example uses output from program JOLLY to illustrate the sequence of Models D, B, and A.

The capture-recapture data in this example are from a study by Spendelow (1982) on roseate terns, *Sterna dougalli*, nesting on Falkner Island, Connecticut. Spendelow's study was directed at a number of aspects of the population ecology of roseate terns, and he began banding adult terns in 1978. Birds were captured on nests, usually a few days before or after hatching occurred, using treadle traps. Trapping was conducted during June, July, and August with most of the captures obtained during mid-June to mid-July.

The data used here cover the period 1978–84 and are summarized in Table 5.5. The individual capture-history information, though not displayed, was available and was used in program JOLLY to compute goodness-of-fit tests. Parameter estimates and estimated standard errors are presented in Table 5.6 for Models A, B, and D. Note that p_k , M_k , and N_k are estima-

Table 5.6. Estimates and approximate standard errors under the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D), for roseate tern data collected by Spendelow (1982) on Falkner Island, Connecticut, from 1978 to 1984.

Model and year	$\hat{\phi}_t$	$\hat{S}E$	\hat{p}_t	$\hat{S}E$	\hat{M}_t	$\hat{S}E$	\hat{N}_t	$\hat{S}E$	\hat{B}_t	$\hat{S}E$
Model A—Jolly-Seber model										
1978	0.74	0.137								
1979	0.52	0.075	0.25	0.068	68	11.9	544	141.8	143	95.6
1980	0.90	0.114	0.23	0.049	101	11.3	426	82.7	200	84.8
1981	0.61	0.085	0.36	0.054	160	17.2	581	80.7	20	45.4
1982	0.55	0.102	0.37	0.056	192	23.2	372	51.3	26	23.6
1983			0.34	0.064	143	21.7	230	38.7		
\bar{x}	0.66	0.033	0.31	0.026						
Model B—constant survival model										
1979			0.27	0.060	64	6.36	525	102.0	192	114.8
1980			0.19	0.037	120	8.80	536	84.9	144	76.1
1981	0.67 ^a	0.028	0.42	0.049	146	9.84	517	49.4	42	41.1
1982			0.36	0.042	190	14.1	376	31.8	28	28.1
1983			0.28	0.043	166	16.6	273	29.5	171	39.1
1984			0.40	0.066	135	16.8	358	50.9		
Model D—constant survival and capture model										
1979					58	6.37	466	44.0	55	33.4
1980					111	9.02	360	33.2	383	43.5
1981	0.69 ^a	0.023	0.31 ^a	0.023	166	12.1	667	55.6	-22	36.6
1982					203	15.1	420	35.3	-6	22.9
1983					171	16.7	268	26.2	242	31.5
1984					175	22.7	462	45.7		

^a These estimates pertain to all years in the study because of the assumptions of constant survival and/or capture.

Table 5.7. Tests for the Jolly-Seber model (A), the constant survival model (B), and the constant survival and capture model (D) for the roseate tern data collected by Spendelow (1982) on Falkner Island, Connecticut, from 1978 to 1984.

Test	χ^2	df	P
Goodness-of-fit to Model A	16.58	13	0.22
Goodness-of-fit to Model B	23.53	17	0.13
Goodness-of-fit to Model D	45.69	22	0.00
Model B vs. Model A	6.94	4	0.14
Model D vs. Model B	21.32	5	0.00

ble under Models B and D, but not A. Results of goodness-of-fit tests and tests comparing models are given in Table 5.7

Note that the standard error associated with the estimate of the constant survival ϕ is smaller for Models B and D than the standard error associated with individual Jolly-Seber (or Model A) estimates, ϕ_i . There is a small gain in precision for individual \hat{p}_i with Model B as compared to Model A. Also there generally is a gain in precision for estimates \hat{M}_i , \hat{N}_i , and \hat{B}_i under Models D and B in comparison to Model A. (Jolly (1982) points out that for the \hat{M}_i , \hat{N}_i , and \hat{B}_i , this gain in precision will not be uniformly good, reduction in variances being limited by the binomial variances of $m_i + z_i$ and u_i .)

Precision of estimators is not the only criterion of importance, however, because unless the model is a reasonable approximation to the biological situation, estimators may be very biased. Thus we look at results in Table 5.7 to assess the adequacy of the 3 models. We see that the goodness-of-fit test produces a significantly large chi-square value for Model D, but not for Models B and A. Also the test comparing Model D to B convincingly rejects the simpler Model D in favor of B ($P < 0.001$); thus D is ruled out as a reasonable model. The test comparing Model B with the more general A (or Jolly-Seber model) does not reject B ($P = 0.14$). With the results for goodness-of-fit to B, this suggests that Model B is the appropriate (i.e., simplest, yet adequate) model for these data. Model B point estimates and confidence intervals can be used in describing the population ecology of these birds.

A final comment concerns average es-

timates under the different models. The simple average of the Jolly-Seber estimates ϕ_i is sometimes reported by biologists because it has better precision than the individual ϕ_i . The Model B estimate ϕ is usually close in value to this average and has comparable or better precision. The estimators \hat{N}_i are uncorrelated under the Jolly-Seber model, but tend to be positively correlated under Models B, C, and D, being based on common estimates ϕ and/or \hat{p} . If interest is in estimating the average population size, a simple average of the Jolly-Seber estimates \hat{N}_i may have better precision than an average of the positively correlated Model B, C, or D estimates.

5.4 Generalizations of the Jolly-Seber Model

5.4.1 Temporary Trap Response Models.—Robson (1969), Pollock (1975), and Brownie and Robson (1983) have shown that it is possible to generalize the Jolly-Seber model to allow marking to have a short-term effect (typically 1 period) on survival and capture probabilities. The estimators still have an intuitive form similar to the original Jolly-Seber estimators. However, because these estimators use only a subset of the marked population (those not newly marked), their precision is lower. Tests for this type of short-term effect of marking on survival and capture probabilities also are given and involve simple contingency table tests.

Using formulae in Brownie and Robson (1983), program JOLLY computes estimates of survival and capture probabilities for a model that assumes marking has a 1-period effect on survival. Following terminology in Brownie and Robson (1983), this model is referred to here and in program JOLLY as Model 2. Tests concerning Model 2, given in Brownie and Robson (1983) also are carried out by program JOLLY. These are (1) a test comparing the Jolly-Seber model to the more general Model 2 and (2) a goodness-of-fit test to Model 2. Note that (1), which tests for whether survival differs for new releases and previous releases, is the same as com-

ponent 1 of the goodness-of-fit test to the Jolly-Seber model (Section 4.5) and (2) is related to component 2 of the same test, but involves less automatic pooling. In fact, tests (1) and (2) can be thought of as a partitioning of the goodness-of-fit test to the Jolly-Seber model.

Our example of the use of Model 2 is based on capture-resighting data for semipalmated sandpipers (*Calidris pusilla*) obtained by Marshall A. Howe at Cobscook Bay, Washington County, Maine, during the summer of 1982. Cobscook Bay is a stopover area for semipalmated sandpipers during their southward migration. Sandpipers were caught in mist nets as they returned to roosts at high tide. Birds were banded with U.S. Fish and Wildlife Service (USFWS) bands and marked with individually coded leg flags. Resighting data were obtained by observation through a spotting scope when birds were on tidal flats at low tide and when they were returning to roosts at high tide. An average of approximately 10 work-hours/day were expended on resighting efforts. The entire effort extended from mid-July through August. In this example, we selected a subset of the data, using 29 July 1982 as the first capture period. Subsequent capture and resighting efforts occurred daily, except for a few cases when 2 days elapsed between efforts. Data included in the example covered 15 consecutive daily (or 2-day) sampling periods.

In a similar study on this species in North Dakota, the investigator, D. Lank, suspected that trauma experienced during capture and marking efforts increased probabilities of departing the area immediately following release (Brownie and Robson 1983:448). Howe (pers. commun.) had similar suspicions about effects of his banding operation; therefore we investigated the use of Model 2 with this data set. Model 2 summary statistics are presented in Table 5.8. The fit of the data to the Jolly-Seber model was poor ($\chi^2 = 54.4$, 23 df, $P < 0.001$), and the test of the Jolly-Seber model versus Model 2 indicated strong rejection of the Jolly-Seber model in favor of Model 2 ($\chi^2 = 27.2$, 9 df, $P <$

Table 5.8. Capture-resighting summary statistics for migrating semipalmated sandpipers at Cobscook Bay, Maine, July-August 1982. The data were collected by Marshall A. Howe.

<i>i</i>	<i>u_i</i> ^a	<i>m_i</i>	<i>r_i*</i> ^b	<i>r_i - r_i*</i> ^c	<i>z_i</i>
1	27	0	17	0	0
2	13	4	8	4	13
3	171	6	90	6	19
4	0	6	0	2	109
5	13	33	8	25	78
6	23	43	10	36	68
7	32	24	27	20	90
8	9	53	7	37	84
9	16	49	8	41	79
10	22	17	11	10	111
11	4	24	3	12	108
12	22	73	5	27	50
13	13	61	2	11	21
14	6	15	1	4	19
15	3	24	0	0	0

^a The notation used here is different than that in Brownie and Robson (1983) but is consistent with that in Chapter 4 of this monograph; the notation is that presented in Table 4.1 except for r_i^* defined below.

^b r_i^* is the total number recaptured from the u_i new releases at *i*, assuming no losses on capture.

^c $r_i - r_i^*$ is the total number recaptured from the m_i recaptures released at *i*, assuming no losses on capture.

0.01). The data did not fit Model 2 well (Brownie-Robson goodness-of-fit $\chi^2 = 45.85$, 28 df, $P = 0.02$) either, although 1 time period contributed over one-third of the total chi-square statistic. Because of the strong test results for the Jolly-Seber versus Model 2 comparison, we believe that Model 2 is the best available model for this data set. (It is possible the marking effect lasts more than 1 period.)

Estimated survival and capture probabilities based on Model 2 are presented in Table 5.9. Note that the survival probabilities refer to 1- or 2-day periods in this situation, and the complement of survival essentially represents the probability of departing the migration stopover area rather than actual mortality. Model 2 has a large number of parameters, and survival probability estimates, both for the period immediately following initial release ($\hat{\phi}_i^*$) and subsequent periods ($\hat{\phi}_i$), have large standard errors. Nevertheless, in 7 of 10 sampling periods for which $\hat{\phi}_i$ and $\hat{\phi}_i^*$ could be compared, $\hat{\phi}_i$ exceeded $\hat{\phi}_i^*$. Thus, these estimates tend to support the hypothesis that capture may have induced increased probabilities of departing the area. Of course, capture also may have increased

Table 5.9. Survival and capture probability estimates and approximate standard errors^a for migrating semipalmated sandpipers at Cobscook Bay, Maine, July–August 1982. The data were collected by Marshall A. Howe.

<i>i</i>	ϕ_i^{*b}	$\hat{S}E$	ϕ_i^c	$\hat{S}E$	p_i^d	$\hat{S}E$
1	0.63	0.093				
2	0.62	0.135	1.00	0.000	0.24	0.103
3 ^e					0.24	0.085
4 ^e					0.02	0.013
5	0.69	0.154	0.85	0.092	0.24	0.042
6	0.50	0.126	0.97	0.098	0.35	0.047
7	1.07	0.106	1.05	0.118	0.18	0.037
8	0.87	0.160	0.78	0.078	0.31	0.042
9	0.80	0.251	1.34	0.265	0.34	0.043
10	0.91	0.256	1.07	0.293	0.08	0.025
11	1.27	0.392	0.85	0.196	0.10	0.027
12	0.49	0.218	0.80	0.205	0.35	0.054
13	0.39	0.291	0.46	0.209	0.34	0.084
14					0.17	0.079
15						

^a SE estimates include both sampling and nonsampling variation (Brownie and Robson 1983).

^b Survival probability estimates for new releases at *i*.

^c Survival probability estimates for previously marked animals alive at *i*.

^d Capture probability estimates apply only to marked birds under Model 2.

^e No survival estimates are presented for these periods because the estimated capture probabilities are low and estimates are unreliable.

the probability of death as it is impossible to separate death from emigration in this model.

5.4.2 Cohort Model.—In Chapter 6 we present in detail an extension of the Jolly–Seber model for the case where there are several identifiable age classes with possibly different survival and capture rates. However, in some cases it may not be possible to easily age animals, but age-dependent survival may be strongly suspected (e.g., many passerine bird species). In this section we show that, based on time of initial marking, one has a measure of minimum age, and age specific survival effects can be investigated by treating a group of animals first marked at a particular time as a cohort and carrying out a Jolly–Seber analysis on each cohort separately. Another potential use of this cohort approach is for situations where animals are easily marked as young (e.g., chicks in nests), but adults are hard to capture. If adults can be resighted without capture (e.g., colonial nesting birds), then exact age-specific survival rates can be obtained. There is noth-

Table 5.10. Structure of marked population size estimators^a for a case where there are 5 cohorts and 6 sampling periods using the cohort version of the Jolly–Seber model.

Cohort	Sampling period				
	1	2	3	4	5
1	R_1	$\hat{M}_2^{(1)}$	$\hat{M}_3^{(2)}$	$\hat{M}_4^{(3)}$	$\hat{M}_5^{(4)}$
2		R_2	$\hat{M}_3^{(1)}$	$\hat{M}_4^{(2)}$	$\hat{M}_5^{(3)}$
3			R_3	$\hat{M}_4^{(1)}$	$\hat{M}_5^{(2)}$
4				R_4	$\hat{M}_5^{(1)}$
5					R_5

^a The notation used in this table is different from that used previously in the monograph. The parenthetical superscript indicates the minimum age of the animal. For example, $\hat{M}_4^{(2)}$ represents the estimated number of marked animals at time 4 that are of minimum age 2 (i.e., originally marked at time 2). We use R_i to represent the number of unmarked animals that are captured, marked, and released at time *i*, which is consistent with previous notation.

ing inherent in the standard Jolly–Seber model that requires releases of newly marked animals at each sampling period, although of course there will be a reduction in the number of marked animals in the population due to deaths, so that precision of survival estimates will decline with time. This is analogous to a life table analysis (Seber 1982:393) where the precision of survival estimates for older age classes is poor due to depletion of the initial cohort.

To illustrate the methodology, let us consider an example where we carry out a capture–recapture study for 6 periods (e.g., years). We treat the newly marked animals in each year as a cohort and apply the Jolly–Seber approach to estimating the number of marked animals of each cohort at each time (Table 5.10). We use the superscript to indicate the time since marking (in some cases this will be minimum age of the animal). For example, $\hat{M}_4^{(2)}$ represents the estimated number of marked animals at time 4 that were initially marked 2 periods earlier at time 2 (these animals are of minimum age 2).

From this matrix (Table 5.10) we can obtain the appropriate survival estimators (Table 5.11). The variances and covariances of the survival estimates use the same equations as in Chapter 4. Successive survival estimates within a cohort are correlated, but survival estimates between cohorts are independent because they are based on different animals.

Table 5.11. Structure of survival rate estimators^a for the cohort version of the Jolly-Seber model when there are 5 cohorts and 6 sampling periods.

Cohort	Survival period			
	1	2	3	4
1	$\hat{\phi}_1^{(1)} = \frac{\hat{M}_2^{(1)}}{R_1}$	$\hat{\phi}_2^{(2)} = \frac{\hat{M}_3^{(2)}}{\hat{M}_2^{(1)}}$	$\hat{\phi}_3^{(3)} = \frac{\hat{M}_4^{(3)}}{\hat{M}_3^{(2)}}$	$\hat{\phi}_4^{(4)} = \frac{\hat{M}_5^{(4)}}{\hat{M}_4^{(3)}}$
2		$\hat{\phi}_2^{(1)} = \frac{\hat{M}_3^{(1)}}{R_2}$	$\hat{\phi}_3^{(2)} = \frac{\hat{M}_4^{(2)}}{\hat{M}_3^{(1)}}$	$\hat{\phi}_4^{(3)} = \frac{\hat{M}_5^{(3)}}{\hat{M}_4^{(2)}}$
3			$\hat{\phi}_3^{(1)} = \frac{\hat{M}_4^{(1)}}{R_3}$	$\hat{\phi}_4^{(2)} = \frac{\hat{M}_5^{(2)}}{\hat{M}_4^{(1)}}$
4				$\hat{\phi}_4^{(1)} = \frac{\hat{M}_5^{(1)}}{R_4}$

^a Notation is explained in Table 5.10.

Buckland (1982) obtained similar types of estimators and presented estimates for 2 examples. He pointed out that a particular survival rate is a function of both time since marking and temporal effects (such as weather) and presented analyses that emphasize one or the other.

To illustrate the methodology, we present estimates obtained from a long-term capture-recapture study of black-capped chickadees (*Parus atricapillus*) carried out by G. Loery in Connecticut. A traditional Jolly-Seber analysis was applied to these data by Loery and Nichols (1985), and they were able to show some very interesting temporal changes in the demographic parameters associated with the invasion of another species, the tufted titmouse (*Parus bicolor*). A more detailed presentation of the cohort analysis is given in Loery et al. (1987).

The banding station is located on a sanctuary owned by the White Memorial Foundation in Litchfield, Connecticut. The habitat around the station was primarily second growth deciduous woods interspersed with red pine plantations and 1 small spruce plantation. The chickadees were captured in single and 3-celled potter traps baited with sunflower seeds and suet. On first capture a USFWS numbered leg band was placed on each bird. For the purposes of this analysis a bird was considered as captured if it was seen at least once during the winter period of November, December, and January. The restriction to this period was an effort to ensure

we were dealing only with resident birds. Assuming that most chickadees are hatched by June each year, the individuals were at least 5 months old at first marking. We were interested in estimating annual survival rates for all cohorts banded between 1958 and 1983. From this analysis we hoped to investigate the effect of age (in fact minimum age). We believe that because of the intensive banding effort most of the birds were banded at or close to the minimum possible age.

For simplicity and to emphasize age effects, we present the first 6 survival estimates for each cohort (Table 5.12). However, we wish to emphasize that these estimates apply to different years and that other methods of presentation emphasizing temporal effects are possible. We also have presented the Jolly-Seber estimates, which are based on pooling over all ages, for comparison. Notice that we also have computed unweighted means of estimates and their standard errors for each age and for the Jolly-Seber estimates. These standard errors are a measure of variability based on year-to-year variation in a particular survival rate, and they also include sampling error. Notice that there appears to be a much lower survival rate in the first year, and after that there is some evidence of a drop in survival with increasing minimum age. However, because of the correlation between estimates within cohorts, we develop further analyses that allow for this below.

We used a paired *t* test (Snedecor and

Table 5.12. Survival estimates for cohorts by minimum age for chickadees banded from 1958 to 1981 and recaptured from 1959 to 1983 by Gordon Loery in Litchfield, Connecticut. Jolly-Seber estimates are presented also.

Cohort	Year	Minimum age survival estimates						Jolly-Seber	Slope
		1	2	3	4	5	6		
1	1958	0.44	1.00	1.06	0.88	0.62	1.08	0.90	-0.028
2	1959	0.53	0.74	0.73	0.78	1.10	0.68	0.64	+0.026
3	1960	0.56	1.08	0.66	0.40	1.05	0.76	0.85	-0.026
4	1961	0.36	0.62	0.27	1.00	0.33	0.00	0.57	-0.118
5	1962	0.45	0.89	0.75	0.60	0.56	1.05	0.58	+0.012
6	1963	0.50	0.56	0.18	1.17	0.57	1.00	0.64	+0.127
7	1964	0.55	0.62	0.48	0.76	0.50	0.00	0.59	-0.122
8	1965	0.50	0.51	0.74	0.49	0.42	0.57	0.51	-0.019
9	1966	0.45	0.82	0.63	1.00	1.30	0.31	0.69	-0.034
10	1967	0.31	0.56	0.40	1.00	0.00		0.49	-0.107
11	1968	0.41	0.54	1.00	0.38	0.67	0.50	0.61	-0.042
12	1969	0.33	0.81	0.41	0.33	0.33	0.00	0.54	-0.169
13	1970	0.40	0.60	0.84	0.67	0.40	0.25	0.50	-0.115
14	1971	0.37	0.77	0.71	0.83	0.59	0.62	0.43	-0.042
15	1972	0.64	0.70	0.50	0.60	0.50	1.00	0.75	+0.061
16	1973	0.45	0.47	0.86	0.88	0.52	0.50	0.54	-0.029
17	1974	0.45	0.45	0.51	0.88	0.29	1.00	0.50	+0.088
18	1975	0.39	0.74	0.61	0.72	1.08	0.14	0.50	-0.072
19	1976	0.66	0.64	0.52	0.72	0.67	0.25	0.70	-0.063
20	1977	0.44	0.67	0.78	0.54	0.50		0.54	
21	1978	0.41	0.67	0.63	0.60			0.48	
22	1979	0.45	0.68	0.42				0.63	
23	1980	0.37	0.67					0.55	
24	1981	0.24						0.47	
\bar{x}		0.44	0.69	0.62	0.73	0.60	0.54	0.59	-0.035
\hat{SE}		0.020	0.033	0.047	0.050	0.071	0.088	0.024	0.017

Cochran 1980:86) to compare minimum age-1 survival with minimum age-2 survival for the 23 cohorts where both estimates were available. We found a highly significant ($P < 0.001$) average increase in survival of 0.23 with $\bar{SE} = 0.036$. This should not be surprising because there is only 1 cohort out of 23 for which the year-1 survival estimate was higher than the year-2 survival estimate (Table 5.12). Therefore the more robust sign test (Snedecor and Cochran 1980:138) was also highly significant ($P < 0.001$).

To address the hypothesis that adult survival is constant irrespective of age, we calculated a simple linear regression on the age-2 through age-6 estimates for each of the 19 cohorts with complete data. We used the equation $Y_i = \alpha + \beta X_i + \epsilon_i$, $i = 1, \dots, 6$, where Y_i is the survival estimate, X_i is the age, and α , β are the intercept and slope parameters, respectively. The slope estimate for each cohort is presented in Table 5.12.

We computed the unweighted average slope estimate to be -0.0354 with estimated $SE = 0.0174$ ($P < 0.05$, one-sided t test). This suggests that survival of adult birds decreases about 3.5% for each year of age. Notice that 14 of the 19 slope estimates were negative so that again the sign test (one-tailed) can be used to show a significant decline with age ($P < 0.05$).

We believe that we have shown convincing evidence that black-capped chickadees banded during their first winter have lower survival probabilities than older birds. It is important to remember, however, that the complement of our survival probability $(1 - \phi_i)$ includes both death and permanent emigration (dispersal). The difference in survival between young and adult birds could thus be due to increased mortality in the first year, increased dispersal, or a combination of the 2 processes. There is no way to distinguish between mortality and dispersal in capture-recapture studies unless marked animals can be

trapped at other locations. Ekman (1984) believed that local winter mortality was substantial among willow tits (*Parus montanus*), especially first-year birds, and he found no evidence of emigration in winter. However, we do not have any evidence that can help us assess the contributions of mortality and emigration to the survival difference between first-year and older black-capped chickadees.

We also have shown some of the first evidence that adult survival is a decreasing function of age. Of course the decline may not be linear; therefore our 3.5% decrease is only an approximation. We do not believe dispersal is important for adult birds and view our estimates as true survival rates.

Heterogeneity of capture probabilities between animals is a problem in survival analyses of this type and produces a negative bias. The bias is greatest for the first estimate and then becomes large again towards the end of the chain of estimates (Buckland 1982). It is important to ask whether such heterogeneity could have produced the age-specific mortality patterns we observed. We did not believe so because of the high capture probabilities in this study (i.e., ~0.9 in the past 10 years, 0.5 earlier). To be sure, however, we decided to conduct a detailed simulation study. We considered our population to be about 150 birds with a constant annual survival of 0.7. We then considered our population as consisting of 100 core animals with high capture probability and 50 fringe animals with lower capture probability. We found that over a wide range of capture probabilities the negative biases were negligible when compared to the size of the effects we observed. To illustrate, we present a table of average survival estimates based on 1,000 simulations for a 10-year study where the core group has capture probability of 0.9 and the fringe group has capture probability of 0.1 (Table 5.13). Notice that for this extreme situation there is little or no evidence of lower apparent survival for first-year birds or a decline in apparent survival with age. We expect simulations may have shown these

Table 5.13. Average survival estimates based on simulated data where there is constant survival (0.7) but extreme heterogeneity of capture probabilities (0.9 vs. 0.1 for the 2 groups). A 10-year study with constant population sizes of 100 and 50 for the 2 groups is considered.

Cohort	Survival estimates by age					
	1	2	3	4	5	6
1	0.676	0.699	0.698	0.709	0.696	0.704
2	0.641	0.706	0.700	0.703	0.703	0.701
3	0.638	0.695	0.698	0.703	0.702	0.708
4	0.643	0.701	0.703	0.703	0.704	0.704
5	0.642	0.701	0.704	0.700		
6	0.638	0.703	0.692			
7	0.639	0.700				
8	0.635					
\bar{x}	0.644	0.701	0.699	0.704	0.701	0.704

effects if survival were higher and capture probability lower as in the examples of Buckland (1982).

Band loss increasing with age also could explain the decline in age-dependent survival. However, in this case there is no evidence of band loss. Loery handled many recaptures and found no evidence of wear or of poorly fitting bands (Loery et al. 1987). In longer-lived species or in species with stronger bills (e.g., raptors, gulls), band loss increasing with age could be a significant problem.

