

CAPTURE-RECAPTURE MODELS: A REVIEW OF CURRENT METHODS,
ASSUMPTIONS AND EXPERIMENTAL DESIGN

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ABSTRACT

The current "state of the art" in capture-recapture sampling methodology is reviewed. An emphasis is placed on model assumptions, model robustness to assumption failure, and in particular on the often neglected topic of study design.

For short term studies, there has been much recent work on closed population models that allow for unequal catchability of individual animals (heterogeneity and or trap response). The closure assumption causes problems for many terrestrial bird population studies. A model which allows a closed population of "residents" plus some short term "wanderers" through the study area is considered.

For long term studies, open population models that assume equal catchability are discussed. They allow estimation of survival and birth rates as well as population sizes. Recent developments which allow some age-dependence of survival and capture probabilities, are reported and related to some recent band recovery models. In terrestrial bird studies resighting of color-marked birds without capture could be potentially useful for estimation of survival rates.

1. INTRODUCTION

Capture-recapture sampling has been widely used and abused for many years in the study of natural animal populations. Excellent reviews are given by Cormack (1968) and Seber (1973). Recently there has been a renewed interest

in the assumptions behind capture-recapture sampling and especially in the assumption of "equal catchability" of all animals in the population. Some new models relaxing this assumption have been proposed, complete with estimators and tests of model fit (Pollock 1974, 1975a, 1975b; Burnham 1972; Burnham and Overton 1978, 1979). Of particular importance is the monograph for biologists by Otis et al. (1978).

Here I concentrate on reviewing the current theory from an applied statistician's viewpoint but for an audience mainly of biologists with some knowledge of statistical thinking. Assumptions, robustness to assumption failure, and design concepts will be emphasized with statistical complexities kept to a minimum. Extensive reference will be made to source materials that may be consulted for more technical details on a particular model or concept.

The review falls naturally into sections on closed and open population models. Here by open we mean additions (birth and/or immigration) into the population are allowed, as are permanent deletions (death and/or emigration) from the population. Closed then means that neither additions nor permanent deletions are permitted. These sections are followed by a general discussion of the important issues raised.

2. SOME DEFINITIONS

Typically a capture-recapture study is carried out in the following way. The population under study is sampled two or more times. At each time, every unmarked animal caught is uniquely marked (usually with a numbered leg band in bird studies); previously marked animals have their capture recorded and then most or all of the animals are released back into the population. Thus at the end of the study the experimenter has the complete capture history of each animal handled. Batch marks where all animals captured in a particular sample cannot be distinguished are sometimes used but provide much less

information and should be avoided if practically feasible.

The typical capture-recapture study described then provides two distinct types of information:

- (i) information from the recovery of marked animals
- (ii) information from comparing numbers of marked and unmarked animals captured at each sampling time.

Data from (i) can be used to estimate survival rates, whereas data from (i) and (ii) are necessary to estimate population size. Sometimes survival rate estimation is of primary concern and the type (ii) information will not be collected. This is typical of the usual band recovery studies where banded birds are recovered dead by hunters or other persons. It is also true for studies where live banded birds are resighted without actual physical capture.

3. SHORT-TERM STUDIES - CLOSED-POPULATION MODELS

3.1 THE PETERSEN MODEL

This simplest form of capture-recapture experiment, which is also often called the Lincoln Index¹ has a long history (see Seber 1973:59). 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 sample should reflect the same ratio in the population so that

$$\frac{m_2}{n_2} \approx \frac{n_1}{N}$$

which gives the estimator (\hat{N})

¹This is really a misuse of the word Index which usually refers to a measure of relative abundance (Caughley 1977:12).

$$\hat{N} = \frac{n_1 n_2}{m_2} . \quad (1)$$

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

$$\hat{N}_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1 , \quad (2)$$

with an unbiased estimate of its variance given by

$$\widehat{\text{Var}}(\hat{N}_c) = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \quad (3)$$

from Seber (1973:60).

These estimators are based on a model in which the following assumptions are made:

- (i) All animals are equally likely to be caught in each sample--The "Equal Catchability" Assumption,
- (ii) The population is closed to additions or deletions--The Closure Assumption,
- (iii) Marks (bands) are visible and are not lost--The Zero Band Loss Assumption.