6. THE AGE-DEPENDENT MODEL

6.1 Introduction

The Jolly-Seber model makes the assumptions (Section 4.2) that all animals in the population of interest have the same survival probability and capture probability for any period. For some species of animals, there are clearly identifiable age classes that are likely to have very different survival rates and, possibly, different capture rates. Here we discuss a model (Pollock 1981b, Stokes 1984) that allows for such age specificity and demonstrate its practical utility. A comprehensive “user friendly” computer program, JOLLYAGE, for 2 age classes has been written to accompany material in this chapter.

We assume for simplicity of illustration that there is 1 capture period per “year”

for k "years." A "year" is used to represent the period of time an animal remains in a single age class and will not necessarily represent a calendar year. There are $(\ell + 1)$ distinguishable age classes of animals ranging from zero up to ℓ (or more) years of age, and each age class moves forward 1 class each "year." We further assume that each age class has a different capture probability in the i th sample ($p_i^{(0)}, p_i^{(1)}, \dots, p_i^{(\ell)}$) and a different survival probability from the i th to the $(i + 1)$ th sample ($\phi_i^{(0)}, \phi_i^{(1)}, \dots, \phi_i^{(\ell)}$). Also, immigration or emigration can occur for each age class of the population. Thus, when referring to "survival," we really mean those animals that have not died or emigrated. Similarly, when referring to "recruitment" into a particular age class, we really mean the combination of immigrants and survivors from the previous time period that have now entered this age class. We will find that under some circumstances it is possible to separate the 2 groups of "recruits," which is not possible under the Jolly-Seber model (Chapter 4).

6.2 Assumptions and Notation

The following assumptions are required by the age-dependent models:

1. Every animal in a particular age class (v) has the same probability of capture ($p_i^{(v)}$), given that it is alive and present in the population at the time the i th sample is taken ($i = 1, 2, \dots, k$).
2. Every marked animal in a particular age class (v) has the same probability ($\phi_i^{(v)}$) of surviving from sampling period i to sampling period $i + 1$, given that it is alive and present in the population at the time the i th sample is taken ($i = 1, 2, \dots, k - 1$).
3. Marks are not lost during the study, and all marks are correctly reported on capture.
4. All emigration is permanent.
5. All animals are correctly aged.

Except for the incorporation of age-specificity in (1) and (2) and the addition of assumption (5), these assumptions are the

same as those for the basic Jolly-Seber model (see Section 4.2).

The following notation (Table 6.1) is used in this chapter and extends in a natural way the notation presented in Chapter 4 (Table 4.1). We present parameters and statistics. In defining the parameters we note that just before sample i , there are no marked animals of age class 0 ($M_i^{(0)} = 0$) because after 1 "year" they will have moved into the next age class (age = 1). It is necessary to identify marked animals up to age $\ell + 1$ ($M_i^{(\ell+1)}$); these include animals of age at least $\ell + 1$ to estimate the survival rate of the age ℓ animals ($\phi_i^{(\ell)}$) as we shall see in the next section. The population size $N_i^{(\ell)}$ includes animals of age at least ℓ . Also notice that under some circumstances we can separately estimate survivors from previous age classes ($B_i^{1(v)}$) and immigrants ($B_i^{11(v)}$), unlike in the Jolly-Seber model. This will be considered in more detail in the next section. The only new statistic defined is $T_i^{(v)}$, the number of marked animals of age v at time i that are caught at or after time i . It follows that $T_i^{(v)} = r_{i-1}^{(v-1)} + z_{i-1}^{(v-1)}$.

6.3 Point Estimation

Except for some simple extensions, the estimators have a simple intuitive structure similar to the Jolly-Seber estimators. The marked population sizes are estimated by

$$\hat{M}_i^{(v)} = m_i^{(v)} + \frac{R_i^{(v)} z_i^{(v)}}{r_i^{(v)}} \quad (6.1)$$

for $v = 1, 2, \dots, \ell - 1$,

$$\hat{M}_i^{(\ell)} + \hat{M}_i^{(\ell+1)} = m_i^{(\ell)} + \frac{R_i^{(\ell)} z_i^{(\ell)}}{r_i^{(\ell)}}, \quad (6.2)$$

and

$$\hat{M}_i^{(\ell)} = \frac{T_i^{(\ell)}}{\frac{T_i^{(\ell)}}{T_i^{(\ell)} + T_i^{(\ell+1)}} \cdot (\hat{M}_i^{(\ell)} + \hat{M}_i^{(\ell+1)})}. \quad (6.3)$$

There is a similar expression for $\hat{M}_i^{(\ell+1)}$ and the estimators are only defined for $i = 2, \dots, k - 1$. The intuition underlying eqs.

Table 6.1. Notation for the age-dependent extension of the Jolly-Seber model described in detail in Chapter 6 of this monograph.

PARAMETERS	
$M_i^{(v)}$	= the number of marked animals of age v in the population just before the i th sample ($v = 1, \dots, \ell + 1$; $M_i^{(0)} \equiv 0$; $i = 2, \dots, k$).
$N_i^{(v)}$	= the number of animals of age v in the population just before the i th sample ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k$).
$\phi_i^{(v)}$	= the probability that an animal of age v , alive at time i , survives until time $(i + 1)$ ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k - 1$).
$p_i^{(v)}$	= the probability that an animal of age v , alive at time i , is captured in the i th sample ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k$).
$B_i^{1(v)}$	= the number of new animals of age v present at time $(i + 1)$ that survived from time i when they were age $(v - 1)$, ($v = 1, \dots, \ell$; $i = 1, \dots, k - 1$).
$B_i^{11(v)}$	= the number of animals immigrating between times i and $(i + 1)$ that are present and of age v at time $(i + 1)$, ($v = 1, \dots, \ell$; $i = 1, \dots, k - 1$).
$B_i^{(v)}$	= the total number of "recruits" to the population between times i and $(i + 1)$ that are present and of age v at time $(i + 1)$. (Note: $B_i^{(v)} = B_i^{1(v)} + B_i^{11(v)}$ and $v = 1, \dots, \ell$; $i = 1, \dots, k - 1$).
STATISTICS	
$m_i^{(v)}$	= the number of marked animals of age v captured in the i th sample ($v = 1, \dots, \ell$; $i = 2, \dots, k$).
$n_i^{(v)}$	= the number of animals of age v captured in the i th sample ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k$).
$R_i^{(v)}$	= the number of animals of age v released after the i th sample ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k - 1$).
$r_i^{(v)}$	= the number of the $R_i^{(v)}$ that are captured again at least once after the i th sample ($v = 0, 1, \dots, \ell$; $i = 1, \dots, k - 1$).
$z_i^{(v)}$	= the number of marked animals of age v caught before time i , not caught at time i , and caught again later ($v = 0, 1, \dots, \ell$; $i = 2, \dots, k - 1$).
$T_i^{(v)}$	= the number of marked animals of age v at time i that are caught at time i or after time i ($v = 1, \dots, \ell + 1$; $i = 2, \dots, k$).

(6.1) and (6.2) is exactly the same as that described for eq. (4.5) for the standard Jolly-Seber model. Eq. (6.3) is then obtained by multiplying the estimated number of marked animals at i that are \geq age ℓ at time i ($\hat{M}_i^{(\ell)} + \hat{M}_i^{(\ell+1)}$) by the estimated proportion of animals in this group that are exactly age ℓ at time i ($T_i^{(\ell)}/[T_i^{(\ell)} + T_i^{(\ell+1)}]$).

The total population sizes are estimated by

$$\hat{N}_i^{(v)} = \frac{n_i^{(v)} \hat{M}_i^{(v)}}{m_i^{(v)}} \quad (6.4)$$

for $v = 1, 2, \dots, \ell - 1$,

and

$$\hat{N}_i^{(\ell)} = \frac{n_i^{(\ell)} (\hat{M}_i^{(\ell)} + \hat{M}_i^{(\ell+1)})}{m_i^{(\ell)}}. \quad (6.5)$$

It is not possible to estimate the number of young animals, $N_i^{(0)}$, because $M_i^{(0)} = 0$ and all the above estimators are only defined for $i = 2, \dots, k - 1$. If there were > 1 capture period/year, then it would be possible to estimate the number of young

animals because the number of marked young animals would be > 0 for all except the first capture period each year (Pollock and Mann 1983, Stokes 1984).

The "survival" rates are estimated by

$$\hat{\phi}_i^{(v)} = \frac{\hat{M}_{i+1}^{(v+1)}}{\hat{M}_i^{(v)} - m_i^{(v)} + R_i^{(v)}} \quad (6.6)$$

for $v = 0, 1, \dots, \ell - 1$,

and

$$\hat{\phi}_i^{(\ell)} = \frac{\hat{M}_{i+1}^{(\ell+1)}}{\hat{M}_i^{(\ell)} + \hat{M}_i^{(\ell+1)} - m_i^{(\ell)} + R_i^{(\ell)}}. \quad (6.7)$$

Notice the need to estimate $M_{i+1}^{(\ell+1)}$ to be able to estimate $\phi_i^{(\ell)}$ as discussed earlier and also that all estimators are only defined for $i = 1, \dots, k - 2$. In some experiments resighting of marked animals without capture is used, and then survival rates can be estimated but not population sizes because we do not have marked to total animal ratios available.

The capture probabilities can be estimated by

$$\hat{p}_i^{(v)} = \frac{m_i^{(v)}}{\tilde{M}_i^{(v)}} \quad (6.8)$$

for $v = 1, \dots, \ell - 1$,

and

$$\hat{p}_i^{(\ell)} = \frac{m_i^{(\ell)}}{\tilde{M}_i^{(\ell)} + \tilde{M}_i^{(\ell+1)}}. \quad (6.9)$$

It is not possible to estimate $p_i^{(0)}$ because $M_i^{(0)} = 0$ and the above estimators are only defined for $i = 2, \dots, k - 1$.

The “birth” numbers are estimated by

$$\hat{B}_i^{1(v)} = \hat{\phi}_i^{(v-1)} \times (\hat{N}_i^{(v-1)} - n_i^{(v-1)} + R_i^{(v-1)}), \quad (6.10)$$

$$\begin{aligned} \hat{B}_i^{11(v)} &= \hat{N}_{i+1}^{(v)} - \hat{\phi}_i^{(v-1)} \times (\hat{N}_i^{(v-1)} - n_i^{(v-1)} \\ &\quad + R_i^{(v-1)}), \end{aligned} \quad (6.11)$$

$v = 2, \dots, \ell - 1$,

$$\begin{aligned} \hat{B}_i^{(\ell)} &= \hat{N}_{i+1}^{(\ell)} - \hat{\phi}_i^{(\ell)} \times (\hat{N}_i^{(\ell)} - n_i^{(\ell)} + R_i^{(\ell)}), \\ & \end{aligned} \quad (6.12)$$

$$\begin{aligned} \hat{B}_i^{1(\ell)} &= \hat{\phi}_i^{(\ell-1)} \times (\hat{N}_i^{(\ell-1)} - n_i^{(\ell-1)} + R_i^{(\ell-1)}), \\ & \end{aligned} \quad (6.13)$$

and

$$\begin{aligned} \hat{B}_i^{11(\ell)} &= \hat{N}_{i+1}^{(\ell)} - \hat{\phi}_i^{(\ell)} \times (\hat{N}_i^{(\ell)} - n_i^{(\ell)} + R_i^{(\ell)}) \\ &\quad - \hat{\phi}_i^{(\ell-1)} \times (\hat{N}_i^{(\ell-1)} - n_i^{(\ell-1)} + R_i^{(\ell-1)}). \end{aligned} \quad (6.14)$$

All estimators are only defined for $i = 2, \dots, k - 2$. If there are only 2 age classes ($\ell = 1$) then only eq. (6.12) is defined, and it is not possible to separate the 2 groups of recruits into the survivors from the previous age and the immigrants. If there are 3 or more age classes ($\ell \geq 2$), then it is possible to separately estimate both classes of recruits. We discuss separation of types of recruits further in Chapter 7 where it

is possible to do more because the young population size ($N_i^{(0)}$) is estimable.

Pollock and Mann (1983) modified the above MLE's and presented the following approximately unbiased estimators:

$$\tilde{M}_i^{(v)} = m_i^{(v)} + \frac{(R_i^{(v)} + 1)z_t}{(r_i^{(v)} + 1)} \quad (6.15)$$

for $v = 1, 2, \dots, \ell - 1$,

$$\begin{aligned} \tilde{M}_i^{(\ell)} + \tilde{M}_i^{(\ell+1)} &= m_i^{(\ell)} + \frac{(R_i^{(\ell)} + 1)z_i^{(\ell)}}{(r_i^{(\ell)} + 1)}, \end{aligned} \quad (6.16)$$

$$\begin{aligned} \tilde{M}_i^{(\ell)} &= \frac{T_i^{(\ell)}}{T_i^{(\ell)} + T_i^{(\ell+1)}} \\ &\quad \cdot (\tilde{M}_i^{(\ell)} + \tilde{M}_i^{(\ell+1)}), \end{aligned} \quad (6.17)$$

$$\tilde{N}_i^{(v)} = \frac{(n_i^{(v)} + 1)\tilde{M}_i^{(v)}}{(m_i^{(v)} + 1)} \quad (6.18)$$

for $v = 1, 2, \dots, \ell - 1$,

$$\tilde{N}_i^{(\ell)} = \frac{(n_i^{(\ell)} + 1)(\tilde{M}_i^{(\ell)} + \tilde{M}_i^{(\ell+1)})}{(m_i^{(\ell)} + 1)}, \quad (6.19)$$

$$\tilde{\phi}_i^{(v)} = \frac{\tilde{M}_{i+1}^{(v+1)}}{\tilde{M}_i^{(v)} - m_i^{(v)} + R_i^{(v)}} \quad (6.20)$$

for $v = 0, 1, \dots, \ell - 1$,

and

$$\tilde{\phi}_i^{(\ell)} = \frac{\tilde{M}_{i+1}^{(\ell+1)}}{\tilde{M}_i^{(\ell)} + \tilde{M}_i^{(\ell+1)} - m_i^{(\ell)} + R_i^{(\ell)}}. \quad (6.21)$$

Unbiased versions of the MLE's of the capture probabilities ($p_i^{(v)}$) and the “birth” numbers ($B_i^{1(v)}$, $B_i^{11(v)}$, and $B_i^{(\ell)}$) follow from eqs. (6.8–6.14) by replacing MLE's by their unbiased forms. Large sample variances and covariances of the estimators can be obtained using a similar approach to that used for the Jolly-Seber model in Chapter 4. They all have been implemented in program JOLLYAGE but are not presented here for the sake of brevity and readability.

Table 6.2. General form of the first set of contingency tables testing for a difference between survival and capture probabilities of animals of different ages.*

Age class	Recaptured after sample i	Not recaptured after sample i	Animals released in sample i
0	$r_i^{(0)}$	$R_i^{(0)} - r_i^{(0)}$	$R_i^{(0)}$
1	$r_i^{(1)}$	$R_i^{(1)} - r_i^{(1)}$	$R_i^{(1)}$
.	.	.	.
.	.	.	.
.	.	.	.
ℓ	$r_i^{(\ell)}$	$R_i^{(\ell)} - r_i^{(\ell)}$	$R_i^{(\ell)}$
Overall	r_i	$R_i - r_i$	R_i

* This test is derived by Pollock (1981b) and described by Pollock and Mann (1983).

6.4 Testing for Age-dependence of Survival and Capture Rates

It is important to be able to test whether survival and capture rates are different between age categories. Pollock (1981b) showed that this is possible using a series of contingency table chi-square tests based on sufficient statistics. For each of the first $(k - 1)$ samples, we have an $(\ell + 1) \times 2$ contingency table of the form shown in Table 6.2. Each table corresponds to a particular sample period (i) and gives rise to an approximate chi-square statistic with ℓ degrees of freedom. In effect we are comparing the recapture rates of the $(\ell + 1)$ different age classes of animals.

For each of the samples 2 to $k - 1$, we have an additional $\ell \times 2$ contingency table of the form shown in Table 6.3. Note that there are no marked animals of age 0, and that this series of tables is used only if there are > 2 age classes. Each table gives rise to an approximate chi-square statistic with $(\ell$

– 1) degrees of freedom. Actually we are comparing the capture rates of known groups of marked animals of each age class.

These chi-square statistics are conditionally independent of each other, and therefore we can obtain an overall chi-square test statistic with $\ell(k - 1) + (\ell - 1)(k - 2)$ degrees of freedom by adding the individual chi-square statistics. In some cases it may be necessary to pool some rows in the tables in which case the degrees of freedom will be reduced.

The computer program JOLLYAGE implementing the age-specific model handles only 2 age classes; therefore only the first set of contingency tables (Table 6.2) is used. A series of 2×2 tables is generated. When the expected value of any cell is < 2 , the table is omitted from the test and the number of degrees of freedom for the overall test statistic is reduced by 1.

6.5 Goodness-of-fit Test

As for the Jolly-Seber model, the age-specific model of Pollock (1981b) makes a number of strong assumptions (Section 6.2) that should be tested whenever possible. Pollock developed a goodness-of-fit test for the age-specific model, and we describe it here for the first time. Although the test was developed for the general case of $\ell + 1$ age classes, the special case of 2 ages ($\ell = 1$) is discussed here and implemented in program JOLLYAGE.

This test is very similar to the Jolly-Seber goodness-of-fit test presented in Section 4.5 and can be best understood by referring to Section 6.7, Example 1. The test for the

Table 6.3. General form of the second set of contingency tables testing for a difference between survival and capture probabilities of animals of different ages.*

Age class	Captured in sample i	Not captured in sample i	Marked animals captured in or after i
1	$m_i^{(1)}$	$T_i^{(1)} - m_i^{(1)}$	$T_i^{(1)}$
2	$m_i^{(2)}$	$T_i^{(2)} - m_i^{(2)}$	$T_i^{(2)}$
.	.	.	.
.	.	.	.
ℓ	$m_i^{(\ell)}$	$T_i^{(\ell)} + T_i^{(\ell+1)} - m_i^{(\ell)}$	$T_i^{(\ell)} + T_i^{(\ell+1)}$
Overall	m_i	$T_i - m_i$	T_i

* This test is derived by Pollock (1981b) and described by Pollock and Mann (1983).

age-specific model has 2 components, the first of which includes $k - 2$ contingency tables. The columns of these contingency tables correspond to the different previous capture histories of animals captured as adults (age class 1) in sampling period i (for $i = 2, \dots, k - 1$) and then released. We recommend pooling to form 3 columns: animals first captured as adults before sampling period i , animals first captured as young (age class 0) before i , and animals captured for the first time in period i as adults (note that the test involves animals that are adults at i and that there is thus no column for animals first caught as young at time i). The 2 rows of these tables correspond to animals that are and are not captured again at some sampling period $>i$, and these require no pooling. The pooling thus results in a 2×3 contingency table for each sampling period ($i = 2, 3, \dots, k - 1$).

The contingency tables of the second test component have columns corresponding to the different previous capture histories of animals captured either at sampling period i or a later period, $>i$. We recommend pooling to form 4 columns: animals first caught as adults (age class 1) at some sampling period before $i - 1$ (i.e., $< i - 1$), animals first caught as young (age class 0) at some period before $i - 1$, animals first caught as adults in period $i - 1$, and animals first caught as young in period $i - 1$. The 2 rows of these tables correspond to animals that are captured in i and animals that are not caught in i but are caught in some later period, $>i$. The pooling thus results in a 2×4 contingency table for each sampling period i ($i = 3, 4, \dots, k - 1$). Only a 2×2 table is available for $i = 2$, as there can be no animals caught before period 1 ($i - 1$) in this instance.

Expected cell values are sometimes small even after the recommended pooling. If an expected cell value is < 2 , we recommend pooling the column containing this cell with the column containing the next smallest expected cell value. This procedure is repeated until all expected cell values are ≥ 2 . One degree of freedom is lost each time 2 columns are pooled. If cell

pooling results in only 1 remaining column, that contingency table is not used in the computation of the overall test statistic. This overall statistic is computed by summing the independent chi-square statistics and their associated degrees of freedom. This entire procedure is conducted by program JOLLYAGE.

6.6 Models with Constant Survival or Capture Rates

To conclude the discussion of age-dependent models we consider models that require survival and capture probabilities to be constant over time. As stated in Sections 5.1 and 5.3, the reason for considering such reduced-parameter models is the gain in precision of estimators that results when the number of parameters to be estimated is decreased.

The simplest reduced-parameter, age-dependent models involve only 2 age classes (0 and 1 or young and adult) and require that the time to mature from age class 0 to 1 is the same as the interval between sampling occasions (usually 1 year). Brownie et al. (1986) developed 2 such models, which can be thought of as generalizations of Models B and D of Section 5.3.3 to the case where young and adult animals are tagged each year. These are referred to as Models B2 and D2 following Jolly's terminology (Section 5.3.3). Assumptions concerning survival and capture probabilities for these models are summarized below with Pollock's (1981b) age-dependent model included for completeness.

1. Model A2, or Pollock's (1981b) generalization of the Jolly-Seber model with $\ell = 1$, assumes time-specific young and adult survival rates ($\phi_i^{(0)}$) and ($\phi_i^{(1)}$) and time-specific adult capture probabilities ($p_i^{(1)}$).
2. Model B2 assumes constant young and adult survival rates ($\phi_i^{(0)} = \phi^{(0)}$, $\phi_i^{(1)} = \phi^{(1)}$, $i = 1, \dots, k - 1$) and time-specific capture probabilities ($p_i^{(1)}$).
3. Model D2 assumes constant young and adult survival ($\phi_i^{(0)} = \phi^{(0)}$, $\phi_i^{(1)} = \phi^{(1)}$, $i =$

$1, \dots, k - 1$) and constant capture probabilities ($p_i^{(1)} = p^{(1)}, i = 2, \dots, k$).

A specialized computer routine is needed to carry out the data analysis for Models B2 and D2. The estimation procedures and tests to aid in model selection are described in Brownie et al. (1986), with the detailed formulae required to develop corresponding computer algorithms given in entirety in Brownie (1985). These algorithms have been incorporated in program JOLLYAGE, which (in addition to performing analyses described in Sections 6.3–6.5) will produce estimates for Models B2 and D2, tests of fit to Models B2 and D2, and tests comparing D2 with B2, D2 with A2, and B2 with A2.

Models D2, B2, and A2 form an increasingly general series. For a given data set, results of the tests in output from program JOLLYAGE should be used to determine the simplest model that adequately describes the data. Inferences are then based on estimates produced under the chosen model. There will of course be data sets where not even the most general of these models (i.e., Model A2) is adequate (e.g., because of heterogeneity or trap response or capture probabilities). Unless the data can be partitioned into more homogeneous subgroups, to be analyzed separately, the methods of this chapter will not apply.

6.7 Examples

Example 1 is from a study on giant Canada geese (*Branta canadensis maxima*) carried out by Raveling (1978) and originally presented by Pollock (1981b). Individually identifiable plastic neck collars were placed on young and adult geese captured on their breeding grounds at Marshy Point Goose Sanctuary on Lake Manitoba in the summers of 1968, 1969, and 1970. Collared birds were resighted in subsequent years on both the breeding and wintering grounds.

To illustrate the importance of the age-dependent model, we use the female resighting data on the breeding grounds (Table 6.4). We consider only 2 age classes,

young (age = 0) and adults (age 1 year or more), because there were not enough subadults (age 1 year) captured to consider them separately.

Obviously, only collared birds can be resighted; therefore estimation of survival rates is the object. Table 6.5 presents the necessary summary statistics. All calculations were done using the program JOLLYAGE. We first tested for age-dependence of survival and capture probabilities (Table 6.6) and found strong evidence of an age-dependent effect ($\chi^2 = 19.43, 3 \text{ df}, P < 0.01$); therefore there is a need for the class of age-dependent models described in this chapter. We next carried out the general goodness-of-fit test to Model A2 described in Section 6.5 (Table 6.7) and found no evidence that the data do not fit the age-dependent model A2 ($\chi^2 = 4.38, 7 \text{ df}, P = 0.74$). We concluded that the class of age-dependent models is appropriate for this data set.

Although the class of age-dependent models is appropriate in general, we still needed to decide whether any of the constant parameter models described in Section 6.6 could be used. In Table 6.8 we present point estimates and approximate standard errors of survival rates (young and adult) and capture rates (adult) for Models A2, B2, and D2. Note that survival here means that a bird survived the year and returned to the breeding grounds. In this study we have good precision on our estimates, because there is a very high probability (>90%) of resighting geese that are still alive and present on the breeding grounds. Note that under Models B2 and D2, precision for the single age-specific survival rate estimates is appreciably better than for individual Model A2 estimates $\hat{\phi}_i^{(0)}$ and $\hat{\phi}_i^{(1)}$, and slightly better than for the means

$$\bar{\phi}^{(0)} = \sum_{i=1}^2 \hat{\phi}_i^{(0)} \div 2,$$

$$\bar{\phi}^{(1)} = \sum_{i=1}^2 \hat{\phi}_i^{(1)} \div 2.$$

Values of the Model B2 estimates are close

Table 6.4. Capture-history data for female Canada geese first captured as young or adults at Marshy Point, Manitoba, 1968–70 and described in Raveling (1978).

Year							
1		2		3		4	
Young	Adults	Young	Adults	Young	Adults	Young	Adults
$R_1 = 129$	67	$X_{11}^a = 67$	47	$X_{111} = 34$	29	$X_{1111} = 17$	18
				$X_{101} = 2$	0	$X_{1011} = 1$	0
		$R_{01} = 190$	54	$X_{011} = 83$	31	$X_{1101} = 2$	1
				$X_{001} = 170$	50	$X_{1001} = 3$	0
						$X_{0111} = 40$	15
						$X_{0101} = 6$	2
						$X_{0001} = 60$	27

^a In this example, all recaptures are by sighting neck-collar numbers, and thus there are no "losses on capture." This means $X_{11} = R_{11}$, etc. To emphasize the notation, $X_{101} = 2$ is the number of birds collared as young in year 1, not seen in year 2, and resighted in year 3.

to the Model A2 mean estimates $\bar{\phi}^{(0)}$ and $\bar{\phi}^{(1)}$, but there is less agreement between the D2 and A2 estimates.

To determine which estimates to use, we examined results of tests in Table 6.9. Goodness-of-fit tests show agreement between model and data for A2 and B2 and an outcome significant at the 10% level for Model D2. The test of B2 against A2 failed to reject the simpler B2, but the test of D2 versus B2 convincingly rejected D2 ($P = 0.004$). Thus both B2 and A2 are satisfactory, but D2 is too restrictive. We selected B2 as being the simplest yet adequate model for these data.

The estimates in Table 6.8 have not been adjusted for collar loss, which is estimated to occur at a rate of about 25%/year (with a large SE of 5%). More recent neck-collar studies probably have lower loss rates. Adjusted survival rates can be obtained by dividing the unadjusted rate by the probability a goose will still have its collar. For Model B2 we obtain adjusted survival rates of $0.52 \div 0.75 = 0.69$ for young and $0.68 \div 0.75 = 0.91$ for adults. As expected the

young have much lower survival rates than the adults. The large sample variances of the adjusted survival rates can be obtained from the equation given in Pollock (1981b), which is

$$\text{var}(\hat{\phi}_i^{(v)*}) = (\phi_i^{(v)*})^2 + \left\{ \frac{\text{var}(\hat{\phi}_i^{(v)})}{(\phi_i^{(v)})^2} + \frac{\text{var}(\hat{\delta})}{(1 - \delta)^2} \right\}, \quad (6.22)$$

with $\phi_i^{(v)*}$, the adjusted survival rate, $\phi_i^{(v)}$, the unadjusted survival rate, and δ , the collar loss rate per year. For young the standard error is 0.060; for adults it is 0.073. Notice that these standard errors are larger than for the unadjusted rates (0.060 vs. 0.029 and 0.073 vs. 0.031, respectively) due to the imprecision of the collar loss estimate.

In Example 2, Mann (1980) used capture-recapture techniques to study northern pike (*Esox lucius*) on the River Frome,

Table 6.6. Contingency chi-square test for age-dependent survival and capture probabilities, female Canada geese, Marshy Point, Manitoba, 1968–70. The data were first described by Raveling (1978).

i	Statistic ^a						
	$R_i^{(0)}$	$r_i^{(0)}$	$T_i^{(1)}$	$R_i^{(1)}$	$r_i^{(1)}$	$T_i^{(2)}$	$m_i^{(1)}$
1	129	72	67	47			
2	190	89	72	168	99	47	114
3	170	60	89	229	118	104	179
						14	

^a Notation is defined in Table 6.1.

i	Contingency table		Test statistic		
	$r_i^{(0)} / R_i^{(1)}$	$R_i^{(0)} - r_i^{(0)} / R_i^{(1)} - r_i^{(1)}$	χ^2	df	P
1	72	57	3.80	1	0.05
	47	20			
2	89	101	5.22	1	0.02
	99	69			
3	60	110	10.41	1	<0.01
	118	111			
Overall test statistic		19.43	3	<0.01	

Table 6.7a. Contingency table goodness-of-fit test for the age-dependent model for female Canada geese, Marshy Point, Manitoba, 1968–70 (Raveling 1978). First component.^a

	Adults first capture before i	Young first capture before i	Adults first capture in i
$i = 2$			
Capture in i and recaptured	30.00	36.00	33.00
Expected value	27.70	39.48	31.82
Capture in i and not recaptured	17.00	31.00	21.00
Expected value	19.30	27.52	22.18
$\chi^2 = 1.32$, 2 df, $P = 0.52$			
$i = 3$			
Capture in i and recaptured	33.00	58.00	27.00
Expected value	30.92	61.32	25.76
Capture in i and not recaptured	27.00	61.00	23.00
Expected value	29.08	57.68	24.24
$\chi^2 = 0.78$, 2 df, $P = 0.68$			
$\chi^2 = 2.10$, 4 df, $P = 0.72$			
Overall $\chi^2 = 4.38$, 7 df, $P = 0.74$			

^a Table contains contingency table entries after pooling.

Dorset, England, between the winters of 1971–72 and 1978–79. Fish were caught each winter (Nov–Mar) using electrofishing techniques. A numbered, metal tag was attached to the maxilla of each fish for identification. Tag loss was estimated to be approximately 0.095 ($\bar{S}E = 0.027$) per year.

Table 6.8. Point estimates and approximate standard errors (in parentheses) of survival and capture rates under Models A2, B2, and D2 for the female Canada geese banded at Marshy Point, Manitoba, 1968–70 and described by Raveling (1978).

Model	Year	Adult survival rates ^a	Young survival rates ^a	Adult capture rates
A2	$\hat{\phi}_i^{(1)}$	$\hat{\phi}_i^{(0)}$	$\hat{p}_i^{(1)}$	
	1968	0.72 (0.058)	0.57 (0.046)	0.93 (0.030)
	1969	0.63 (0.042)	0.50 (0.040)	0.87 (0.033)
B2	Mean	0.68 (0.035)	0.54 (0.030)	
	$\hat{\phi}^{(1)}$	$\hat{\phi}^{(0)}$	$\hat{p}_i^{(1)}$	
	Overall	0.68 (0.031)	0.52 (0.029)	0.94 (0.026)
D2				0.85 (0.035)
	$\hat{\phi}^{(1)}$	$\hat{\phi}^{(0)}$	$\hat{p}_i^{(1)}$	0.73 (0.053)
Overall		0.62 (0.025)	0.49 (0.026)	0.88 (0.023)

^a Survival rate estimates not adjusted for neck-collar loss (see Section 6.7).

The relevant data for this analysis are the capture histories for individual fish. For these histories, we only need information on whether a fish was captured at least once in a given winter. Young of the year fish could not be marked with the metal tags and were not considered in the analysis. We used 2 age classes: fish of age 1 year ($v = 0$) and fish of age at least 2 years ($v = 1$). It was suspected a priori that older fish would have higher capture probabilities (because of the size-selective nature of electrofishing) and higher survival probabilities than the younger fish, and

Table 6.7b. Contingency table goodness-of-fit test for the age-dependent model for female Canada geese, Marshy Point, Manitoba, 1968–70 (Raveling 1978). Second component.^a

	Adults first capture before $i - 1$	Young first capture before $i - 1$	Adults first capture in $i - 1$	Young first capture in $i - 1$
$i = 2$				
Capture in i	0.00	0.00	47.00	67.00
Expected value	0.00	0.00	45.03	68.97
Capture after i , not in i	0.00	0.00	0.00	5.00
Expected value	0.00	0.00	1.97	3.03
$\chi^2 = 0.00$, 0 df, $P = 1.00$				
$i = 3$				
Capture in i	29.00	36.00	31.00	83.00
Expected value	27.82	38.03	30.61	82.54
Capture after i , not in i	1.00	5.00	2.00	6.00
Expected value	2.18	2.97	2.39	6.46
$\chi^2 = 2.28$, 3 df, $P = 0.52$				
$\chi^2 = 2.28$, 3 df, $P = 0.52$				
Overall $\chi^2 = 4.38$, 7 df, $P = 0.74$				

^a Table contains contingency table entries after pooling.

Table 6.9. Results of goodness-of-fit tests and tests comparing models for the female Canada geese banded at Marshy Point, Manitoba 1968–70 and studied by Raveling (1978).

Model	Goodness-of-fit test			Tests between models			
	x ²	df	P	Models	x ²	df	P
A2	4.38	7	0.74	B2 vs. A2	3.92	3	0.270
B2	8.30	10	0.60	D2 vs. B2	10.96	2	0.004
D2	19.23	12	0.08	D2 vs. A2	14.85	5	0.011

that the age-specific model would thus be needed for the proper analysis of the data (Pollock and Mann 1983). The necessary summary statistics are presented in Table 6.10.

The contingency table test statistic for age-dependent capture and survival probabilities was not significant ($P = 0.43$) (Table 6.11). This is surprising, as the survival probability estimates for young fish were lower than those for adults in all of the 6 years for which they could be estimated under Model A2 (Table 6.12). The contingency table test results of Table 6.11 may thus reflect low power because of the small sample sizes rather than a true lack of age dependence. This possibility was investigated by computing $r_i^{(v)} \div R_i^{(v)}$ (the estimated probability of capturing a fish of age v after sampling period i , given that the fish was alive and in the population immediately after release in period i). As shown in Table 6.11, 6 of the 7 values of $r_i^{(v)} \div R_i^{(v)}$ were larger for adults than for young fish. If the true probabilities were equal for young and adult fish, the binomial

Table 6.11. Contingency chi-square test for age-dependent survival and capture probabilities for northern pike tagged in the Frome River, Dorset, England, 1971–79 (Mann 1980).

i	Contingency table		Test statistic			$r_i^{(0)}/R_i^{(0)a}$
	$r_i^{(0)}$	$R_i^{(0)} - r_i^{(0)}$	x^2	df	P	
1	6	14	0.11	1	0.74	0.30
	10	19				0.34
2	4	25	0.69	1	0.41	0.14
	5	17				0.23
3	3	18	3.68	1	0.06	0.14
	11	17				0.39
4	4	25	0.46	1	0.50	0.14
	5	19				0.21
5	3	8	0.08	1	0.78	0.27
	8	17				0.32
6	13	34	0.54	1	0.46	0.28
	11	20				0.35
7	4	18	1.43	1	0.23	0.18
	3	35				0.08
Overall test statistic		6.98	7	0.43		

^a This denotes the estimated probability of capturing a fish of age v after sampling period i , given that the animal was alive and in the population immediately after release in period i ($v = 0$ or 1).

mial probability of obtaining a result this extreme is approximately 0.06. We conclude that there is evidence of age-specificity of survival and capture probabilities in this data set, and that the class of age-dependent models is more appropriate for these data than the Jolly-Seber model (Pollock and Mann 1983).

Although we believe that the class of age-dependent models is appropriate, we still need to decide whether any of the constant parameter models described in Section 6.6 could be used. This is especially relevant here because the numbers of recoveries ($r_i^{(0)}$ and $r_i^{(1)}$) are so small (Table 6.10). Table 6.12 contains estimates and standard errors for Models A2, B2, and D2. Table 6.13 contains results of the various tests outlined in Section 6.6.

The tests indicate no reason to reject Model B2 or D2. We conclude the Model D2 estimates may be used and compare precision for the D2 estimates $\hat{\phi}^{(0)}$, $\hat{\phi}^{(1)}$ and individual A2 estimates $\hat{\phi}_i^{(0)}$, $\hat{\phi}_i^{(1)}$ and their averages $\hat{\phi}^{(0)} = \sum \hat{\phi}_i^{(0)} \div 6$, $\hat{\phi}^{(1)} = \sum \hat{\phi}_i^{(1)} \div 6$. The confidence interval for $\hat{\phi}^{(1)}$ based on the Model D2 estimate will be about

Table 6.10. Capture-recapture summary statistics for northern pike tagged in the Frome River, Dorset, England, 1971–79 (Mann 1980).

Year	i	$R_i^{(0)a}$	$r_i^{(0)}$	$T_i^{(1)b}$	$R_i^{(1)a}$	$r_i^{(1)}$	$T_i^{(2)b}$	$m_i^{(1)}$	$z_i^{(1)}$
1971–72	1	20	6		29	10			
1972–73	2	29	4	6	22	5	10	12	4
1973–74	3	21	3	4	28	11	9	11	2
1974–75	4	29	4	3	24	5	13	14	2
1975–76	5	11	3	4	25	8	7	9	2
1976–77	6	47	13	3	31	11	10	11	2
1977–78 ^c	7	22	4	13	38	3	13	24	2

^a There were no "losses on capture" so that $n_i^{(0)} = R_i^{(0)}$ and $n_i^{(1)} = R_i^{(1)}$.

^b Recall that $T_i^{(v)} = r_{i-1}^{(v-1)} + z_{i-1}^{(v-1)}$ for $v = 1$ and 2. Also note that $T_i^{(1)} + T_i^{(2)} = m_i^{(1)} + z_i^{(1)}$, $T_i^{(1)} = r_{i-1}^{(0)}$, and $T_i^{(2)} = r_{i-1}^{(1)} + z_{i-1}^{(1)} = m_i^{(1)} + z_i^{(1)} - r_{i-1}^{(0)}$.

^c 1978–79 was just a recapture year. No new animals were marked.

Table 6.12. Estimates^a and approximate standard errors under Models A2, B2, and D2 for northern pike tagged in the Frome River, Dorset, England, 1971–79 (Mann 1980).

	$\hat{\phi}_t^{(0)}$	$\hat{S}E$	$\hat{\phi}_t^{(1)}$	$\hat{S}E$	$\hat{p}_t^{(1)}$	$\hat{S}E$	$\hat{N}_t^{(1)}$	$\hat{S}E$	$\hat{B}_t^{(1)}$	$\hat{S}E$
Model A2—time-specific survival and capture rates										
1971	0.51	0.234	0.59	0.234						
1972	0.17	0.082	0.28	0.114	0.44	0.172	48	17.8	25	15.2
1973	0.20	0.119	0.55	0.192	0.69	0.171	38	8.2	16	19.1
1974	0.19	0.095	0.28	0.125	0.63	0.200	37	11.3	28	12.0
1975	0.34	0.178	0.40	0.134	0.61	0.199	38	11.3	28	18.0
1976	0.46	0.218	0.59	0.281	0.67	0.177	44	10.2	42	30.7
1977					0.55	0.228	68	29.2		
\bar{x} estimate	0.31	0.068	0.45	0.064	0.60	0.078				
Model B2—constant adult and young survival rates										
1972					0.57	0.128	41	7.7	37	10.5
1973					0.54	0.148	50	11.8	16	6.2
1974					0.64	0.144	37	7.1	42	13.4
1975	0.31 ^b	0.053	0.42 ^b	0.044	0.45	0.143	53	14.9	28	10.5
1976					0.61	0.156	50	11.6	28	6.3
1977					0.73	0.124	53	8.2	5	2.2
1978					0.34	0.115	27	12.4		
Model D2—constant survival and constant capture rates										
1972							40	6.04	35	12.6
1973							48	7.50	19	4.3
1974							40	6.18	33	5.4
1975	0.30 ^b	0.052	0.40 ^b	0.042	0.58 ^b	0.073	43	7.05	33	6.2
1976							53	8.19	33	5.1
1977							62	8.77	3	2.7
1978							15	3.69		

^a Estimates have not been adjusted for 9.5% tag loss (see Pollock and Mann 1983 and the previous example).

^b These estimates pertain to all years in the study because of the assumptions of constant survival and/or capture.

two-thirds the length of the interval based on $\hat{\phi}^{(1)}$. For these data, the advantages of a reduced-parameter model are apparent.

Let us now consider the estimates under Models B2 and D2 presented in Table 6.12 in more detail. Estimates of adult and young survival rates were used to carry out a 1-tailed approximately normal test of equality of young and adult survival rates versus the alternative that adults had a higher survival rate. Thus we tested

$$H_0 \phi^{(1)} \leq \phi^{(0)}$$

against

$$H_1 \phi^{(1)} > \phi^{(0)},$$

using the test statistic

$$Z = \frac{\hat{\phi}^{(1)} - \phi^{(0)}}{\hat{S}E(\hat{\phi}^{(1)} - \phi^{(0)})}$$

where

$$\begin{aligned} \hat{S}E(\hat{\phi}^{(1)} - \phi^{(0)}) &= [\hat{var}(\hat{\phi}^{(1)}) + \hat{var}(\phi^{(0)}) \\ &\quad - 2 \hat{cov}(\hat{\phi}^{(1)}, \phi^{(0)})]^{0.5}. \end{aligned}$$

Using Model D2 estimates gives

$$Z = \frac{0.401 - 0.303}{[0.0017 + 0.0027 - 2(0.00032)]^{0.5}} = 1.60.$$

Using the standard normal tables the 1-tailed P value is 0.055. Using the Model B2 estimates gives $Z = 1.73$ with a P value of 0.042, providing further evidence of age-dependent survival. Note that the covariance between $\hat{\phi}^{(1)}$ and $\phi^{(0)}$ is not given in Table 6.12 but is contained in the output from JOLLYAGE. The estimates of the

Table 6.13. Results for goodness-of-fit tests and tests comparing models for northern pike tagged in the Frome River, Dorset, England, 1971–79 (Mann 1980).

Model	Goodness-of-fit tests			Tests between models			
	χ^2	df	P	Models	χ^2	df	P
A2	3.15	5	0.68	B2 vs. A2	9.83	10	0.46
B2	12.97	15	0.60	D2 vs. B2	4.26	4	0.37
D2	19.78	21	0.53	D2 vs. A2	16.64	16	0.41

adult population ($\hat{N}_i^{(1)}$) suggest that we have a very small population of around 30–50 fish. Also, capture rates are very high for a fisheries study (0.34–0.64). It is interesting that the number of new recruits into the adult class ($\hat{B}_i^{(1)}$) appears to be significantly larger than zero in all years except 1977.

7. COMBINATION CLOSED AND OPEN POPULATION MODELS

7.1 Introduction

We believe that the design of capture-recapture experiments deserves much more attention from statisticians and biologists. Study design should be oriented around satisfaction of as many model assumptions as practically possible so that a simple and reasonably efficient model can be used for estimation.

At the basis of many capture-recapture sampling models is the assumption that all animals are equally likely to be caught in each sample (the equal catchability assumption), which was discussed in Chapter 2. This assumption is most unlikely to be realistic in natural animal populations, and either 1 or both of the heterogeneity and trap-response alternatives may be acting in a particular animal population.

The capture-recapture model most frequently used by biologists for open populations in long-term studies is the Jolly-Seber model, which was discussed in detail in Chapter 4. This model requires the equal catchability assumption and although some weakening of the assumption is possible (Section 5.3 and Chapter 6), the complexity of open population models is likely to preclude general models that allow heterogeneity and/or permanent trap response. However, some closed models discussed in Chapter 3 do permit relaxation of the equal catchability assumption in a biologically realistic manner.

Pollock (1981a) asserted that statisticians have drawn a sharp distinction between closed and open population models, which is perhaps rather artificial. To quote (Pollock 1981a:435), ‘In practice a series

of short-term studies may be carried out. One approach to analysis would be to analyze each short-term study using the closed population models . . . which allow unequal catchability. Then all the sampling periods in each short-term study could be pooled and survival estimators between these short-term studies could be estimated using the Jolly-Seber Model. This approach allows population size estimation under models allowing unequal catchability while survival estimation, which is not so affected by unequal catchability, is under the Jolly-Seber Model.’

In this chapter, we describe the design discussed above. The design was originally published by Pollock (1982) and was motivated by the desire to find a design for long-term studies that is robust to heterogeneity and/or trap response. We examine its robustness properties using simulation, and examples are given in some detail to illustrate the methodology for biologists.

7.2 The Design

Consider the following representation of a capture-recapture sampling experiment (Fig. 7.1) where we have k primary sampling periods (e.g., years), and within each one of these we have ℓ secondary sampling periods that are very close to each other in time (e.g., ℓ consecutive days of trapping). It is not necessary that the number of secondary periods be equal in all the primary periods.

The design can be used to estimate the population size for each of the primary sampling periods (N_1, N_2, \dots, N_k) assuming that the population is constant over the secondary sampling periods within each primary sampling period. We also can estimate survival rates ($\phi_1, \phi_2, \dots, \phi_{k-2}$) and numbers of new individuals entering the population between the primary sampling periods (B_1, B_2, \dots, B_{k-2}).

It would be possible to estimate all of these parameters except N_1 and N_k using the standard Jolly-Seber model of Chapter 4. In order to use the Jolly-Seber model with the described design, all the second-

DIAGRAMMATIC REPRESENTATION OF THE ROBUST CAPTURE-RECAPTURE DESIGN

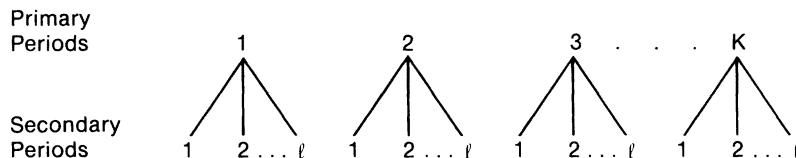


Fig. 7.1. Diagrammatic representation of the robust design of a capture-recapture study that allows combination of closed and open population models for analysis.

ary sampling periods within a primary sampling period would be "pooled." Here by "pooled" we mean that we are just interested in whether or not an animal is captured at least once during the primary sampling period.

When considering the use of the Jolly-Seber model, it is important to keep in mind requisite assumptions and model robustness. In Chapter 4 it was pointed out that heterogeneity and/or trap response will have a large effect on the population size estimators (eq. 4.1) because the sample ratio (m_i/n_i) will no longer accurately reflect the population ratio (M_i/N_i). The marked population estimators (eq. 4.5) will not be so affected by unequal catchability because the 2 ratios of recoveries of marked animals will both tend to be influenced similarly. It follows that the survival rate estimators (eq. 4.2), which are simply ratios of the M_i 's, also will be less affected by unequal catchability than the population size estimators. Cormack (1972) suggested this using an intuitive argument and Carothers (1973) documented it for heterogeneity of capture probabilities using analytic approximations and computer simulation. In the case of permanent trap response, survival rate estimates are not affected at all (Nichols et al. 1984a).

In the robust design we attempt to minimize the influence of unequal catchability on our estimators by exploiting our 2 levels of sampling. Survival rate estimators, which are not so influenced by unequal catchability, will be estimated exactly as under the Jolly-Seber procedure using pooled

captures within a primary period. Recall that these survival estimators will be available only for $i = 1, 2, \dots, k - 2$.

We suggest that population size estimators for each primary sampling period ($\hat{N}_1, \dots, \hat{N}_k$) be obtained using closed population models allowing for unequal catchability (Chapter 3). These estimates use only the captures and recaptures within a primary sampling period. The easiest way for a biologist to obtain these estimates is to use the program CAPTURE developed by Otis et al. (1978) (also White et al. 1982). It considers a range of different models allowing for heterogeneity and/or trap response and also gives an objective method of choosing the most appropriate model to use. Notice that an additional advantage of this approach is that population size estimators are available for all primary periods ($i = 1, \dots, k$), whereas under the Jolly-Seber approach, estimators are only available for $i = 2, \dots, k - 1$. Once again, however, we suggest caution in the use of the model selection procedure from CAPTURE (Chapman 1980, Menkins and Anderson 1988). The tests are not independent and often have low power, especially for small populations (Menkins and Anderson 1988).

Finally, the birth rate estimators can be obtained from eq. (4.3) as before, but now the population size estimators used are those described in the preceding paragraph. Notice that it is possible to estimate B_1, \dots, B_{k-2} , whereas under Jolly-Seber it is only possible to estimate B_2, \dots, B_{k-2} . If we had an estimator of ϕ_{k-1} then B_{k-1}

would also be estimable. In some experiments, it may be reasonable to estimate ϕ_{k-1} by $\hat{\phi}_{k-2}$ or perhaps by an average of $\hat{\phi}_1, \dots, \hat{\phi}_{k-2}$. Another possibility that bears further investigation is to estimate M_k using recaptures of previously marked animals during primary period k in conjunction with closed models and then to use this estimate in eq. (4.2) to estimate ϕ_{k-1} .

The approximate variance of the $\hat{\phi}_i$ estimator is given in Section 4.4 (eq. 4.13). The variance estimators for the \hat{N}_i are obtained from the closed models as described by Otis et al. (1978) and Chapter 3 and computed in program CAPTURE. The variances of the \hat{B}_i given here can thus be obtained as

$$\begin{aligned} \text{var}(\hat{B}_i) &= \text{var}(\hat{N}_{i+1}) + \phi_i^2 \text{var}(\hat{N}_i) \\ &\quad + (N_i - n_i + R_i)^2 \text{var}(\hat{\phi}_i) \\ &\quad + \text{var}(\hat{\phi}_i) \text{var}(N_i). \end{aligned} \quad (7.1)$$

To obtain eq. (7.1) we assume independence of the estimators $\hat{\phi}_i$ and \hat{N}_i .

7.3 Simulation Example

A small simulation study is presented to illustrate the robustness properties of this design. Consider a population that is sampled for 3 years and within each year there are 5 sampling periods close enough together so that closure can be assumed. Further assume that the population is subject to heterogeneity alone (Model M_h of Otis et al. 1978) and that each animal has the same capture probability for all 15 (3×5) sampling periods. The 7 trials we consider are all taken from table N.4.a of Otis et al. (1978:128) and have differing degrees of heterogeneity as can be seen from Table 7.1. For each trial we also consider 2 different birth and death processes acting on the population:

1. There are no births or deaths so that the population stays constant from year to year.
2. There is a survival rate of 0.5 for all animals in the population, and births

exactly match deaths to keep the population constant in size from year to year.

Using the simulation procedure of PO-PAN-3 (Arnason and Schwarz 1987), approximate means and standard errors were obtained for \hat{N}_2 , the Jolly-Seber estimator given by eq. (4.1). These values were based on 99 simulation runs. If we consider the 5 sampling periods within year 2, the appropriate estimate of N_2 is the jackknife estimator (\hat{N}_h), and Otis et al. (1978:128) have derived approximate means and standard errors for our trials using simulation.

In Table 7.2 the 2 estimators described above are compared. When the population has no births and deaths, the Jolly-Seber estimators have smaller standard errors than the jackknife estimators, but in the more realistic case when survival is 0.5 and births match deaths, the standard errors of both estimators are very similar. Under both types of birth and death processes, the Jolly-Seber estimators typically have a much larger bias than the jackknife estimators.

7.4 Examples

In Example 1 Fuller (1981) carried out a capture-recapture study on a population of American alligators (*Alligator mississippiensis*) in the vicinity of Lake Ellis Simon, North Carolina, during 1976–79. The study was not designed exactly as we suggest here, but it does illustrate that the suggested methodology has advantages. The data on between-year captures and recaptures (Table 7.3) were used to obtain the Jolly-Seber estimates of population size in year 2 (1977) and year 3 (1978) and survival estimates for 1976–77 and 1977–78. In 1978 there were enough within-year captures and recaptures to apply the closed population models of Otis et al. (1978). The model selection procedure in CAPTURE chose Model M_h , the heterogeneity model, and hence the jackknife estimator (\hat{N}_h) was computed.

The Jolly-Seber population estimates for 1977 and 1978 are given with their stan-

Table 7.1. Description of simulation trials of model M_h ^a useful for comparison with the Jolly-Seber model.

Trial	N ^b	$p_j, j = 1, 2, \dots, N$	
1	400	$p_j = 0.05, j = 1, 200; p_j = 0.15, j = 201, 300; p_j = 0.50, j = 301, 400.$	
2	400	$p_j = 0.01, j = 1, 100; p_j = 0.05, j = 101, 200; p_j = 0.10, j = 201, 300; p_j = 0.20, j = 301, 400.$	
3	400	$p_j = 0.10, j = 1, 100; p_j = 0.20, j = 101, 200; p_j = 0.25, j = 201, 300; p_j = 0.30, j = 301, 400.$	
4	400	$p_j = 0.01, j = 1, 50; p_j = 0.15, j = 51, 200; p_j = 0.25, j = 201, 300; p_j = 0.30, j = 301, 400.$	
5	400	$p_j = 0.20, j = 1, 100; p_j = 0.30, j = 101, 200; p_j = 0.40, j = 201, 300; p_j = 0.50, j = 301, 400.$	
8	100	$p_j = 0.05, j = 1, 40; p_j = 0.10, j = 41, 80; p_j = 0.30, j = 81, 100.$	
12	100	$p_j = 0.10, j = 1, 40; p_j = 0.20, j = 41, 80; p_j = 0.30, j = 81, 100.$	

^a From Otis et al. (1978:128).^b N denotes the total number of animals in the simulated population, and j is used to denote different individuals.

dard errors together with the jackknife estimator for 1978 and its standard error in Table 7.4. The jackknife estimate is double the Jolly-Seber estimate, which is consistent with the hypothesis that there is strong heterogeneity of capture probabilities for this population. Fuller (Fla. Wildl. Fed., pers. commun.) also suggested that the jackknife estimate is more consistent with other independent estimates of population size based on other sampling techniques.

Lefebvre et al. (1982) in a study of hispid cotton rat (*Sigmodon hispidus*) populations did a similar comparison of closed population model estimates and Jolly-Seber estimates over a series of months. In their case they found both sets of estimates to be very similar.

In Example 2 the livetrapping grid study of *Microtus pennsylvanicus* at Patuxent Wildlife Research Center described earlier (Section 3.9, Example 1; Section 4.7, Example 3) was used to examine the utility of the robust design (Nichols et al. 1984b). For each of the 6 monthly (primary) sampling periods from June 1981 through De-

cember 1981, trapping was carried out for 5 consecutive days (secondary sampling periods). A raccoon (*Procyon lotor*), which was later caught, visited the grid and tipped over a large number of traps on the final 2 days of trapping during the second of the 6 months. These 2 days had to be discarded leaving only 3 trapping days in the second month. In the analyses reported here, data on both sexes were combined, and young animals <22 g body weight were omitted.

Jolly-Seber estimates for survival rates, population sizes, and numbers of new animals based on captures and recaptures in the primary (monthly) sampling periods were presented in Table 4.8. Capture frequency data for the secondary (daily) sampling periods within each primary period are shown in Table 7.5. Test statistics associated with population closure, heterogeneity of capture probability, and fit of M_h for these secondary periods are shown in Table 7.6.

This example illustrates very clearly the advantages of the robust procedure we

Table 7.2. Comparison of M_h and Jolly-Seber population size estimators based on simulated capture-recapture studies.

Trial	N	\hat{N}_h^a	\hat{SE}	Jolly-Seber			
				$\hat{N}_2^b (\phi = 1)$	\hat{SE}	$\hat{N}_2^b (\phi = 0.5)$	\hat{SE}
1	400	331.06	23.99	250.99	13.22	244.38	22.96
2	400	298.06	24.52	257.08	26.23	258.14	52.74
3	400	461.22	32.64	367.06	12.44	369.04	35.79
4	400	417.08	30.91	338.07	12.07	338.27	29.19
5	400	443.95	19.71	386.89	4.94	387.83	17.81
8	100	84.66	14.32	70.17	10.49	72.93	30.74
12	100	107.57	16.80	89.98	7.83	84.13	16.54

^a Simulation results from Otis et al. (1978:128).^b Simulation results used POPAN-3 (Arnason and Schwarz 1987).

Table 7.3. Alligator between-year capture-history data collected by Fuller (1981) for a population at Lake Ellis Simon, North Carolina, from 1976 to 1979.

1976	1977	1978	1979
$n_1^a = 20$	$n_2 = 51$	$n_3 = 41$	$n_4 = 25$
$R_1^b = 17$	$R_2 = 49$	$R_3 = 37$	$R_4 = 25$
$X_{11} = 9$	$X_{111}^c = 4$	$X_{1111} = 1$	
$X_{01} = 42$	$X_{101} = 1$	$X_{1011} = 1$	
	$X_{011} = 18$	$X_{0111} = 6$	
	$X_{001} = 18$	$X_{0011} = 5$	
		$X_{1001} = 0$	
		$X_{1101} = 2$	
		$X_{0101} = 4$	
		$X_{0001} = 5$	

^a n_i = the number of alligators captured in year i (e.g., $n_1 = 20$ is the number of alligators captured in year 1).

^b R_i = the number of alligators released in year i (e.g., $R_1 = 17$ is the number of alligators released in year 1).

^c $X_{ijk\ell}$ = the number of alligators with capture history $ijk\ell$, where $ijk\ell$ denotes years 1, 2, 3, 4 and where "1" denotes capture and "0" indicates that the animal was not captured (e.g., $X_{111} = 4$ is the number of alligators first captured in year 1 that are recaptured in year 2 and then again in year 3).

have just described. In all periods except month 2, the model selection procedure of program CAPTURE chose Model M_h , the heterogeneity model. As month 2 had only 3 trapping days for analysis, we decided to use model M_h there also, because the model selection procedure does not work well with such a small number of sampling periods. The M_h goodness-of-fit statistics generally supported the use of this model, and the M_o versus M_h test (essentially a test for heterogeneity of capture probability) results provided strong evidence of heterogeneity in every month (Table 7.6). As reported in Section 4.7, the Jolly-Seber goodness-of-fit statistic indicated rejection of this model ($\chi^2 = 30.9$, 5 df, $P < 0.01$). This test is sensitive to heterogeneity of capture probability when average capture probability is high, and test results are thus consistent with the evidence of heterogeneity provided by the closed models.

Table 7.4. Comparison of population size estimators for the alligator data collected by Fuller (1981) for a population at Lake Ellis Simon, North Carolina, from 1976 to 1979.

Estimator	\hat{N}	\hat{SE}	95% CI
Jolly-Seber 1977	56	6.7	43–69
Jolly-Seber 1978	69	12.6	44–94
Jackknife 1978	140	28.5	84–197

Table 7.5. Meadow vole capture-frequency data for the secondary sampling periods within each primary period, Patuxent Wildlife Research Center, Laurel, Maryland, June–December 1981. The data were collected by J. D. Nichols.

Primary period (month)	Statistic ^a	Secondary period (day)				
		1	2	3	4	5
1	Animals caught	63	72	74	65	63
	Frequency	20	15	21	21	28
2	Animals caught	66	81	82	^b	^b
	Frequency	35	37	40	^b	^b
3	Animals caught	53	54	46	47	43
	Frequency	37	23	16	13	12
4	Animals caught	60	62	61	52	68
	Frequency	29	15	15	16	27
5	Animals caught	60	67	65	56	64
	Frequency	19	19	19	17	26
6	Animals caught	87	89	79	85	64
	Frequency	40	28	32	28	20

^a Animals caught denotes the number of animals caught on each day of trapping. Frequency denotes the number of animals caught on 1, 2, 3, 4, and 5 occasions.

^b A raccoon tipped over traps on the final 2 days of the second primary period, and these data were omitted from the analysis.

Population size estimates from both the Jolly-Seber open model and the closed model, M_h , are compared in Table 7.7. Jolly-Seber estimates can be computed for months 2–5, and closed model estimates can be computed for each period, 1–6. The M_h estimates of average capture probability (this represents the probability that an animal will be caught on any particular day or secondary sampling period) ranged from 0.35 to 0.56 and produced precise values of \hat{N}_i . The Jolly-Seber estimates of capture probability (this represents the probability that an animal will be captured at least once during a 5-day or primary sampling period) are very high (mean = 0.91), and the Jolly-Seber population size estimates, \hat{N}_i , are thus very precise having small standard errors. Jolly-Seber \hat{N}_i are negatively biased in the presence of heterogeneity, but bias should be relatively small when capture probability is high (Section 4.6) (Carothers 1973, Gilbert 1973). Nevertheless, in every month for which a comparison is possible, the population estimate based on M_h is higher than the Jolly-Seber estimate (Table 7.7). Thus despite the greater precision of the Jolly-Seber estimates, we prefer the M_h estimates, which should exhibit lower bias.

Table 7.6. Test statistics for population closure and M_h goodness-of-fit based on meadow vole data in Table 7.5. The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, by James D. Nichols from June to December 1981.

Primary period (month)	Closure test		M_h goodness-of-fit			M_o vs. M_h^a		
	<i>z</i>	<i>P</i>	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
1	-1.90	0.03	5.7	4	0.22	73.0	3	0.00
2	-1.16	0.12	6.7	2	0.04	8.1	1	0.00
3	0.59	0.72	4.1	4	0.39	67.6	3	0.00
4	0.65	0.74	7.3	4	0.12	120.8	3	0.00
5	-0.52	0.30	4.2	4	0.39	66.9	3	0.00
6	-1.13	0.13	12.9	4	0.01	62.8	3	0.00

^a M_o vs. M_h essentially tests for heterogeneity of capture probabilities (Otis et al. 1978:52–56).

The Jolly-Seber survival rate estimator, $\hat{\phi}_i$, is robust to heterogeneity of capture probability (Section 4.6) (Carothers 1973) and is not biased by permanent trap response (Nichols et al. 1984a). We thus believe that our survival estimates should exhibit little bias (Table 7.8). Because of our high capture probabilities, these estimates are very precise (Table 7.8).

Recruitment, B_i , or the number of individuals entering the population between times i and $i + 1$, and present at time $i + 1$, is estimated using eq. (4.3). Jolly-Seber \hat{B}_i are estimated by using Jolly-Seber \hat{N}_i in eq. (4.3), whereas the robust design uses \hat{N}_i from the closed models (in this case, M_h). An estimate of B_1 is possible with the robust design but not with the Jolly-Seber model. For the 3 periods in which a comparison is possible, the robust design yields higher estimates of B_i in 2 periods, whereas the Jolly-Seber \hat{B}_i is higher in 1 period (Table 7.8). Jolly-Seber \hat{B}_i are more precise

than the robust \hat{B}_i , but the latter should exhibit less bias.

7.5 Extension to More Than 1 Age Class

The previous design description and examples apply to situations where only a single age class of animals is considered. However, as pointed out by Pollock and Mann (1983), this design also should be useful in studies of age-stratified populations. In such situations, age-specific survival rates can be estimated using the model of Chapter 6 in conjunction with capture-recapture data over the primary sampling periods. Population size then can be estimated for each age class separately, using capture-recapture data over the secondary sampling periods.

The Jolly-Seber \hat{B}_i can contain animals from 2 different sources: (1) animals that result from production within the population and (2) animals that immigrate from areas outside that occupied by the studied

Table 7.7. Comparison of meadow vole population size estimates using closed population model M_h (heterogeneity model) and using the Jolly-Seber model. The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June to December 1981 by J. D. Nichols.

Primary period	Model M_h^a		Jolly-Seber model	
	\hat{N}_i	$\hat{S}E$	\hat{N}_i	$\hat{S}E$
1	123	5.2		
2	144	6.9	138	4.3
3	141	10.0	118	4.5
4	140	10.9	109	3.1
5	115	4.7	111	3.1
6	189	10.3		

^a Trap losses in each month of 3, 6, 1, 1, 2, 1 were added to the M_h estimates.

Table 7.8. Estimates of meadow vole survival rates and then birth numbers using both M_h (heterogeneity model) and the Jolly-Seber model. The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June to December 1981 by J. D. Nichols.

Primary period	Jolly-Seber				Model M_h	
	$\hat{\phi}_i$	$\hat{S}E$	\hat{B}_i	$\hat{S}E$	\hat{B}_i	$\hat{S}E$
1	0.88	0.021			39	8.7
2	0.66	0.023	31	3.6	50	11.5
3	0.69	0.022	29	2.9	43	13.2
4	0.63	0.015	43	3.1	28	8.5

population. Knowledge of the relative contributions of animals from these 2 different sources is extremely important to obtaining a mechanistic understanding of population dynamics (Connor et al. 1983). In Section 6.3 we showed that the age-dependent model allowed separate estimation of these 2 components when there were at least 3 age classes. Here we consider this topic further and show that separate estimation of the 2 components is possible even when there are only 2 age classes.

Assume that we are dealing with 2 effective age classes, young and adults, denoted as age classes 0 and 1, respectively. Define $B_i^{1(1)}$ as those members of the adult population at sampling period $i + 1$ that were young animals in the population at time i . This component of recruitment, $B_i^{1(1)}$, is simply estimated as the number of young animals in the population at sampling period i that survive until period $i + 1$:

$$\hat{B}_i^{1(1)} = (\hat{N}_i^{(0)} - n_i^{(0)} + R_i^{(0)})\hat{\phi}_i^{(0)}, \quad (7.2)$$

where $\hat{N}_i^{(0)}$ is estimated using a closed population model, $\hat{\phi}_i^{(0)}$ is estimated using the model of Pollock (1981b), see Chapter 6, and $(n_i^{(0)} - R_i^{(0)})$ simply denotes young animals caught at i but not released back into the population. The immigration component of recruitment, $B_i^{11(1)}$, can then be estimated as

$$\hat{B}_i^{11(1)} = \hat{N}_{i+1}^{(1)} - (\hat{N}_i^{(1)} - n_i^{(1)} + R_i^{(1)})\hat{\phi}_i^{(1)} - (\hat{N}_i^{(0)} - n_i^{(0)} + R_i^{(0)})\hat{\phi}_i^{(0)}, \quad (7.3)$$

where the population size estimates again come from closed models and the survival rate estimates are obtained from the model of Pollock (1981b). These definitions also were described in Section 6.2 and the notation presented in Table 6.1.

Approximate large sample variances for these 2 estimators are given by

$$\begin{aligned} \text{var}(\hat{B}_i^{1(1)}) &= (\phi_i^{(0)})^2 \text{var}(\hat{N}_i^{(0)}) \\ &+ (N_i^{(0)} - n_i^{(0)} + R_i^{(0)})^2 \times \text{var}(\hat{\phi}_i^{(0)}) \\ &+ \text{var}(\hat{N}_i^{(0)}) \times \text{var}(\hat{\phi}_i^{(0)}), \end{aligned} \quad (7.4)$$

and

$$\begin{aligned} \text{var}(\hat{B}_i^{11(1)}) &= \text{var}(\hat{N}_{i+1}^{(1)}) + (\phi_i^{(1)})^2 \text{var}(\hat{N}_i^{(1)}) \\ &+ (N_i^{(1)} - n_i^{(1)} + R_i^{(1)})^2 \text{var}(\hat{\phi}_i^{(1)}) \\ &+ \text{var}(\hat{N}_i^{(1)}) \text{var}(\hat{\phi}_i^{(1)}) \\ &+ (\phi_i^{(0)})^2 \text{var}(\hat{N}_i^{(0)}) \\ &+ (N_i^{(0)} - n_i^{(0)} + R_i^{(0)})^2 \text{var}(\hat{\phi}_i^{(0)}) \\ &+ \text{var}(\hat{N}_i^{(0)}) \text{var}(\hat{\phi}_i^{(0)}) \\ &+ 2(N_i^{(1)} - n_i^{(1)} + R_i^{(1)}) \\ &\times (N_i^{(0)} - n_i^{(0)} + R_i^{(0)}) \\ &\times \text{cov}(\hat{\phi}_i^{(0)}, \hat{\phi}_i^{(1)}). \end{aligned} \quad (7.5)$$

Although the 2-age situation is by far the most frequently encountered in age-stratified capture-recapture studies, the methods described above are easily extended to >2 age classes.

7.6 Example for the Robust Design with 2 Age Classes

Here we again use the meadow vole livetrapping grid data from near Laurel, Maryland, 1981 (Sections 3.9, 4.7, 7.4). All previous examples with this data set have been restricted to animals of ≥ 22 g body weight and thus categorized as subadults and adults (Krebs et al. 1969). Here we also use data from animals <22 g (juveniles; Krebs et al. 1969) and divide the population into 2 age categories based on this criterion. We combine sexes and denote all animals of ≥ 22 g as adults and all animals <22 g as young. The young animals obviously have to be of sufficient size or age to be considered part of the trapable population. Data from 7 monthly (primary) sampling periods were used in this example. Each of the first 6 periods contained 5 secondary sampling periods (days), whereas the seventh period contained only a single day of trapping. Adult data from the first 6 periods have been analyzed in Sections 4.7 and 7.4.

Young and adult summary statistics for the 7 primary periods are presented in Table 7.9. Adult sample sizes were good in all 7 periods, but fair numbers of young voles were obtained only in periods 4 and

Table 7.9. Capture-recapture statistics for young and adult meadow voles. The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June to December 1981 by J. D. Nichols.

Date	<i>i</i>	$n_t^{(0)}$	$R_t^{(0)}$	$r_t^{(0)}$	$n_t^{(1)}$	$R_t^{(1)}$	$r_t^{(1)}$	$m_t^{(1)}$	$z_t^{(1)}$
27 Jun-1 Jul 81	1	9	8	8	108	105	89		
1 Aug-5 Aug 81	2	4	4	2	127	121	76	92	5
29 Aug-2 Sep 81	3	3	3	1	102	101	68	75	8
3 Oct-7 Oct 81	4	29	27	22	103	102	63	74	3
31 Oct-4 Nov 81	5	31	30	27	102	100	86	79	9
4 Dec-8 Dec 81	6	5	4	1	149	148	67	119	3
2 Jan 82	7	0	0	0	78	78		71	

5. The data in Table 7.9 were used with the age-specific model of Chapter 6 to estimate young and adult survival rates. For some periods, young and adult survival estimates do appear to differ substantially, although the direction of the differences is not consistent from 1 period to another (Table 7.10). The test for age-specificity of survival and capture probabilities (Chapter 6) (Pollock 1981b) failed to reject the null hypothesis of no age-specific differences ($\chi^2 = 7.9$, 6 df, $P = 0.25$). The goodness-of-fit test for the age-specific model (Chapter 6) indicated rejection ($\chi^2 = 45.9$, 23 df, $P < 0.01$), a result consistent with the earlier rejection of the Jolly-Seber model and the finding of heterogeneity of capture probability among adults (see Section 7.4, Example 2).

Closed model estimates of adult population size were obtained for periods 1–6 (Section 7.4, Example 2), but reasonable estimates for young voles were obtained only for periods 4 and 5. The model selection procedure in program CAPTURE selected M_o for the young voles in both of these periods, unlike for the adults where CAPTURE selected M_h for all periods. In period 4, 27 young voles were captured 48 times yielding an estimate of $\hat{N}_4^{(0)} = 34$. In period 5, 31 young voles were caught 56 times yielding $\hat{N}_5^{(0)} = 36$. (The model selection procedure often chooses M_o for small populations even if there is heterogeneity or trap response as we described in Section 3.8)

The evidence for age-specificity of survival and capture probabilities in the studied vole population is not very strong. The test of Pollock (1981b) failed to detect age-

specificity. However, survival rate estimates for specific periods did appear to differ between young and adults. In addition, the closed models provided strong evidence of heterogeneity of capture probabilities for adult voles but not as strong for young, although this may have been due to the smaller sample sizes for young animals. Also, the daily capture probability estimates for young animals ($\hat{p}_4^{(0)} = 0.30$, $\hat{p}_5^{(0)} = 0.31$) were considerably lower than the averages for adults (avg $\hat{p}_4^{(1)} = 0.44$, avg $\hat{p}_5^{(1)} = 0.55$). In any case, we concluded that there was sufficient evidence of age-specificity to warrant an age-stratified analysis for illustrative purposes.

The age-specific survival rate estimates (Table 7.10) were used with the closed model population size estimates (Table 7.11) for periods 4–6 to obtain estimates of reproductive recruitment, $\hat{B}_i^{1(1)}$, and immigration, $\hat{B}_i^{11(1)}$ (Table 7.11). Reproductive recruitment differed significantly from zero for both periods 4 and 5 and was similar in magnitude, whereas immigran-

Table 7.10. Survival rate estimates for young and adult meadow voles. The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June to December 1981 by J. D. Nichols.

Primary period	Young		Adults			
	(<i>i</i>)	$\hat{\phi}_t^{(0)}$	$\widehat{SE}(\hat{\phi}_t^{(0)})$	$\hat{\phi}_t^{(1)}$	$\widehat{SE}(\hat{\phi}_t^{(1)})$	$\text{cov}(\hat{\phi}_t^{(0)}, \hat{\phi}_t^{(1)})$
1	1.00	0.064		0.87	0.020	0.0001777
2	0.52	0.079		0.66	0.022	0.0001085
3	0.34	0.053		0.69	0.022	0.0000472
4	0.83	0.023		0.63	0.014	0.0000255
5	0.93	0.034		0.89	0.023	0.0002411

Table 7.11. Estimates of young and adult population size, immigration, and reproductive recruitment for meadow voles.^a The data were collected at Patuxent Wildlife Research Center, Laurel, Maryland, from June to December 1981 by J. D. Nichols.

Primary period (<i>i</i>)	Population size							
	Young		Adult		Reproductive recruitment		New immigrants	
	$\hat{N}_i^{(0)}$	$\hat{SE}(\hat{N}_i^{(0)})$	$\hat{N}_i^{(1)}$	$\hat{SE}(\hat{N}_i^{(1)})$	$\hat{B}_i^{1(1)}$	$\hat{SE}(\hat{B}_i^{1(1)})$	$\hat{B}_i^{11(1)}$	$\hat{SE}(\hat{B}_i^{11(1)})$
4	34	3.4	140	10.9	26.5	2.9	1.2	9.0
5	36	3.4	115	4.7	32.4	3.4	56.5	12.0
6			189	10.3				

^a Animals not released (trap mortality) include 2 young and 1 adult in period 4, and 1 young and 2 adults in period 5.

tion differed significantly from zero in period 5, but not 4. Immigration appeared to be negligible in 1 period, but in the next period it appeared to be very important, perhaps more so than reproductive recruitment. Estimates of these 2 components of recruitment in this population over an extended period of time could prove very useful in understanding microtine population fluctuations.

7.7 Discussion

We believe that the simulation study and examples presented in this chapter suggest that the proposed design and modified estimation procedure should be useful in many situations. Heterogeneity and trap response in capture probabilities are believed to be very common among vertebrate populations (Smith et al. 1975, Otis et al. 1978, Tanaka 1980, Nichols et al. 1981, Seber 1982), and the proposed design yields estimators that are robust to these forms of unequal capture probability.

Although the original motivation underlying this design involved robust parameter estimation (Pollock 1982), the design also has other advantages. One advantage is the ability to estimate quantities that cannot be estimated by either the Jolly-Seber model or closed population models, separately. For example, in the single-age case, the Jolly-Seber model does not permit estimation of N_1 , N_k , or B_1 , all of which are estimable using the robust

design. (Also this design allows estimation of ϕ_{k-1} if we use the secondary captures in period k to estimate M_k , the number of previously marked animals still alive at time k . This point should be investigated further.) In the 2-age case, the ability to obtain separate estimates for numbers of immigrants and numbers of new animals resulting from reproduction within the population is potentially very important. The importance of immigration and emigration to population regulation in small mammals has been recognized for some time (Krebs et al. 1973, Lidicker 1975, Gaines and McClenaghan 1980). However, many ecological models of population dynamics, predator-prey relationships, and competitive relationships assume that immigration is not important to population growth and persistence and that all new individuals result from in situ reproduction (Connor et al. 1983). It is important to estimate the contributions of these 2 sources of new animals and thus to test this critical assumption. Connor et al. (1983) suggest that the difficulty in obtaining such estimates (see techniques cited in Gaines and McClenaghan 1980:165) is at least partially responsible for our ignorance of this important aspect of animal population dynamics. We believe that the design described here can be useful in providing such estimates.

Another advantage of the robust design involves the testing of hypotheses about possible functional relationships between estimated quantities of interest. For example, an important question in animal

population ecology involves the possibility that survival rate and/or reproductive rate are functionally related to population size. Although such density dependence is believed to be widespread, such relationships are difficult to estimate and even detect in natural animal populations. A major difficulty with such efforts is that the quantities of interest often are estimated from the same data set and, in many cases, have non-negligible sampling covariances. Inference procedures based on correlated estimators may be misleading and may reflect sampling correlation rather than any true relationships between underlying parameters (e.g., see discussion in Anderson and Burnham 1976:31). For example, Jolly-Seber estimators for population size and survival rate are based on the same set of capture-recapture data. Jolly-Seber \hat{N}_i and ϕ_i exhibit a non-negligible sampling correlation, and any correlation analysis between vectors of these estimates will be influenced by this sampling correlation. However, with the robust design, N_i is estimated using capture-recapture data over secondary sampling periods, whereas ϕ_i is estimated using captures over primary periods. There is thus no sampling correlation between \hat{N}_i and ϕ_i , and these estimators can be more reasonably used to draw inferences about the true relationship between N_i and ϕ_i . With the robust design, it is thus possible to exploit the 2 levels of sampling to obtain independent estimators, which can then be used in inference procedures directed at functional relationships between underlying parameters.

8. DESIGN OF CAPTURE-RECAPTURE EXPERIMENTS

Although study design is the first task a biologist has to consider, we have left this topic until after all of the models have been presented. We believe that a biologist has to be aware of the different models and their assumptions before he or she can seriously design a capture-recapture study.

In this chapter we first present some comments on selection of an estimation method for studying animal populations. We then narrow the focus to capture-recapture studies and consider questions of how to avoid or at least minimize assumption violations when designing a study. This is followed by a detailed presentation of how comprehensive a study is required in terms of sampling intensity to achieve given levels of precision of parameter estimators.

8.1 Selection of an Estimation Method

One of the most important decisions a biologist must make when beginning an investigation involves the selection of methods best suited to the attainment of study objectives. As we have discussed, open capture-recapture models can be used to estimate population size, survival rate, and number of new recruits to the population. These quantities also can be estimated using methods other than capture-recapture. Here we present a very brief general discussion of some other methods and of the strengths and weaknesses of capture-recapture relative to these methods.

A number of alternative methods exist for estimating size and density (population size per unit area) of free-ranging animal populations. Most of these alternatives involve counts or observations of animals. Some methods assume that all animals located within sample quadrats or transects are detected and seen with probability 1.0. In such instances, traditional sampling techniques (e.g., Cochran 1977) are used to “expand” these sample counts to estimate total population size over some area of interest (Eberhardt 1978, Seber 1982). In situations where animals are easily observed and detected with probability 1.0, such sample counts will almost certainly provide the best method of estimating population size.

In most field situations involving observations of animals, however, it is not re-

alistic to assume a detection probability of 1.0. In these situations detection probability must be estimated and then used in conjunction with count data to estimate population size or density. A variety of methods are available for estimating detection probability. These include comparison of standard counts and intensive counts on sample areas, use of a subpopulation of marked animals, mapping with multiple observers, formal line transect sampling, and multiple counts on the same areas (Eberhardt 1978, Eberhardt et al. 1979, Seber 1982, Pollock and Kendall 1987).

The method for estimating detection probability that has received the most detailed statistical development is line transect sampling (Gates 1979, Burnham et al. 1980). In line transect sampling, the observer travels along the transect line counting animals. All animals located directly on the line are assumed to be detected with probability 1.0, and detection probability is assumed to decrease with distance away from the line. Perpendicular distances or paired sighting angles and distances are then used to estimate the detection function, which expresses detection probability as a function of distance from the transect line. The estimated detection function is then used with the total number of animals observed to estimate density. We believe the main limitations of line transect sampling models are (1) the assumption of all animals on the line being seen and (2) the practicality of recording distances. These limitations are particularly severe in aerial surveys.

When animals are readily observable, observation-based methods for estimating population size often will be preferable to capture-recapture methods. Field workers generally have recognized this and have tended to use observation-based methods for estimating population size for birds and large mammals. However, other vertebrates (small mammals, reptiles, amphibians, and fish) and most invertebrates are not so easily observed, and capture-recapture methods provide the most reasonable

means of estimating population size for many such organisms.

Capture-recapture and band-recovery models are commonly used to estimate survival and mortality probabilities for animal populations. Band-recovery models (Brownie et al. 1985) represent special cases of general capture-recapture models in which all recaptures involve removal of the tagged animals from the population (e.g., removal usually occurs via fishing, hunting, trapping, or some other form of human exploitation). Generally, such data are not used to estimate population size or recruitment, although exceptions exist in special application areas (Brownie and Pollock 1985, Nichols et al. 1986). The relationship between band-recovery and more general capture-recapture models is discussed by Brownie and Pollock (1985) and Brownie et al. (1985).

Despite their close conceptual relationship, band-recovery and capture-recapture models often are applied to very different kinds of field sampling situations, and hence, often yield estimates that carry different interpretations. Band recovery models often utilize data supplied by members of the general public involved in the exploitation process (e.g., hunters report bands of shot migratory birds; fishermen report tags of fish in the catch). Thus, the sample of recovered animals is drawn from a large geographic area, which often covers the entire range of the studied population. Capture-recapture models, on the other hand, typically utilize samples provided by the efforts of a single investigator or team and thus often are restricted to local study areas. As a result, the complement of a survival rate estimate from a capture-recapture study ($1 - \phi_i$) generally includes both mortality and permanent emigration (failure of an animal to return to the area exposed to capture efforts), whereas the complement of survival estimates from many band-recovery studies (e.g., many studies of hunted migratory birds) includes only mortality. With regard to selecting an estimation method, if strict mortality rate is the parameter of

interest and if permanent emigration is both likely to occur and difficult to estimate, then band-recovery models may provide the preferred means of estimation. Tag-recovery rates are low in many applications of band-recovery models, however, producing low precision in resulting survival rate estimates. Thus, in situations where permanent emigration does not present a problem or can be estimated, capture-recapture survival estimators often will be preferred to band-recovery estimators because of their greater precision.

In cases where both local recaptures and widespread exploitation recoveries occur for animals marked in a particular study, the distinction between band-recovery and capture-recapture survival estimates permits inference about permanent emigration (Anderson and Sterling 1974, Hepp et al. 1987). Specifically, the ratio of the capture-recapture survival estimate to the band-recovery survival estimate should estimate the conditional probability that an animal alive at the time of recapture sampling efforts is in the local area exposed to these efforts. The complement of this conditional probability can be thought of as an estimate of the probability of permanent emigration.

Historically, band-recovery and capture-recapture models have been the 2 most important general methods for estimating survival and mortality rates in free-ranging animal populations. Recently, field researchers have begun to use another technique, based on radiotelemetry, to estimate mortality rates (Trent and Rongstad 1974). This direct approach involves attaching radio transmitters to animals in the population of interest and then making frequent (daily or weekly) determinations of whether or not each instrumented animal is alive. Initial approaches to estimating mortality rate from such data involved the estimation of daily mortality probability as number of animals lost divided by total days at risk. Bart and Robson (1982) and Heisey and Fuller (1985) discuss statistical aspects of this basic approach and present some extensions. Pol-

lock et al. (1989a,b) point out the relationship between telemetry-based mortality estimation and the estimation of survival in medicine and engineering, and then exploit this relationship to provide general and flexible nonparametric models for estimation of animal mortality that are much more realistic than earlier models.

Radiotelemetry methods provide good estimates of survival probabilities if reasonable numbers of animals are followed, and we suspect that this method will be used with increasing frequency in the future. Telemetry offers advantages over capture-recapture because it often provides insight into sources of mortality (and sometimes even estimates of source-specific mortality risks) and information about emigration. The use of radiotelemetry is relatively expensive, however, in both equipment costs and the substantial field effort needed to obtain frequent locations of large numbers of animals. In addition, it is possible that there is sometimes a lack of independence between losses of contact (i.e., failure to relocate a transmitted animal) and animal status (alive or dead), and such a dependence could cause problems in estimation. Nevertheless, radiotelemetry offers a good means of estimating mortality in many situations and will become increasingly important in the future. Winterstein et al. present a detailed discussion of nonparametric methods for estimating mortality rate from telemetry data under a variety of field situations (S. R. Winterstein, K. H. Pollock, and C. M. Bunck. Analysis of survival data from studies using radio telemetry. Unpublished manuscript). These methods are based on those used in medicine and engineering.

There are a variety of approaches available for estimating reproductive rate (we can define this as number of young produced per breeding age female) and number of new recruits entering a population. However, no single approach other than capture-recapture is very general; instead methods are tailored to meet specific field situations. If alternative (i.e., not using capture-recapture models) methods are

used to estimate both population size and survival rate, then number of new recruits can be estimated by subtraction as for the capture-recapture \hat{B}_i . For exploited populations it is sometimes possible to estimate an age ratio (young per adult or adult female at a particular time of the year), an indicator of reproductive rate, using harvest age ratios and age-specific band-recovery data (Martin et al. 1979). For easily observed animals, it is sometimes possible to estimate an age ratio using direct field observations.

Reproductive rate and numbers of young animals are frequently estimated by combining estimates of the various components of reproductive rate. For example, in many bird species the number of eggs in a typical clutch has been well estimated. There are also an increasing number of studies providing good estimates of nesting success (the probability that a newly initiated nest "succeeds" to produce at least 1 fledgling). When these estimates are combined with estimates of the proportion of adult females breeding and an estimate of postfledgling survival, an estimator for reproductive rate or number of young can be developed. However, estimates of these latter 2 quantities (proportion breeding and postfledgling survival) can be difficult to obtain.

When a biological question of interest involves a specific component of reproductive rate, then it generally will be best to try to estimate that component directly, rather than make indirect inferences using capture-recapture \hat{B}_i . When estimates of total new recruits are needed, capture-recapture \hat{B}_i frequently may be the only available estimator. It should be remembered, however, that B_i is estimated using estimates of both population size and survival rate, and hence has a large sampling variance. The standard capture-recapture \hat{B}_i also includes animals entering the population via both immigration and in situ reproduction. However, the age-dependent model (Chapter 6) and the robust design (Chapter 7) permit separate estimation of these 2 components of recruitment in some situations.

8.2 Minimization of Assumption Violations

When capture-recapture is selected for use in a particular investigation, it is important to try to minimize violations of the model assumptions on which the estimators are based. We believe that the problem of assumption violations should be considered at 3 different stages of the capture-recapture study. First, possible violations should be considered when developing the field sampling design for the study. Second, when the data are analyzed it is important to use general model goodness-of-fit tests, between-model tests, and tests of specific assumptions to aid in deciding which model is most appropriate for the data and to provide insight into whether specific assumptions of the selected models have been violated. Third, if it is concluded that specific assumptions have been violated, then it is important to use information from studies on effects of assumption violations when interpreting the estimates and using them to draw inferences. For example, if we conclude that heterogeneity of capture probabilities exists in our data, we still may be able to use resulting Jolly-Seber survival estimates, as they tend to exhibit relatively small bias under heterogeneity (Carothers 1973, 1979). On the other hand, if heterogeneity occurs and capture probabilities are not high (<0.5), then we would not be able to rely on our Jolly-Seber population size estimates although we would know that they likely underestimate true population size. In some cases, it is even possible to "correct" capture-recapture estimators for specific violations (Carothers 1979, Arnason and Mills 1981). Tests of assumptions and effects of assumption violations on capture-recapture estimates have been discussed elsewhere. Here we briefly discuss aspects of study design that relate to model assumptions and their violation.

Heterogeneity of survival and capture probabilities is likely to exist in all capture-recapture studies to some degree. Although there is no study design that can completely eliminate such heterogeneity,

there are certainly ways to reduce it. When it is suspected that survival or capture probabilities are associated with some measurable characteristic of individual animals (e.g., age, sex, size), then such characteristics should be recorded so that the sample can be stratified for analysis. When animals cannot change strata during the course of the study (e.g., sex, also age and size in sufficiently short studies), the appropriate approach simply involves separate analyses for the different strata. When animals change strata during the course of a study, as with age, then special models such as those of Chapter 6 must be developed to incorporate such heterogeneity. For example, the models of Chapter 6 permit heterogeneity of capture and survival probabilities for different identifiable age classes. Although these models are very useful in some cases, there will be other cases where there is heterogeneity due to age but where the age classes cannot be identified in the field.

Heterogeneity of capture probabilities can occur as a result of heterogeneous sampling intensities; therefore efforts should be made to ensure that all sections of the study area are sampled with equal intensity. When traps, mist nets, or other stationary capture devices are used, it is important that all animals in the sampled area be exposed to the devices. For example, even in trapping grids where traps are placed at equal intervals in a checkerboard pattern, it is important that the distance between traps be smaller than the average home range radius of the studied animal. If traps are spaced too far apart, then capture probability can vary substantially as a function of the location of an animal's home range. It is important to have at least 1 trap, and preferably more, within each animal's home range. If sufficient traps are not available for such intense sampling, then traps can be moved during the course of each sampling period to ensure adequate coverage.

In a 2-sample Lincoln-Petersen experiment (Chapter 2), a good method to eliminate bias due to heterogeneity is to use 2 different sampling methods. Unfortu-

nately, open population models require at least 3 sampling periods and often have many more; therefore it is not feasible to use different methods in each sample.

As noted in the previous chapter, we believe that the robust design represents a very useful approach to dealing with heterogeneous capture probabilities. At this time, we believe that implementation of this design is the best available means of minimizing estimation problems associated with such heterogeneity.

Trap response in capture or survival probabilities is another problem that occurs commonly in capture–recapture studies. Evidence of trap response in capture probability has been found in a number of studies of vertebrates (Otis et al. 1978: 29, Tanaka 1980:42–52, Nichols et al. 1981: 123, Seber 1982:83–85). Trap-happy responses often are associated with the use of baited traps. Although such response could be eliminated by not baiting at all, this usually is a poor alternative because of the large losses of data (few animals are captured) that result. Prebaiting, the placement of traps that are baited and locked open in the study area prior to the initiation of trapping, is thought to reduce trap-happiness in some situations, but can lead to other problems (Tanaka 1980:52–55). When considering a trap-happy response, it is important to recall that survival rate estimators are not biased by trap response and that a trap-happy response results in higher precision of the survival rate estimator. Trap-shyness also is a common response and can be minimized by using capture and handling techniques that exert minimal stress on animals. Minimization of capture and handling stress also helps protect against a trap response in survival rate, in which animals show low survival probabilities for the period immediately following initial capture.

Sometimes use of only resighting data (without capture) may be possible as, for example, with color-marked birds, and this method avoids the problem of trap response. Typically, studies using this design have obtained only survival rate estimators (Cormack 1964), but sometimes it is pos-

sible to get ratios of marked to unmarked animals at the same time and estimate population size as well. This was the situation in the study of rock doves described in detail in Section 4.3. This design has good precision if it is possible to obtain high resighting probabilities. One possible disadvantage is that some biologists believe that color-marked animals may have lower survival rates than unmarked animals (Burley 1985).

Temporary (e.g., lasting 1 or perhaps 2 periods after marking) changes in capture and survival probability can be handled using the general models of Robson (1969), Pollock (1975), and Brownie and Robson (1983), and hence require no special design considerations. Permanent trap response in capture probability cannot be handled using available open models, but the robust design of Chapter 7 permits both testing for such response and estimating parameters of interest without bias when it does occur.

An important practical consideration when designing a study is to use a good marking method. The marking method needs to be such that it does not influence the animal's survival, but at the same time mark loss should be negligible. If a new marking method is being used, it would be advisable to carry out a small pilot study and investigate its practicality. If mark loss cannot be avoided completely, it should be estimated through techniques such as double marking (Chapter 2). Estimates of tag loss then can be used to correct open model estimates using methods such as those in Arnason and Mills (1981).

Most capture-recapture models cannot distinguish between births and immigration and between deaths and emigration. As noted in Chapter 7, the robust design permits separation of recruits arising from birth and immigration in some situations. In some cases migration may be ruled out on biological grounds by a careful choice of study area to take account of natural boundaries. This was the case for the study on the gray squirrel described in Section 4.7. The problem of temporary emigration also should be considered. This can be es-

pecially severe in small mammal studies and suggests the use of large grids, natural boundaries, and even "semipermeable" fences to minimize the problem. In cases where migration has the potential to cause large problems, it may be worthwhile to accompany the capture-recapture work with a radiotelemetry study designed to estimate the magnitude of both permanent and temporary emigration.

We believe that in some cases the biologist may be able to choose a population so that no births or immigration are occurring. In such cases the model that only allows losses (Section 5.3.1) can be used. It has the advantage of giving higher precision to population size and survival rate estimators. We believe that the model that only allows gains (births or immigrants) is less likely to be useful (Section 5.3.2).

Finally we emphasize that simulation can be a useful tool at the design stage to evaluate assumption violations. POPAN-3 (Arnason and Schwarz 1987) has a flexible, powerful, simulation component as part of the program.

8.3 Sampling Intensity

In this section we consider the question of what sampling intensity is required to reach a specified level of precision for all parameter estimates. We shall use the quantity, coefficient of variation (CV), or proportional standard error as our measure of precision. We define

$$CV(\hat{\theta}) = \frac{SE(\hat{\theta})}{\theta},$$

which is just the standard error of the estimator of θ divided by θ , the parameter itself. Lowering CV indicates increasing precision for the study. A rough rule of thumb is that a study that provides a CV of 20% is reasonable. Many wildlife and fisheries studies will not achieve this level because of cost constraints. Of course the precision of our estimator will depend on the values of the various parameters in our model. Therefore we present a variety of

graphs of the precision of various estimators as we allow the parameters in the models to change. For an experimenter to use our graphs, he or she would need to come up with reasonable guesses for the parameters in the study. This may seem somewhat of a “catch 22” situation, as the experimenter is doing the study to estimate the parameters! However, for planning purposes even very approximate guesses often will be sufficient.

First of all, we consider the Jolly-Seber model (Chapter 4) in some detail because it is the model central to this monograph. Then we consider the gain in precision possible when the Deaths Only model (Section 5.3.1) can be used.

8.3.1 Jolly-Seber Model.—Figures 8.1–8.9 illustrate the precision of population size, survival rates, and birth number estimators for a range of conditions. For simplicity we assume the population size is constant at 50, 100, 200, or 500 during the course of the study with births matching deaths. We consider 4 different survival rates, $\phi = 0.25, 0.50, 0.75$, and 0.90 , and 3 different numbers of samples, $k = 5, 10$, or 20 . For each set of conditions of the parameters we plot the CV of 1 of our estimators versus capture probability p as it increases from zero to 1. These figures are based on large-sample approximations (Carothers 1973). Nichols et al. (1981) compared these approximations with Monte Carlo simulation results and concluded that the approximations performed well. Finally, note that the SE ($\hat{\theta}$) include both sampling and nonsampling variation for ϕ_i , but only sampling variation for \hat{N}_i and \hat{B}_i . We will first give a summary of general results obtained from the figures and then illustrate the use of the figures.

1. For any set of conditions the CV decreases as the capture probability increases. That is, the precision of any estimator increases as the capture probability increases.
2. The precision increases as the number of samples increases.
3. The precision increases as the survival rate of the animals increases. If animals

have high survival rates, then once they are marked they will contribute more information throughout the experiment.

4. The precision increases as population size increases for fixed capture and survival probabilities and fixed number of samples.

Now consider an example to illustrate the use of the figures. Suppose a biologist has a population of about 100 animals with a survival rate of about 0.75/month with births matching deaths and he plans to sample for about 1 year (12 months). We have graphs with $N = 100$, $\phi = 0.75$, and $k = 10$, which will be good enough for planning purposes. Let us ask the question as to what capture probability he would require to reach a 20% CV for the middle population size estimate (\hat{N}_5), survival estimate ($\hat{\phi}_5$), and birth numbers estimate (\hat{B}_5). Let us consider Figures 8.2, 8.5, and 8.8, respectively, to obtain the information. For population size and survival estimates the precision is similar with a capture probability of approximately 0.38 being required. For birth numbers, a capture probability of 0.76 is required. Therefore, with a small mammal population of this size, an intensive study with more than 1 day of trapping each month would likely be required, and even then it might not be feasible to get birth number estimates with this precision. Of course for large populations, the precision would be better.

In Figure 8.10 we illustrate the difference in precision between population size, survival, and birth number estimates for the case where $k = 10$, $N = 200$, and $\phi = 0.75$. As noted above, the precision for population size and survival estimates is comparable, whereas that for birth numbers is much worse. However, recall that we are including both sampling and non-sampling variation in CV ($\hat{\phi}_i$), but only sampling variation in CV (\hat{N}_i) and CV (\hat{B}_i). If we restricted CV ($\hat{\phi}_i$) to only sampling variation, then we would see that survival estimates are somewhat more precise than estimates of population size.

8.3.2 Deaths Only Model.—Here we

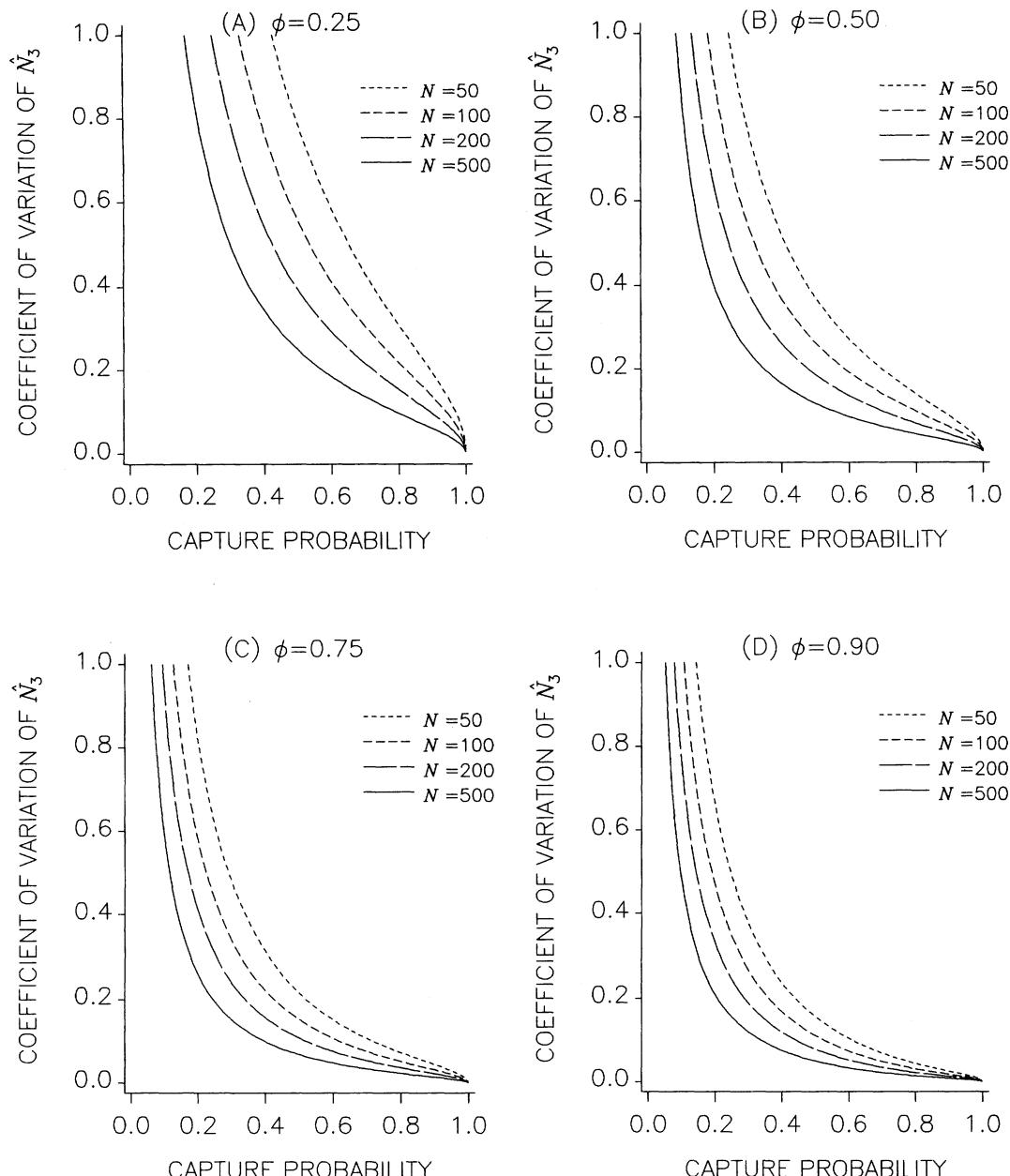


Fig. 8.1. Comparison of the precision of the population size estimator (\hat{N}_3) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 5$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

consider briefly the precision of estimates for the Deaths Only model discussed in Section 5.3.1. In that section we noted that it is possible to increase precision of population size and survival estimates by using this model over the general Jolly-Seber

model. Of course, one needs to be reasonably confident that the critical additional assumption of no new animals coming into the population is justified.

In Figures 8.11 and 8.12 we present similar curves to those given in 8.1–8.9 for the

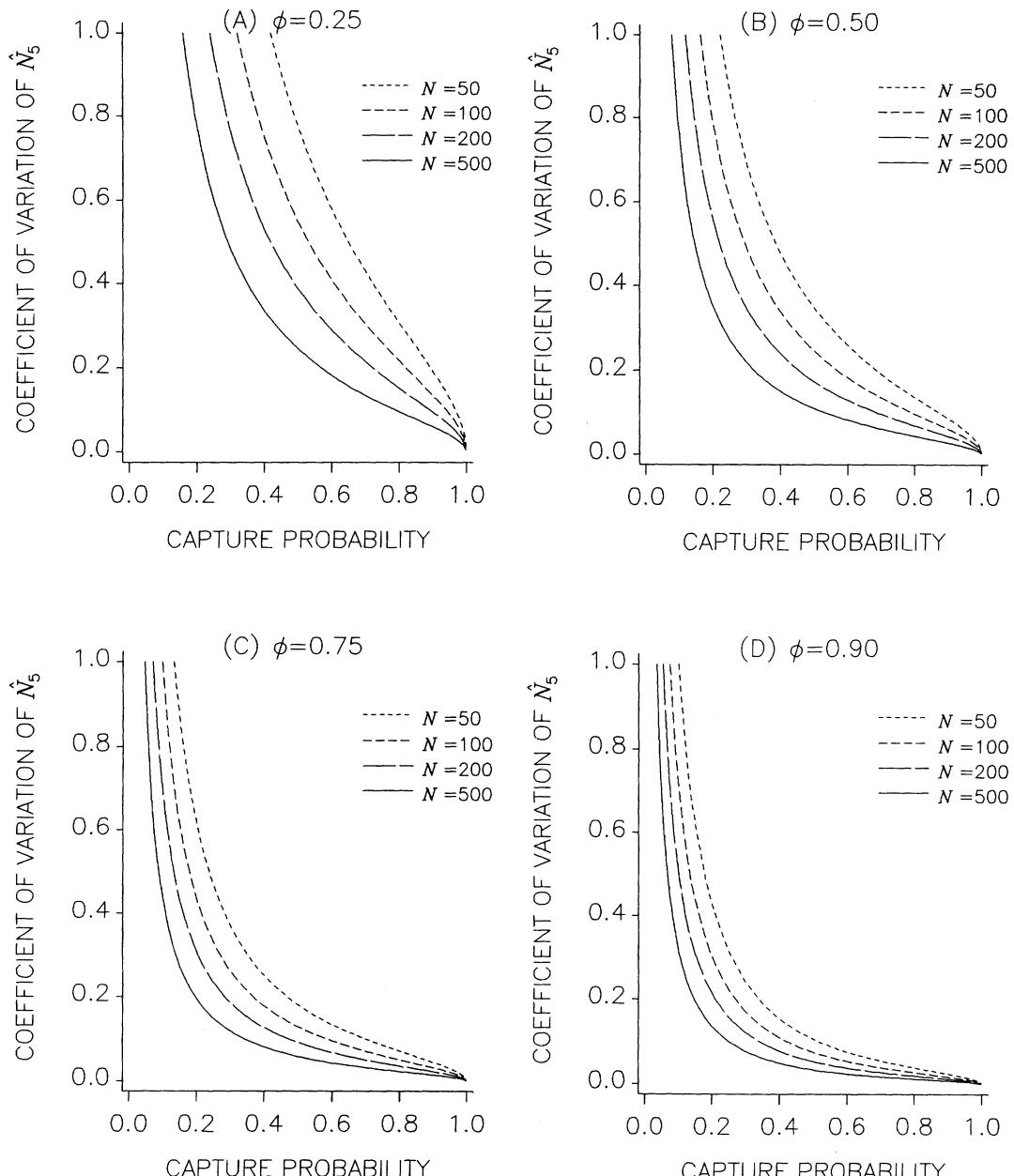


Fig. 8.2. Comparison of the precision of the population size estimator (\hat{N}_s) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 10$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

Jolly-Seber model. We only consider 3 cases, ($k = 5$, $\phi = 0.75$; $k = 5$, $\phi = 0.90$; and $k = 10$, $\phi = 0.90$) for illustrative purposes. For each case we present plots of CV versus capture probability for $N = 50$, 100, 200, and 500.

To get an approximate comparison of the Deaths Only model and the Jolly-Seber model, consider the following example. Consider a population sampled 5 times ($k = 5$) with a survival rate (ϕ) of 0.75. For the Deaths Only model consider $N = 200$,

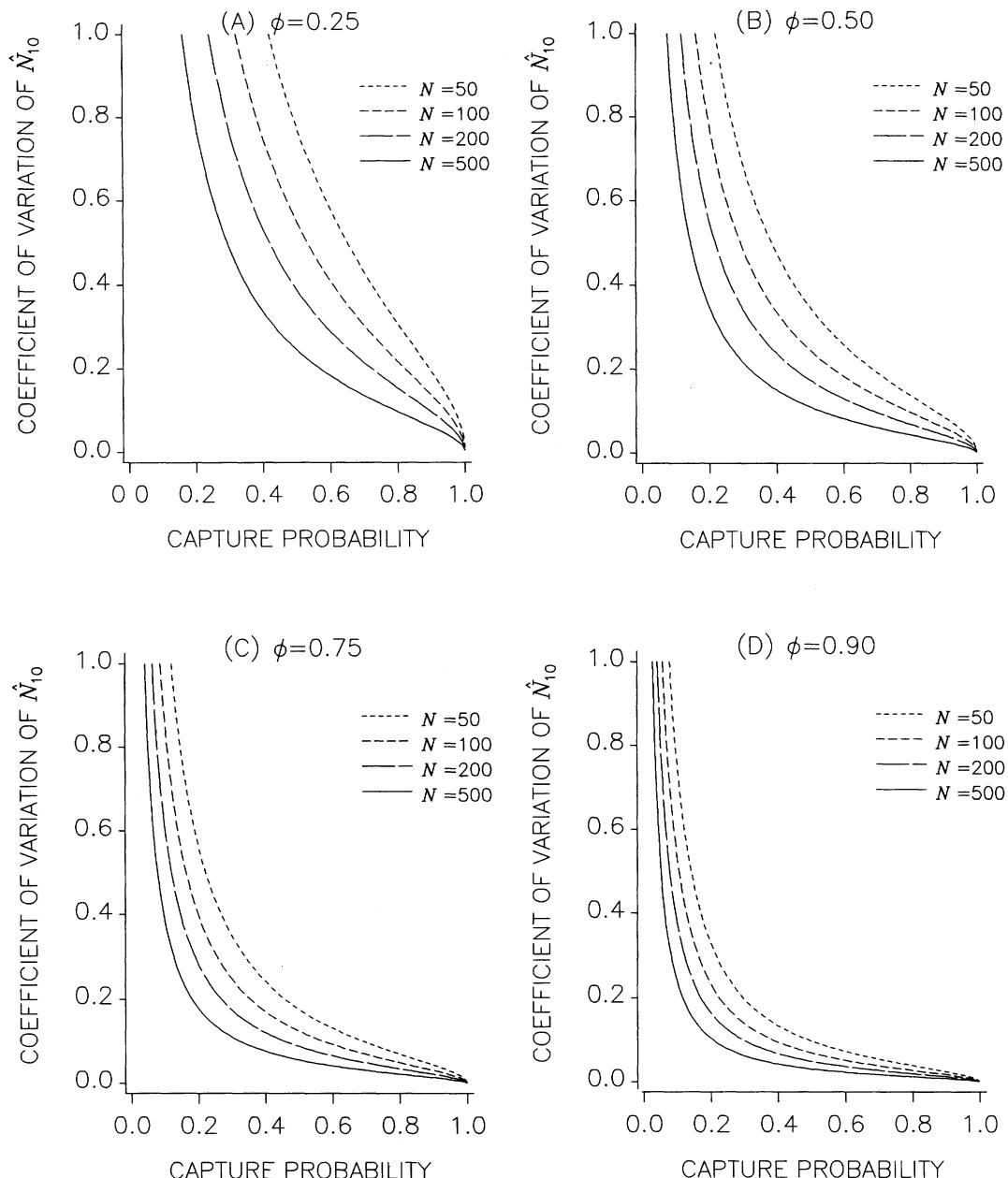


Fig. 8.3. Comparison of the precision of the population size estimator (\hat{N}_{t_0}) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 20$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

the initial population size, which is reduced to slightly more than 100 by time 3. For the Jolly-Seber consider $N = 100$, with births matching deaths. A comparison of the precision of N_3 , the third population size estimate, shows that a capture prob-

ability of 0.29 is required to produce a CV of 20% for the Deaths Only model, whereas a capture probability of 0.46 is required for the Jolly-Seber model. A comparison of the precision of $\hat{\phi}_3$, the third survival estimate, shows a capture probability of

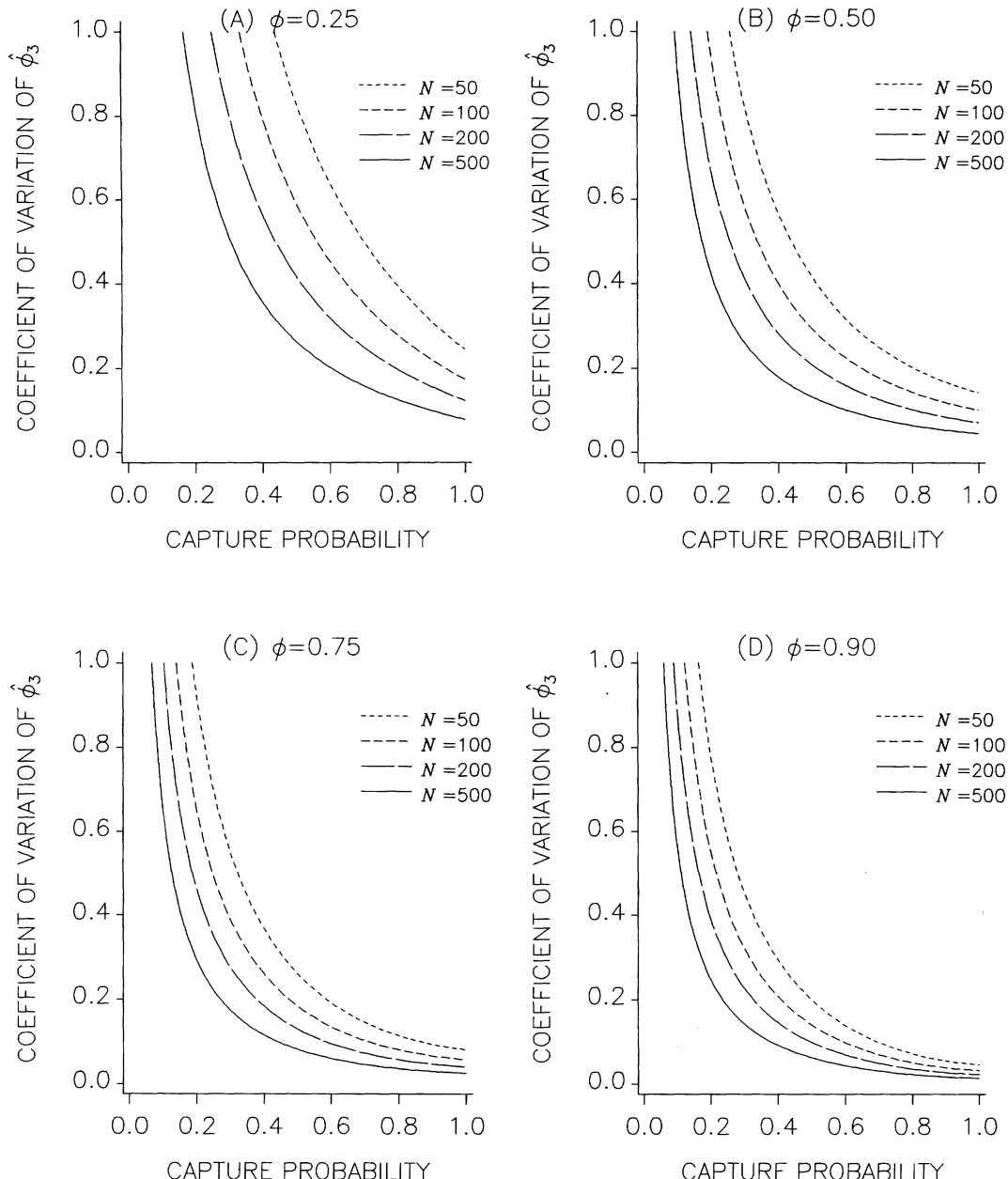


Fig. 8.4. Comparison of the precision of the survival rate estimator ($\hat{\phi}_3$) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 5$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

0.40 required for the Deaths Only model and a capture probability of 0.46 for the Jolly-Seber model.

8.3.3 Simulation.—We believe that the figures presented in this chapter will be useful in the planning of long-term capture–recapture studies. Sometimes the bi-

ologist also may find it feasible to use simulation to check the feasibility of various design options in terms of parameter estimator precision. The program POPAN-3 (Arnason and Schwarz 1987) again can be used for this purpose for Jolly-Seber and related models.

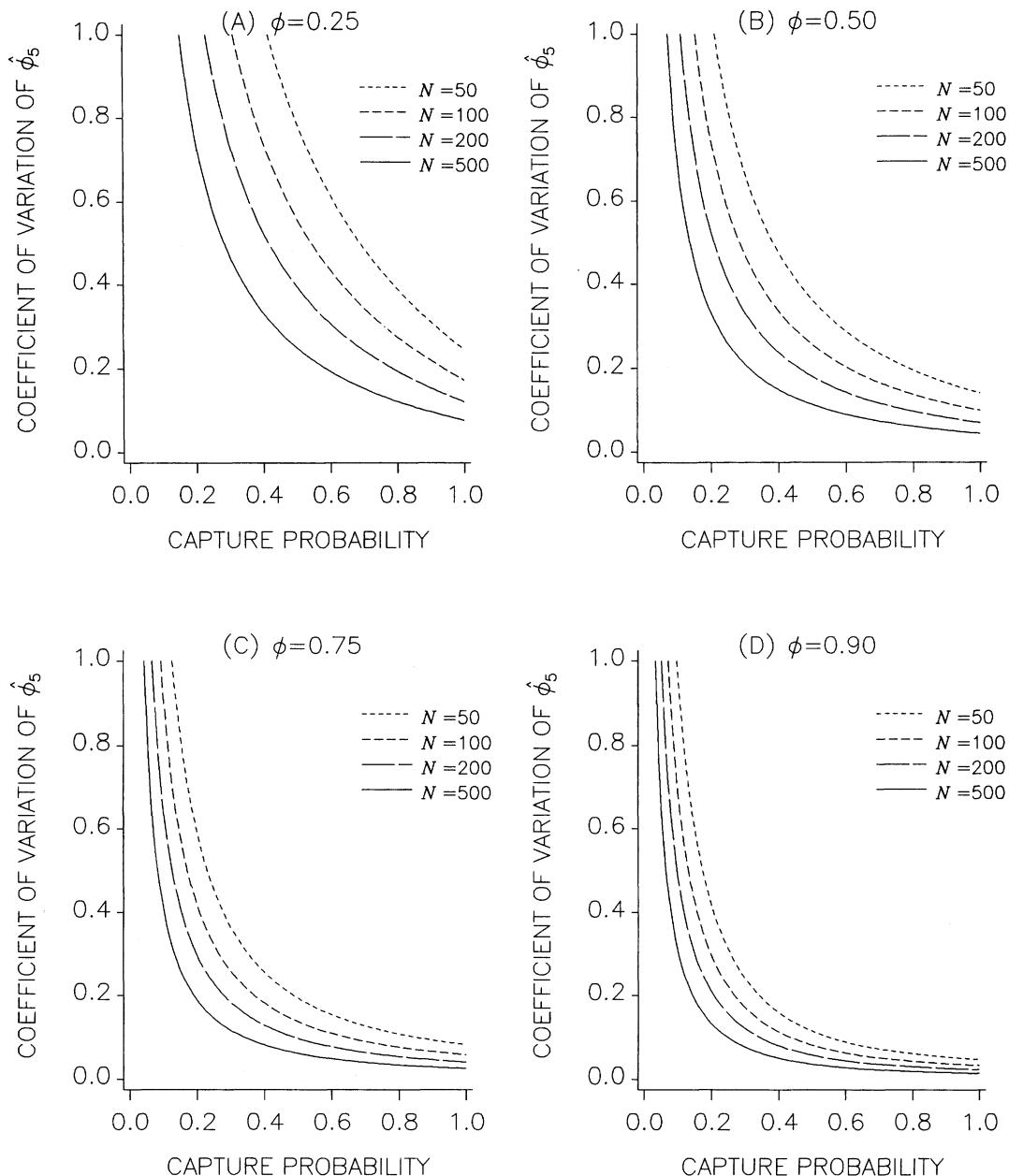


Fig. 8.5. Comparison of the precision of the survival rate estimator ($\hat{\phi}_5$) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 10$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

8.3.4 The Robust Design.—For the robust design described in Chapter 7 where a combination of closed and open models is used, design strategies are more complex. Design considerations for closed models were considered by Otis et al.

(1978). Design considerations for the Jolly-Seber model were considered earlier in this chapter.

The major practical difficulty in using this design obviously is its large size. Otis et al. (1978) suggest that a closed popu-

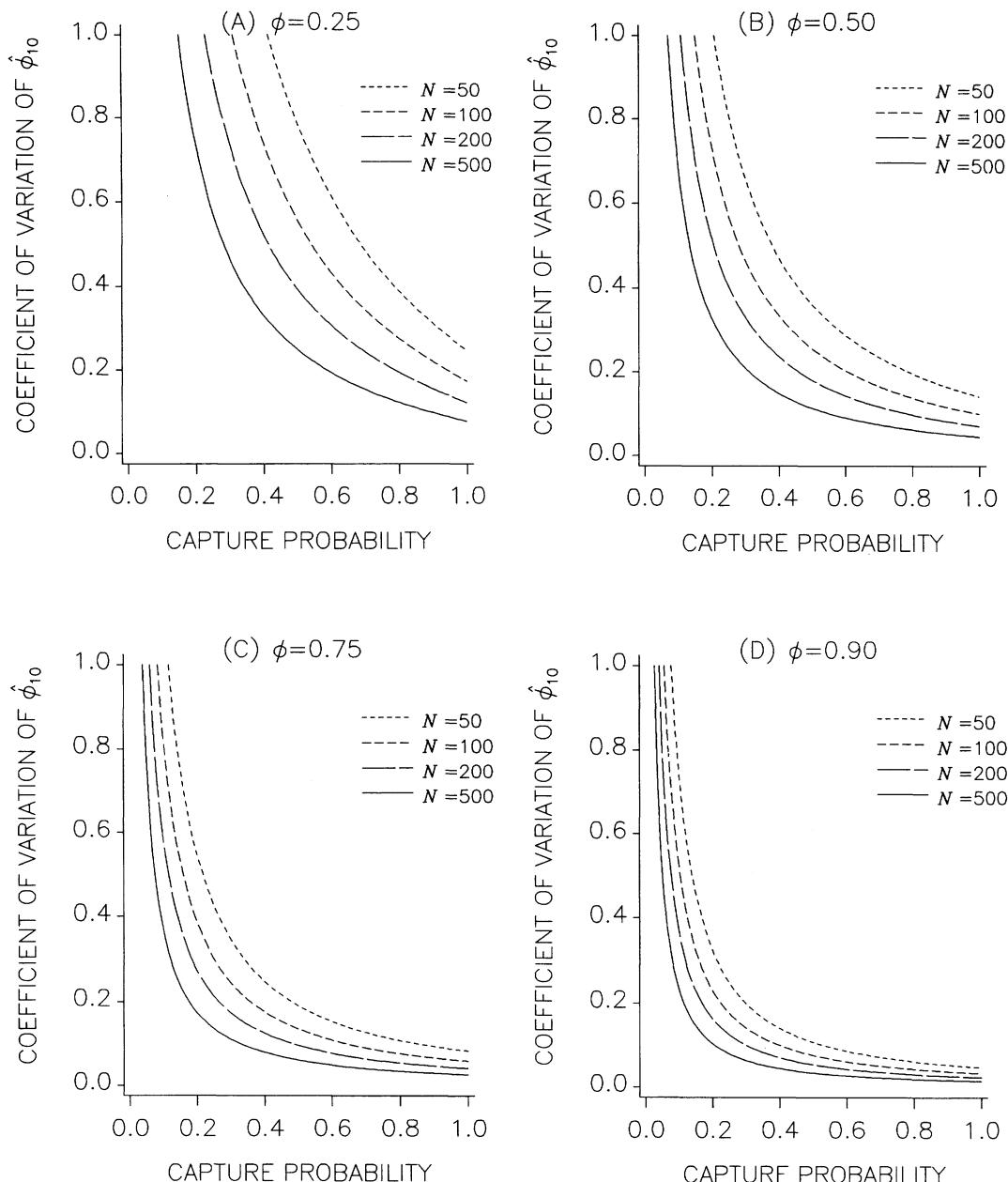


Fig. 8.6. Comparison of the precision of the survival rate estimator ($\hat{\phi}_{10}$) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 20$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

lation model requires 5–10 sampling periods with average capture probabilities of at least 0.1/period for reasonable results. Thus, the smallest practical design would be 3 primary periods, each containing 5 secondary sampling periods. We note that

in some cases, the effort required for the recommended design is similar to that currently expended on other designs. For example, many current small mammal capture-recapture studies involve 2–3 days of trapping every 2 weeks. Redistribution of

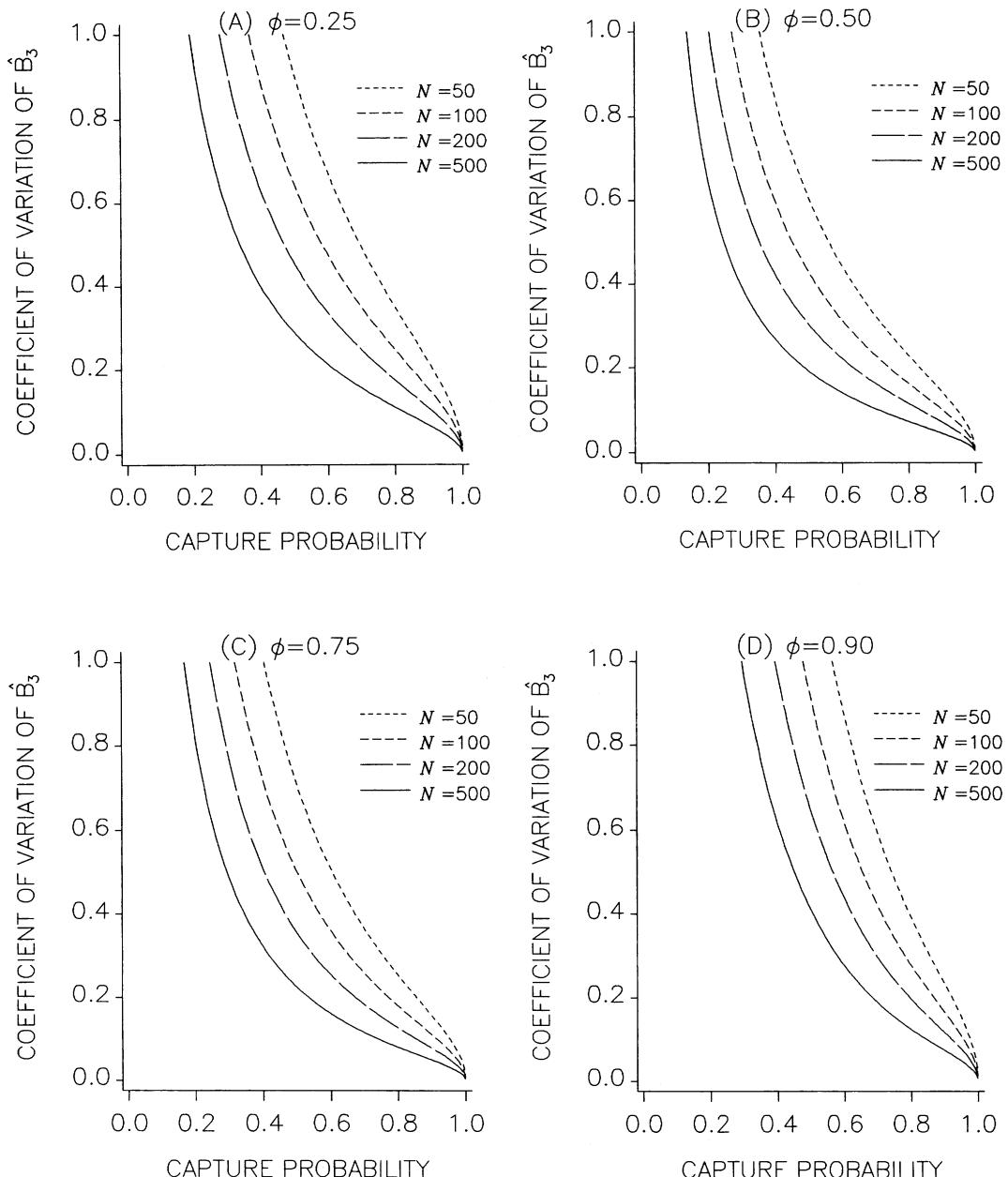


Fig. 8.7. Comparison of the precision of the birth number estimator (\hat{B}_3) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 5$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

sampling to 5 days every month would represent similar effort and would produce the advantages of robust estimation of population size, survival rate, and recruitment. Nevertheless, the effort required for the

recommended design certainly exceeds that currently expended on many studies. If, however, this is the size design necessary for robust estimation of population parameters, it is important for the biologist

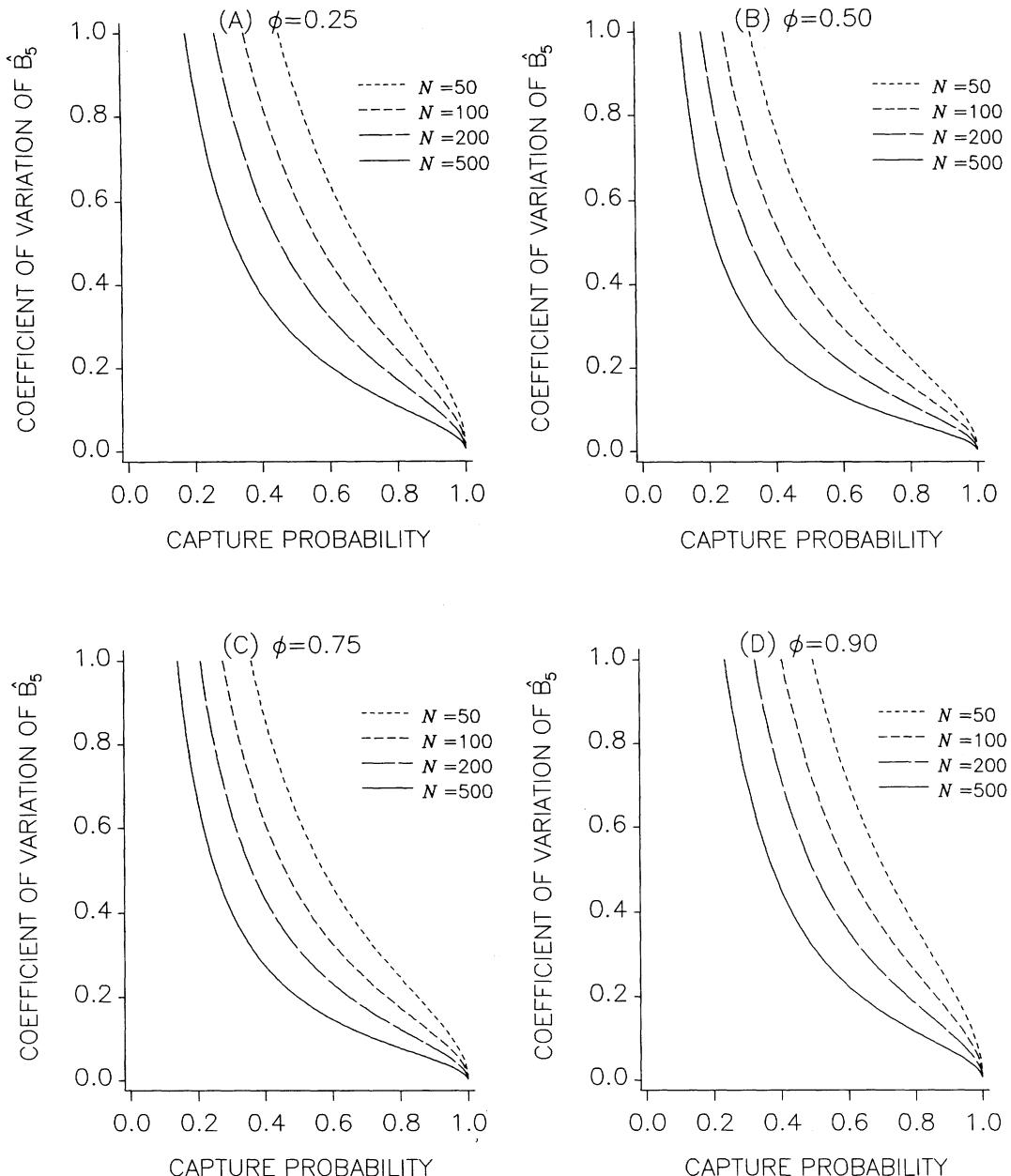


Fig. 8.8. Comparison of the precision of the birth number estimator (\hat{B}_5) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 10$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

to be aware of it. The biologist also should be aware that the size of the population is important. Small populations require much higher capture probabilities than larger ones. In the past there have been too many

small inadequate studies carried out. This may be because statisticians have not given biologists good design guidelines or it may be because biologists have ignored the statisticians!

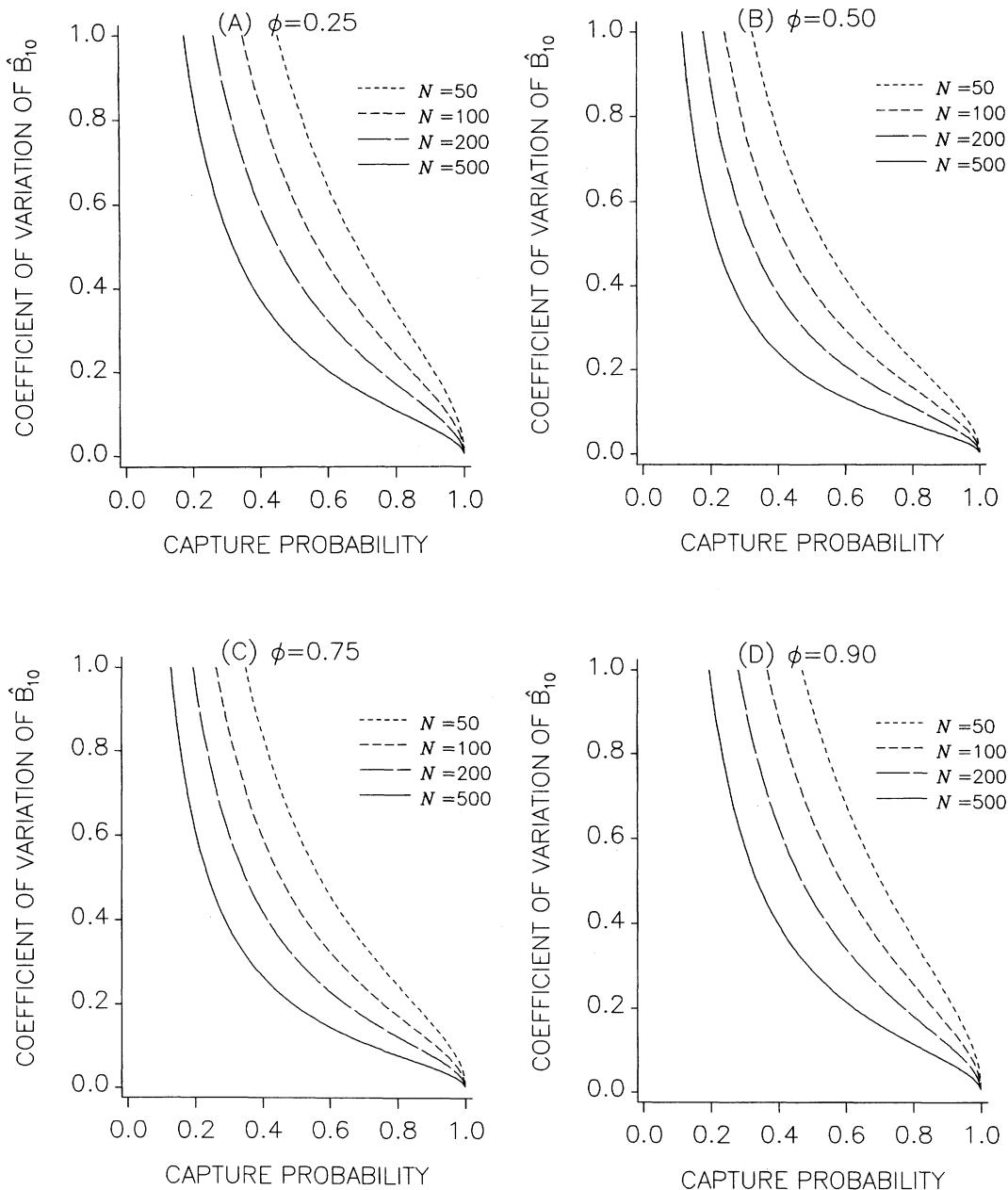


Fig. 8.9. Comparison of the precision of the birth number estimator (\hat{B}_{10}) for a range of population sizes ($N = 50, 100, 200, 500$) when $k = 20$ and survival rate takes the range of values $\phi = 0.25$ (A), 0.50 (B), 0.75 (C), and 0.90 (D). (Jolly-Seber model)

8.4 Capture–Recapture for Treatment Comparisons

In this monograph, and in particular in this chapter, we have considered the question of how to design long-term capture–recapture experiments. The emphasis has

been on how to reduce the variation and the bias in demographic parameter estimates for a particular study area. Burnham et al. (1987) discuss the design of long-term capture–recapture experiments where the purpose is comparison of survival rates under different treatments. For

example, the survival of marked fish passing through turbines of a hydroelectric plant might be compared to the survival of marked fish that did not pass through the turbines. Skalski and Robson also discuss the design of capture-recapture studies useful in the assessment of environmental impact and other treatment comparisons (J. R. Skalski and D. S. Robson. Design and analysis of field studies which use capture data to test hypotheses concerning the abundance of wild populations. Unpublished manuscript.). Their work concentrates on short-term capture-recapture experiments and is closely related to the Lincoln-Petersen model discussed in Chapter 2.

9. COMPREHENSIVE COMPUTER PROGRAMS

Although point estimates and their associated variances and covariances could be calculated for the full rank models by hand, the iterative procedures used in the reduced-parameter models necessitate the aid of a computer. Computer programs JOLLY and JOLLYAGE were written to provide parameter estimates under many of the models described in this monograph (Fig. 9.1).

Program JOLLY computes estimates and test statistics for data that contain only 1 age class. Point estimates of parameters and their variances and various test statistics are computed under Models A, A', B, D, and 2. Program JOLLYAGE computes estimates and test statistics under the 2-age-class models (A2, B2, and D2). Both programs compute goodness-of-fit tests and tests between models to enable the researcher to choose the most appropriate model for the data.

9.1 Program Input

The input data file for programs JOLLY and JOLLYAGE should contain "control" records and "data" records. Control records are used to describe the structure or format of the data records. All control records must precede any data records in the

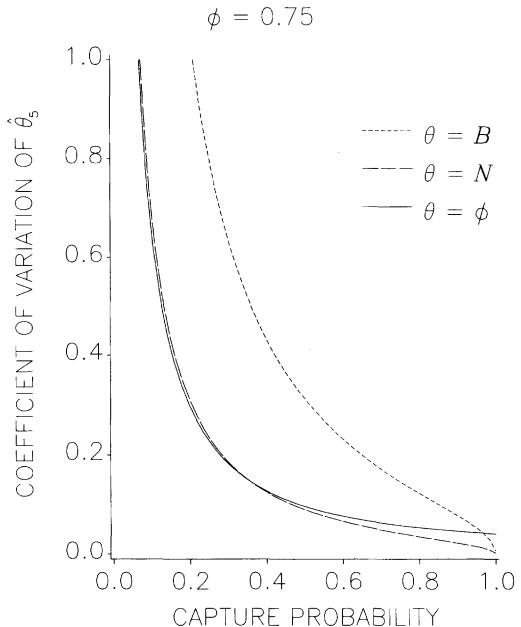


Fig. 8.10. Comparison of the precision of survival rate ($\hat{\theta}_s$), population size (\hat{N}_s), and birth numbers (\hat{B}_s) for the case where $N_i = N = 200$, $\phi_i = \phi = 0.75$, and $k = 10$. (Jolly-Seber model)

input file. Figure 9.2 describes the function of each of the possible control records.

The data records must be in 1 of 3 possible formats. The most common type of data records are capture-history records. Originally, capture-history records were strings of ones and zeros indicating the status of an animal at each sampling period. The data file contained 1 record for each individual captured, and its status at each sample was recorded as 1 if captured and zero if not captured. (If desired, age at first capture also may be recorded.)

Although capture-history records may be entered in this way, a few modifications have been made to allow for special situations and reduce the amount of input. Because many animals may have the same capture history, a weighting variable may be used to indicate the number of animals with a particular capture history. Three other codes to indicate the status of an animal in a particular sample have been added to account for special situations. See Figure 9.3 for definitions of all capture-history status codes.

An example showing input for program JOLLY is shown in Figure 9.4. The first

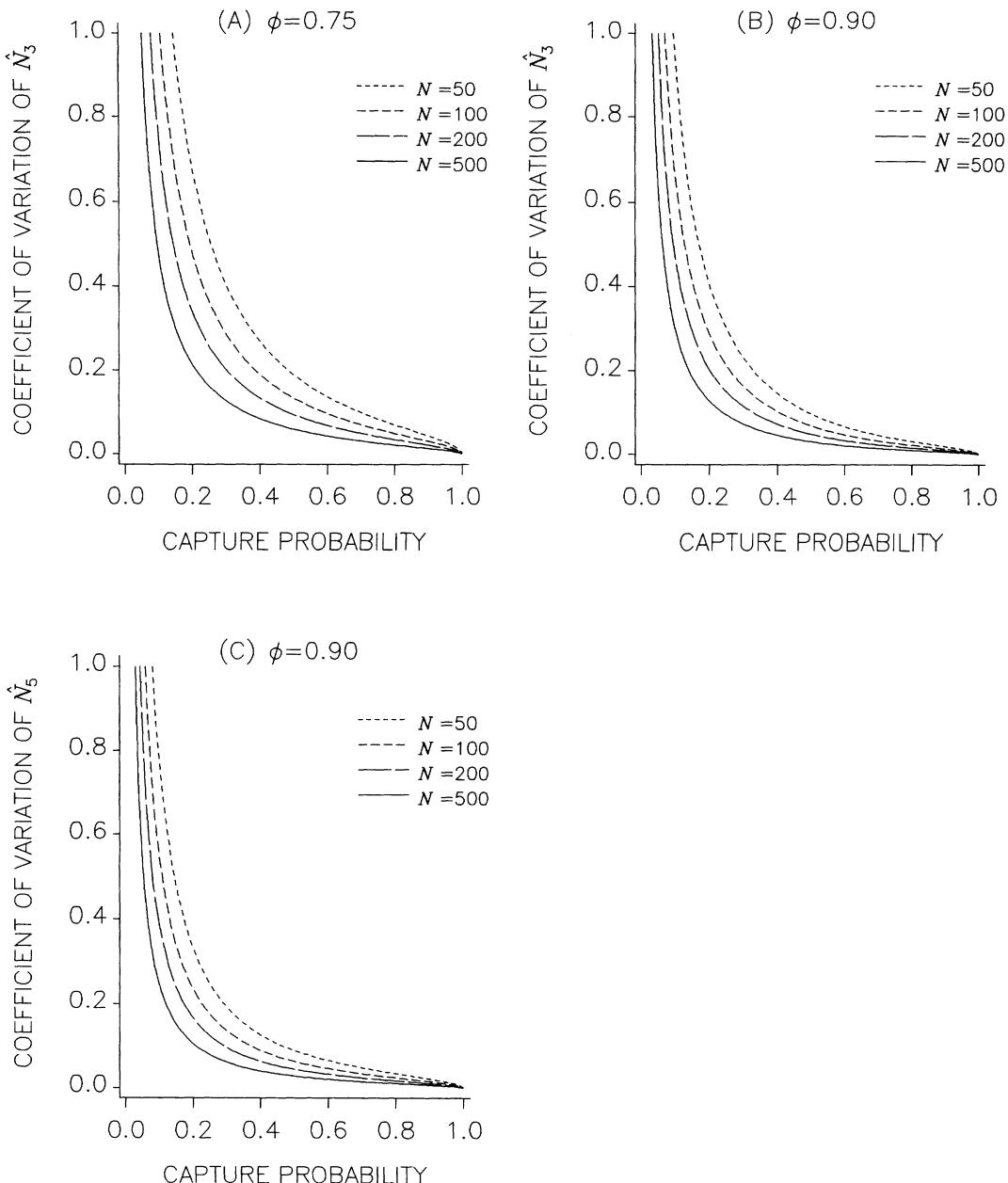


Fig. 8.11. Comparison of precision of population size estimators for a range of population sizes. In case (A) $k = 5$, $\phi = 0.75$, (B) $k = 5$, $\phi = 0.90$, and (C) $k = 10$, $\phi = 0.90$. (Darroch Death Only model)

line in the example in Figure 9.4 will cause program JOLLY to print the title on the first page of output for each model. The second line indicates how many sampling periods there were in the experiment. Because there were 5 sampling periods, there

must be 4 intervals. The lengths of the 4 intervals are given in the third record. The fourth record describes the format of the capture-history records. It was written this way so nonprogrammers may better understand it. The "11" in the format state-

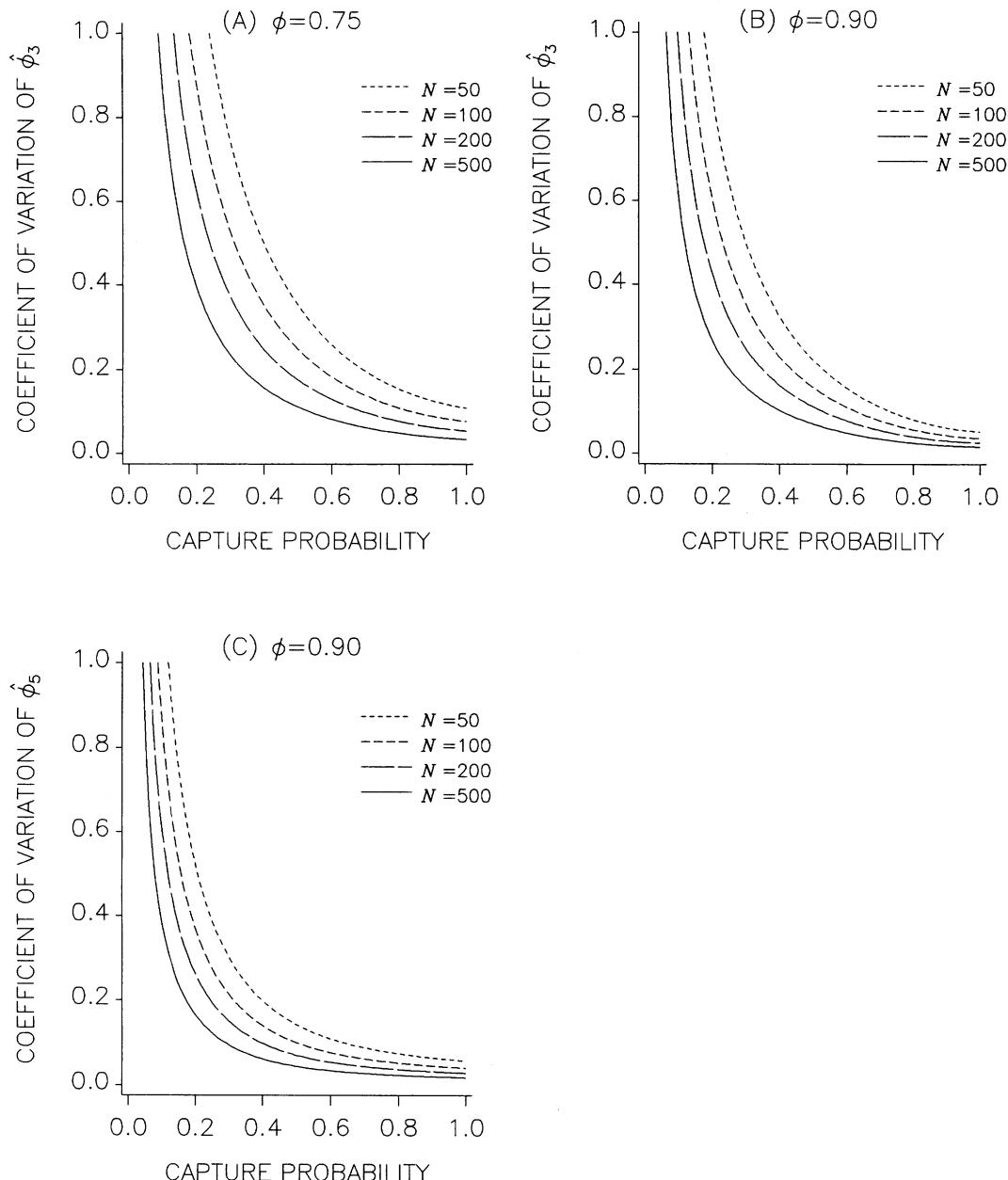


Fig. 8.12. Comparison of precision of survival rate estimators for a range of population sizes. In case (A) $k = 5$, $\phi = 0.75$, (B) $k = 5$, $\phi = 0.90$, and (C) $k = 10$, $\phi = 0.90$. (Darroch Death Only model)

ment tells the program to read a 1-digit integer, the “1X” means skip 1 column, and the “I2” means read a 2-digit integer. So, the status of the animals at each sampling period will be read from columns 1 through 5, and the number of animals with

that capture history will be read in columns 7 and 8.

The first data record indicates that 5 animals were not captured in samples 1 through 3 and were captured and released in samples 4 and 5. Record 2 indicates 12

Program Model Parameters			Description
<hr/>			
JOLLY	A	ϕ_i, p_i	Full Jolly-Seber model
	A'	ϕ_i, p_i	Jolly-Seber "Death only" model
	B	ϕ_i, p	Time-specific survival and constant capture probability
	D	ϕ, p	Constant survival and capture probability
	2	ϕ_i, ϕ^*, p_i	Jolly-Seber model with "trap-response"
JOLLYAGE	A2	ϕ_i, ϕ_i^*, p_i	2-age, time-specific survival and capture probability
	B2	ϕ, ϕ^*, p_i	2-age, constant survival, time-specific capture probability
	D2	ϕ, ϕ^*, p	2-age, constant survival and capture probability

Fig. 9.1. Summary of models in JOLLY and JOLLYAGE.

animals were captured and released in samples 2 and 4 only. The next record shows that 1 individual was captured in sample 1, not captured in sample 2, and captured but not released in sample 3. The last record indicates that 1 animal was cap-

tured in the first sample, not captured in sample 2, resighted between periods 2 and 3, captured in sample 3, and resighted again between samples 3 and 4.

If the individual capture-history records are not available, JOLLY and JOLLYAGE

Control record	Function/comments
<hr/>	
PERIODS=k	Number of sampling periods=k (required, no default)
TITLE=text	Title to appear on output (default:no title)
FIRST=n	First period will be numbered n (default:1)
INTERVALS= x_1, x_2, \dots, x_{k-1}	Specifies interval lengths between sampling periods (default:all lengths=1, used in JOLLY only)
INTER(j)= x_{j+1}, \dots	If only j interval lengths fit on a line, more interval lengths may be specified by using this control record (used in JOLLY only)
[CAPHIS] [or] TYPE=[B-TABLE] [or] [TOTALS]	Specifies the structure of the data records (B-TABLE used in JOLLY only, default:CAPHIS, TOTALS used in JOLLYAGE only)
FORMAT=text	FORTRAN format of data records (default:free)
ADULTS=code	Age-code representing adults (default:1)
YOUNG=code	Age-code representing young (default:2)
ITERATIONS=m	Sets maximum number of iterations for reduced- parameter models to m (default:100)
CONVERG=z	Sets convergence criterion for reduced- parameter models to z (default:.00001)

Fig. 9.2. Description of control records for JOLLY and JOLLYAGE.

Code	Definition
<hr/>	
0	Not captured in sample
1	Captured and released in sample
2	Captured and not released in sample
3 ^a	Not captured in sample, resighted after sample and before next sample
4 ^a	Captured and released in sample and resighted after sample and before next sample

^a Status codes 3 and 4 are intended for use in capture-resighting studies in which all observations do not occur within well-defined sampling periods.

Fig. 9.3. Definitions of capture-history status codes.

```

TITLE=Jolly test data using capture-history records
PERIODS=5
INTERVALS=0.5,1,.8,2
FORMAT=(I1,I1,I1,I1,I1,1X,I2)
00011 5
01010 12
10200 1
13400 1

```

Fig. 9.4. Example of input for program JOLLY.

Last captured in sample	Number captured in sample			
	1	2	3	4
1	0	$m_{1,2}$	$m_{1,3}$	$m_{1,4}$
2	0	0	$m_{2,3}$	$m_{2,4}$
3	0	0	0	$m_{3,4}$
4	0	0	0	0

Number captured	n_1	n_2	n_3	n_4
Number released	R_1	R_2	R_3	R_4

where $m_{i,j}$ = number captured in sample j which were last captured in sample i ,

n_i = number captured (marked+unmarked) in sample i ,

R_i = number released in sample i .

Fig. 9.5. Format of summary table for program JOLLY.

Sample	<i>m</i>	<i>n</i>	<i>n'</i>	<i>R</i>	<i>R'</i>	<i>r</i>	<i>r'</i>	<i>z</i>
1	m_1	n_1	n'_1	R_1	R'_1	r_1	r'_1	z_1
2	m_2	n_2	n'_2	R_2	R'_2	r_2	r'_2	z_2
3	m_3	n_3	n'_3	R_3	R'_3	r_3	r'_3	z_3
4	m_4	n_4	n'_4	R_4	R'_4	r_4	r'_4	z_4

where

m_i = number of marked animals caught in sample *i*,
 n_i = number of adults caught in sample *i*,
 n'_i = number of young caught in sample *i*,
 R_i = number of adults released in sample *i*,
 R'_i = number of young released in sample *i*,
 r_i = number of adults caught in sample *i* which were later recaptured,
 r'_i = number of young caught in sample *i* which were later recaptured,
 z_i = number of adults caught before and after, but not in sample *i*.

Fig. 9.6. Format of summary table for program JOLLYAGE.

will accept table summaries for input. Descriptions of these table summaries are provided in Figures 9.5 and 9.6.

9.2 Program Operation

Programs JOLLY and JOLLYAGE start by presenting a menu to the user. This menu allows the user to specify the input file, output file, models, and output of definitions and covariances. Each item in the menu contains a default value, and the

user may either use this value or change it. To change a value in the menu, type an item number and enter a new value for that item at the prompt. When ready to run the program, type the item number that says "RUN." An example of the menu and steps needed to run JOLLY are given in Figure 9.7.

9.3 Program Output

Output from both programs is summarized in Figure 9.8. The estimates com-

```
Program JOLLY <10/07/88>
-----
1) Data filename:JOLLYINP
2) Name of print file:LPT1
3) Models:A,B,D
4) Print definitions:NO
5) Print Covariance matrices:NO
6) Run...
7) Quit
Choice(1...7)? _

To change the input data file, type:
1 [Enter]
JLYEXMPL [Enter]

To instruct the program to print a page of definitions and include
model A', type:
4 [Enter]
3 [Enter]
A' [Enter]

To begin the analysis, type:
6 [Enter]
```

Fig. 9.7. Example of menu and steps needed to run JOLLY.

JOLLY	JOLLYAGE
- Page of definitions (if desired)	- Page of definitions (if desired)
- Summary of input	- Summary of input
- Model A	- Model A2
- Estimates of survival rate, population size, and capture probability with standard errors and approximate 95% confidence intervals	- Estimates of survival rate, population size, and capture probability with standard errors and approximate 95% confidence intervals
- 'Goodness-of-fit' test	- 'Goodness-of-fit' test
- Model A' (if desired)	- Test of model A vs. A2
- Model 2 (if desired)	- Model B2 (if desired)
- Model D (if desired)	- Model D2 (if desired)
- Model B (if desired)	- Tests between models
- Tests between models	

Fig. 9.8. Summary of output for programs JOLLY and JOLLYAGE.

puted by the programs for models A, A', and A2 are “bias-adjusted” to compensate for small sample sizes. For some estimates, 2 different standard errors are computed. One is the standard error that accounts for both sampling and nonsampling variation, and the other includes only nonsampling variation (Chapter 4). These standard errors are defined on the page of definitions.

When sample sizes are small and the summary table contains zeros, some of the estimates cannot be computed. When this happens, the programs will print “Undef” to indicate that a particular estimate is undefined. Another result of small sample sizes is that the goodness-of-fit test can yield zero (or negative) degrees of freedom after cell pooling, indicating that a proper test cannot be conducted with the data.

9.4 Example

Figures 9.9 and 9.10 contain the input and output for program JOLLYAGE for the northern pike data set used as an example in Chapter 6 (Pollock and Mann 1983). Figure 9.9 shows the 2 possible ways in which data can be input. Note that the TOTALS input option does not provide all of the data needed for model testing. The program output in Figure 9.10 was based

on capture-history input data. The detailed output follows the sequence described in Figure 9.8, and the estimates and test statistics correspond to those presented in Figures 6.11, 6.12, and 6.13.

9.5 Programming Details

Programs JOLLY and JOLLYAGE were written in FORTRAN and contain 3,200 and 2,100 lines of code, respectively. Users of IBM PC and compatibles may obtain these programs by sending a formatted blank diskette to James E. Hines, Patuxent Wildlife Research Center, Laurel, MD 20708.

Usually, the user will receive the executable code files for the programs along with documentation files and some sample data files. The FORTRAN source code also is available upon request. Users with modems may download the software from SESAME (SouthEastern Software And Message Exchange), which is a free online bulletin board and public software library service for fisheries and wildlife resource managers who use microcomputers (phone [919]737-3990; 1,200 baud, 8 data bits, no parity). Mainframe users who have a FORTRAN compiler may obtain the programs by sending a blank computer tape and specifying the required format.

TITLE=CANADIAN JOURNAL EXAMPLE							
PERIODS=8							
FORMAT=(A1,8I2,I3)							
ADULT=1							
YOUNG=2							
2 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	14
2 1 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	4
2 1 1	1 1 1	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
2 1 0	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
2 0 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	25
2 0 1	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	3
2 0 1	0 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
2 0 0	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	18
2 0 0	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	2
2 0 0	1 0 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
2 0 0	0 0 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	25
2 0 0	0 1 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	2
2 0 0	0 1 1	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	1
2 0 0	0 1 1	0 0 1	0 0 0	0 0 0	0 0 0	0 0 0	1
2 0 0	0 0 1	0 0 0	1 0 0	0 0 0	0 0 0	0 0 0	8
2 0 0	0 0 0	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	2
2 0 0	0 0 0	0 1 1	1 0 0	0 0 0	0 0 0	0 0 0	1
2 0 0	0 0 0	0 1 1	1 1 0	0 0 0	0 0 0	0 0 0	1
2 0 0	0 0 0	0 0 0	1 0 0	0 0 0	0 0 0	0 0 0	34
2 0 0	0 0 0	0 0 0	1 1 0	1 0 0	0 0 0	0 0 0	12
2 0 0	0 0 0	0 0 0	1 1 1	1 0 0	0 0 0	0 0 0	1
2 0 0	0 0 0	0 0 0	1 1 0	0 1 0	0 0 0	0 0 0	18
2 0 0	0 0 0	0 0 0	0 1 1	0 1 0	0 0 0	0 0 0	4
1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	19
1 1 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	5
1 1 1	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	2
1 1 0	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	2
1 1 0	0 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
1 0 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	8
1 0 1	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	2
1 0 0	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	9
1 0 0	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	4
1 0 0	1 0 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
1 0 0	0 1 1	1 0 0	0 0 0	0 0 0	0 0 0	0 0 0	1
1 0 0	0 0 1	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	11
1 0 0	0 0 0	1 1 0	0 0 0	0 0 0	0 0 0	0 0 0	11
1 0 0	0 0 0	0 1 1	0 0 0	0 0 0	0 0 0	0 0 0	2
1 0 0	0 0 0	0 0 1	1 1 0	0 0 0	0 0 0	0 0 0	3
1 0 0	0 0 0	0 0 0	1 0 0	0 0 0	0 0 0	0 0 0	14
1 0 0	0 0 0	0 0 0	1 1 0	0 0 0	0 0 0	0 0 0	5
1 0 0	0 0 0	0 0 0	1 0 1	0 0 0	0 0 0	0 0 0	1
1 0 0	0 0 0	0 0 0	0 0 1	0 0 0	0 0 0	0 0 0	12
1 0 0	0 0 0	0 0 0	0 0 0	1 0 1	0 0 0	0 0 0	2

TITLE=CANADIAN JOURNAL EXAMPLE							
PERIODS=8							
FORMAT=(8F4.0)							
TYPE=TOTALS							
0	29	20	29	20	10	6	0
12	22	29	22	29	5	4	4
11	28	21	28	21	11	3	2
14	24	29	24	29	5	4	2
9	25	11	25	11	8	3	2
11	31	47	31	47	11	13	2
24	38	22	38	22	3	4	2
9	9	0	9	0	0	0	0

Fig. 9.9. Sample input data files for program JOLLYAGE.

10. OTHER APPROACHES

In this monograph we have emphasized material that is useful to the biologist. We have available 2 computer programs, JOLLY and JOLLYAGE, that increase the utility of our monograph. It has not been possible for us to give a comprehensive description of all possible analyses of open population models. Here we briefly mention some significant approaches that we have not considered.

Fienberg (1972) applied log-linear models to the estimation of population size in a closed population. Cormack (1981, 1985) showed how the statistical package GLIM could be applied to capture-recapture problems and extended the use of log-linear models to open populations. Some of these models have been implemented in POPAN-3 (Arnason and Schwarz 1987).

Bonett et al. (1986) also developed a more general log-linear model for a closed population. Cormack (1989) provides a general review of the current use of log-linear models for capture-recapture studies. Although the log-linear model approach is extremely useful, we do not think it will replace other approaches. It has not been applied to the age-dependent models (Chapter 6) or the robust design (Chapter 7). In fact, we do not see how it could be applied easily to the robust design. Also it is difficult to implement if the number of samples is large, and it is difficult to get parameter estimates and their variances from the GLIM output.

Crosbie and Manly (1985) present a version of the Jolly-Seber model with a program, CMR, that allows the user to put restrictions on the birth and death processes. This means that parsimonious

```

-----  

INPUT==>TITLE=CANADIAN JOURNAL EXAMPLE  

CONTROL RECORD: TITLE=CANADIAN JOURNAL EXAMPLE  

INPUT==>PERIODS=8  

CONTROL RECORD: PERIODS= 8  

INPUT==>FORMAT=(A1,8I2,I3)  

CONTROL RECORD: FORMAT=(A1,8I2,I3)  

INPUT==>ADULT=1  

CONTROL RECORD: ADULT=1  

INPUT==>YOUNG=2  

CONTROL RECORD: YOUNG=2  

INPUT==>2 1 0 0 0 0 0 0 14  

1st DATA RECORD:2 1 0 0 0 0 0 0 14  

JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE 2/23/89 15:49

NUMBER OF TRAPPING PERIODS = 8  

DATA TYPE = CAPTURE-HISTORY RECORDS  

INPUT FORMAT = (A1,8I2,I3)  

MAX ITERATIONS = 100  

CONVERGENCE CRITERION = 0.1000E-04

SUMMARY OF DATA:

Time # Marked # Caught # Released # Caught & seen later # Not caught
Period Adlt Adlt Yng Adlt Yng Adlt Yng & seen later
-----
1 0 29 20 29 20 10 6 0
2 12 22 29 22 29 5 4 4
3 11 28 21 28 21 11 3 2
4 14 24 29 24 29 5 4 2
5 9 25 11 25 11 8 3 2
6 11 31 47 31 47 11 13 2
7 24 38 22 38 22 3 4 2
8 9 9 0 9 0 0 0 0

45 Input records read
45 Records used

```

Fig. 9.10. Sample output from either of the input files in Fig. 9.9. (Fig. 9.10 continues through page 93.)

models with better precision than the Jolly-Seber model can be obtained. These models allow more flexibility than those we have programmed into JOLLY, which are presented in Section 5.3. The program is not generally available.

Brownie et al. (1985) present a detailed monograph describing analysis of band-

return data complete with 2 programs, ESTIMATE and BROWNIE, which are analogs of JOLLY and JOLLYAGE for capture-recapture data. We recommend that the practice of analyzing capture-recapture data with these programs by only using first and last capture times be abandoned. Brownie and Pollock (1985) found

```

JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE 2/23/89 15:49

Model A2 - Time-specific survival rates for adults young, time-specific adult
capture probabilities.

Parameters: PHI(i) = Adult survival rate in period i
            PHI'(i) = Young survival rate in period i
            P(i) = Adult capture probability in period i

      i    PHI'     SE(PHI')    SE'(PHI')    95% confidence interval
-----
1  0.5125    0.2344    0.2060    0.0531 - 0.9719
2  0.1680    0.0817    0.0431    0.0787 - 0.3282
3  0.1994    0.1186    0.0803    -0.0330 - 0.4318
4  0.1853    0.0948    0.0614    -0.0004 - 0.3710
5  0.3427    0.1778    0.1056    -0.0059 - 0.6912
6  0.4628    0.2181    0.2056    0.0353 - 0.8902
MEAN  0.3118    0.0675    0.0548    0.1795 - 0.4440

      I    PHI     SE(PHI )    SE'(PHI )    95% confidence interval
-----
1  0.5891    0.2342    0.2156    0.1301 - 1.0480
2  0.2768    0.1143    0.0895    0.0528 - 0.5008
3  0.5484    0.1920    0.1714    0.1720 - 0.9248
4  0.2799    0.1251    0.0983    0.0346 - 0.5251
5  0.4021    0.1339    0.1011    0.1397 - 0.6644
6  0.5937    0.2814    0.2695    0.0421 - 1.1452
MEAN  0.4483    0.0644    0.0548    0.3220 - 0.5746

```

I	N	SE(N)	SE'(N)	95% confidence interval	
2	48.36	18.14	17.81	12.80	- 83.91
3	38.26	8.79	8.16	21.04	- 55.49
4	37.22	11.84	11.29	14.02	- 60.42
5	38.42	11.68	11.31	15.53	- 61.32
6	43.56	10.68	10.17	22.63	- 64.49
7	67.86	29.46	29.21	10.13	- 125.59
MEAN	45.61	6.93	6.66	32.03	- 59.19

I	p	SE(p)	95% confidence interval	
2	0.4390	0.1720	0.1019	- 0.7762
3	0.6947	0.1705	0.3606	- 1.0289
4	0.6269	0.1998	0.2352	- 1.0185
5	0.6090	0.1987	0.2196	- 0.9984
6	0.6735	0.1772	0.3261	- 1.0209
7	0.5517	0.2278	0.1051	- 0.9983
MEAN	0.5991	0.0784	0.4454	- 0.7528

I	B	SE(B)	95% confidence interval	
2	24.88	15.20	-4.91	- 54.66
3	16.24	19.07	-21.14	- 53.62
4	28.00	11.99	4.51	- 51.50
5	28.11	17.98	-7.13	- 63.35
6	42.00	30.70	-18.17	- 102.17
MEAN	27.85	8.53	11.13	- 44.56

that to be a very inefficient procedure, and now it is totally unnecessary.

White (1983) has written a general program for band-recovery data called SURVIV that can be used to obtain survival rates for capture-recapture data. Without additional programming, however, it cannot currently be used to obtain population

size estimates. SURVIV can be difficult for a biologist to use, although it is an incredibly powerful program.

The use of auxiliary variables to improve precision in capture-recapture studies was considered by Pollock et al. (1984) for closed populations. Currently there is no easy way to use a program that incor-

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JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE      2/23/89 15:49
Test of the hypothesis that adult and young survival and capture
probabilities are the same (from Pollock 1981; Biometrics 37:521-529)

i= 1
          Adults   Young
          Released  1st Cap
          in i     in i
+-----+
! 10.00! 6.00!
! 9.47! 6.53!
+-----+
! 19.00! 14.00!
! 19.53! 13.47!
+-----+
Chi-square = 0.1082 with 1 degrees of freedom, Probability = 0.7422

i= 2
.
.
.
i= 8
          Adults   Young
          Released  1st Cap
          in i     in i
+-----+
! 0.00! 0.00!
! 0.00! 0.00!
+-----+
! 9.00! 0.00!
! 9.00! 0.00!
+-----+
Chi-square = 0.0000 with 0 degrees of freedom, Probability = 0.0000

Total chi-square = 6.98
Degrees of freedom= 7.
Overall Prob. = 0.4310
```

JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE 2/23/89 15:49

Contingency table goodness-of-fit test

i= 2	Adults 1st cap	Young 1st cap	Adults before i before i in i	2.00! 1.59!	1.00! 1.14!	2.00! 2.27!
Cap in i, released & recap						
Expected value						
Cap in i, released & not recap				5.00! 5.41!	4.00! 3.86!	8.00! 7.73!
Expected value						

Chi-square = 0.0776 with 1 degrees of freedom (Prob.=0.7805)

	Adults 1st cap	Young 1st cap	Adults 1st cap	Young 1st cap	before i-1 before i-1 in i-1 in i-1
Cap in i	! 0.00!	0.00!	7.00!	5.00!	
Expected value	! 0.00!	0.00!	7.50!	4.50!	
Cap after, not in i	! 0.00!	0.00!	3.00!	1.00!	
Expected value	! 0.00!	0.00!	2.50!	1.50!	

Chi-square = 0.0000 with 0 degrees of freedom (Prob.=1.0000)

i= 3

i= 7	Adults 1st cap	Young 1st cap	Adults before i before i in i	2.00!	1.00!	2.00!
Cap in i, released & recap	! 0.00!	1.00!	2.00!			
Expected value	! 0.71!	1.18!	1.11!			
Cap in i, released & not recap	! 9.00!	14.00!	12.00!			
Expected value	! 8.29!	13.82!	12.89!			

Chi-square = 0.0000 with 0 degrees of freedom (Prob.=1.0000)

	Adults 1st cap	Young 1st cap	Adults 1st cap	Young 1st cap	before i-1 before i-1 in i-1 in i-1
Cap in i	! 4.00!	2.00!	5.00!	13.00!	
Expected value	! 3.69!	2.77!	5.54!	12.00!	
Cap after, not in i	! 0.00!	1.00!	1.00!	0.00!	
Expected value	! 0.31!	0.23!	0.46!	1.00!	

Chi-square = 0.0000 with 0 degrees of freedom (Prob.=1.0000)

Chi-square = 3.1456 with 5 degrees of freedom (Prob.=0.6776)

Chi-square = 0.0000 with 0 degrees of freedom (Prob.=1.0000)

Overall chi-square = 3.1456 with 5 degrees of freedom (Prob. =0.6776)

JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE

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Model D2 - Constant survival rate per unit time, constant capture probability per unit time.

Parameters: PHI = Adult survival rate per unit time
 PHI' = Young survival rate per unit time
 P = Adult capture probability per unit time

Starting values of PHI (adult, young), and p: 0.4483 0.3118 0.5700

Final values after 10 iterations

Parm	Estimate	Var	Std.error	95% conf int	Cov W/ PHI	Cov W/ PHI'
PHI	0.4012	0.0017	0.0416	0.3198 - 0.4827		0.00032212
PHI'	0.3033	0.0027	0.0522	0.2009 - 0.4056	0.00032212	
p	0.5839	0.0054	0.0733	0.4402 - 0.7276		

Period	M	Variance	Standard error	95% confidence interval	Covariance(p,M(i))
2	22.83	12.32	3.51	15.95 - 29.71	-0.12
3	18.55	10.24	3.20	12.27 - 24.82	-0.12
4	22.83	13.05	3.61	15.75 - 29.91	-0.14
5	15.71	8.43	2.90	10.01 - 21.40	-0.10
6	18.63	10.35	3.22	12.33 - 24.94	-0.12
7	38.16	29.63	5.44	27.49 - 48.83	-0.26
8	15.41	13.58	3.69	8.19 - 22.64	-0.12
MEAN	21.73	36.95	6.08	9.82 - 33.65	

Period	N	Variance	Standard error	95% Confidence interval
2	39.96	36.45	6.04	28.12 - 51.79
3	47.66	56.27	7.50	32.96 - 62.37
4	39.96	38.20	6.18	27.84 - 52.07
5	43.11	49.64	7.05	29.30 - 56.92
6	52.89	67.12	8.19	36.83 - 68.95
7	62.14	76.91	8.77	44.95 - 79.33
8	15.41	13.58	3.69	8.19 - 22.64
MEAN	43.02	158.84	12.60	18.32 - 67.72

Period	B	Variance	Standard error	95% Confidence interval	Covar(B(i-1),B(i))
2	35.05	31.59	12.60	18.32 - 67.72	*****
3	18.63	18.88	4.34	10.12 - 27.15	-6.97
4	33.34	29.27	5.41	22.73 - 43.94	-3.65
5	33.01	37.83	6.15	20.96 - 45.07	-1.08
6	32.51	25.78	5.08	22.56 - 42.46	-6.79
7	2.67	7.22	2.69	-2.60 - 7.93	-8.08
MEAN	25.87	16.24	4.03	17.97 - 33.77	

porates this option for open populations. Program SURVIV (White 1983) can be used for this purpose if survival and recapture rates are the only parameters of interest. Program MULT (Conroy and Williams 1984) also can be used to incorporate auxiliary information but is designed for band-return data.

Clobert and Lebreton (1985) describe a program for use with resighting data that permits models with constant survival and/or capture rates, and models with survival expressed as a function of environmental variables. This program is being modified to cope with losses on capture so that it will handle live recapture data. Other in-

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JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE          2/23/89 16:13
Model B2 - Constant survival rate per unit time, time-specific capture
probabilities.

Parameters: PHI = Adult survival rate per unit time
            PHI' = Young survival rate per unit time
            P(i) = Adult capture probability in sample i

Starting values of PHI (Adult, Young):    0.4483    0.3118
Starting values of p:
  0.4054   0.6836   0.5932   0.5902   0.6612   0.4865   0.5700
Final values after      6 iterations

  Parm Estimate   Var Std.Error 95% conf int      Cov w/ PHI      Cov W/ PHI'
  PHI     0.4209   0.0019  0.0435  0.3355 - 0.5062           0.00034621
  PHI'    0.3103   0.0029  0.0534  0.2057 - 0.4150           0.00034621
  p( 2)  0.5663   0.0163  0.1278  0.3158 - 0.8168  -0.00062506  -0.00105495
  p( 3)  0.5433   0.0218  0.1475  0.2542 - 0.8325  -0.00106927  -0.00208030
  p( 4)  0.6411   0.0208  0.1444  0.3582 - 0.9240  -0.00142772  -0.00203748
  p( 5)  0.4495   0.0204  0.1429  0.1694 - 0.7296  -0.00119694  -0.00206639
  p( 6)  0.6101   0.0244  0.1563  0.3037 - 0.9165  -0.00168732  -0.00186946
  p( 7)  0.7326   0.0154  0.1242  0.4893 - 0.9759  -0.00158096  -0.00249410
  p( 8)  0.3369   0.0133  0.1153  0.1108 - 0.5629  -0.00161452  -0.00157676
  Avg p  0.5543   0.0266  0.1631  0.2346 - 0.8739
```

Period	M	Variance	Standard error	95% confidence interval	
2	23.15	13.58	3.69	15.92	- 30.37
3	18.99	10.67	3.27	12.59	- 25.39
4	21.78	12.84	3.58	14.75	- 28.80
5	17.74	11.95	3.46	10.96	- 24.51
6	17.65	9.66	3.11	11.56	- 23.74
7	33.74	24.55	4.96	24.03	- 43.46
8	26.72	152.92	12.37	2.48	- 50.95
MEAN	22.82	67.22	8.20	6.75	- 38.89

Period	N	Variance	Standard error	95% Confidence interval	
2	40.80	59.76	7.73	25.65	- 55.96
3	50.28	140.30	11.84	27.06	- 73.50
4	37.37	50.71	7.12	23.42	- 51.33
5	53.33	222.31	14.91	24.11	- 82.56
6	50.43	133.73	11.56	27.76	- 73.10
7	52.85	67.18	8.20	36.79	- 68.92
8	26.72	152.92	12.37	2.48	- 50.95
MEAN	44.54	236.56	15.38	14.40	- 74.69

Period	B	Variance	Standard error	95% Confidence interval	
2	37.07	109.78	10.48	16.53	- 57.60
3	16.10	38.02	6.17	4.02	- 28.19
4	42.24	179.86	13.41	15.95	- 68.53
5	27.95	110.19	10.50	7.37	- 48.52
6	28.32	39.90	6.32	15.94	- 40.70
7	4.68	4.66	2.16	0.44	- 8.91
MEAN	26.06	136.39	11.68	3.17	- 48.95

teresting and flexible models that can be implemented using this program are described in Clobert et al. (1987). Though not yet generally available, we believe the Clobert-Lebreton program has the potential to be very useful for biologists.

Recently Burnham et al. (1987) published an important monograph on com-

parison of survival rates from different populations using capture-recapture methods. To accompany this monograph, White produced a new program, RELEASE, which produces survival rate and capture rate estimates under a series of increasingly complex models and also provides tests to assist in model selection.

JOLLYAGE (Ver 8/10/88) CANADIAN JOURNAL EXAMPLE						2/23/89 16:13			
Test of Model D2 vs A2			Test of Model B2 vs A2			Test of Model D2 vs B2			
Per	T1	T1	T2	T1	T1	T2	T1	T1	T2
1	0.5806	0.9139	0.0000	0.4085	0.8671	0.0000	0.0135	0.0005	0.0000
2	0.3166	0.9646	0.7933	0.3969	0.9624	0.5182	0.0052	0.0000	0.0219
3	1.7278	0.6090	0.0160	0.9165	0.8655	0.2184	0.1091	0.0302	0.1448
4	0.6272	0.9610	0.2016	0.3451	0.5548	0.0009	0.0475	0.0688	0.1785
5	0.1994	0.2467	0.0000	0.0117	0.1216	0.4806	0.1122	0.0191	0.0000
6	1.0356	1.4038	0.0008	0.1321	0.3628	0.0290	0.4043	0.3028	0.0000
7	5.1101	0.0034	0.9280	1.2327	1.4033	0.0000	1.8121	0.7940	0.1972
Tot	9.5973	5.1024	1.9397	3.4435	5.1373	1.2472	2.5039	1.2154	0.5424
Total chi-square =	16.6394			Total chi-square =	9.8280		Total chi-square =	4.2617	
Deg of freedom =	16			Deg of freedom =	10		Deg of freedom =	4	
Probability =	0.4093			Probability =	0.4557		Probability =	0.3717	
Goodness-of-fit tests:									
Model	Chi-square	df	Probability						
A2	3.15	5	0.6776						
B2	12.97	15	0.6043						
D2	19.78	21	0.5349						

Finally, we mention the work of Skalski and Robson (see page 81). In their monograph they consider the use of simple capture-recapture methods in the design and analysis of ecological field studies such as environmental impact assessment.

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