Clearly these assumptions are not always satisfied in practice and in the following sections we consider in detail each assumption and models allowing some relaxation of them. It should be emphasized that usually we consider a general K-sample capture-recapture experiment with more than two samples. This is often referred to as the Schnabel Census.²

3.2 THE EQUAL CATCHABILITY ASSUMPTION

This assumption is very unlikely in most wildlife populations. Two

²Census has been an extremely misused term in this literature. A census is defined to be a complete enumeration of a population, whereas capture-recapture methods involve sampling only part of a population.

general types of alternatives exist:

(i) Heterogeneity: the probability of capture in any sample is a property of the animal and may vary over the population. That is animals may vary in capture probability according to age, sex, social status and many other factors.

(ii) Trap Response: the probability of capture in any sample depends on the animal's prior history of capture. That is, animals may become "trap shy" or "trap happy" depending on the type of trapping method used.

Either one or both of these two types of alternatives may be acting in a particular animal population.

Here we discuss the following series of mutually exclusive models first considered by me (Pollock 1974) and later by Otis et al. (1978) in an excellent monograph for biologists interested in detailed study.

M_0 : no trap response, no heterogeneity

M_b : trap response, no heterogeneity

M_h : no trap response, heterogeneity

M_{bh} : trap response, heterogeneity

3.2.1 M_0 : THE EQUAL CATCHABILITY MODEL

This model does not allow heterogeneity or trap response of the individual animal capture probabilities and makes the following assumptions:

(i) Every animal in the population has the same probability of capture at each sampling time, p_i ; $i = 1, \dots, K$.

(ii) The probability of capture does not change over sampling times;
 $p_i = p$; $i = 1, \dots, K$.

Otis et al. (1978) call the model using only assumption (i) above M_t , and it is the classical capture-recapture model for a closed population with a history going back to Schnabel (1938). A detailed statistical treatment is

given by Darroch (1958) (who refers to it as Model A) and Seber (1973:164).

An application involving red-winged blackbirds (Agelaius phoeniceus) is given by Hewitt (1967). M_0 which requires assumptions (i) and (ii) is a special case of M_t with capture probabilities constant over time.

An approximate maximum likelihood (M.L.) estimator of N for Model M_0 is the solution of

$$\left(1 - \frac{M_{k+1}}{\hat{N}}\right) = (1-\hat{p})^K, \quad (4)$$

which must be found iteratively. Note that $\hat{p} = n./K\hat{N}$ with M_{k+1} the number of distinct animals captured in the whole experiment and $n.$ the sum of the numbers of animals captured in each sample. The approximate estimated large sample variance is

$$\widehat{\text{Var}}(\hat{N}) = \hat{N} \left[\frac{1}{(1-\hat{p})^K} + (K-1) - \frac{K}{(1-\hat{p})} \right]^{-1}. \quad (5)$$

Otis et al. (1978) compute the M. L. estimator directly using a numerical method.

It should be emphasized that this estimator can be highly biased if there is unequal catchability. Heterogeneity causes a negative bias, while trap response can cause positive or negative bias depending on whether the animals are "trap shy" or "trap happy" respectively.

3.2.2 M_b : THE TRAP RESPONSE MODEL

This model, allowing trap response but no heterogeneity, makes the following assumptions:

(i) Every unmarked animal in the population has the same probability of capture (p) for all samples

(ii) Every marked animal in the population has the same probability of recapture (c) for all samples after it has been captured once.

An approximate M. L. estimator of N is the solution of

$$\left(1 - \frac{M_{K+1}}{\hat{N}}\right) = (1-\hat{p})^K, \quad (6)$$

where \hat{p} is now given by $M_{K+1}/(\hat{N} - \sum_{i=1}^K M_i)$ and M_i is the number of marked animals available for capture in the i th sample. The M. L. estimator has an estimated approximate variance of

$$\widehat{\text{Var}}(\hat{N}) = \frac{\hat{N}(1-(1-\hat{p})^K)(1-\hat{p})^K}{[1-(1-\hat{p})^K]^2 - (\hat{p}K)^2(1-\hat{p})^{K-1}}. \quad (7)$$

Notice that the recapture probability \hat{c} , does not appear in (6). In fact 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 1973:309) in which an animal is considered removed by marking rather than physically removed.

Typically in the biological literature a linear regression method has been used to estimate N in removal studies. It has intuitive appeal and also is easy to compute. However, if computer programs are available it is probably better to use the M. L. estimator. In practice I have found that there is usually little difference between the two estimators.

The regression method is presented briefly here because of its intuitive appeal and because it will be helpful when we come to discuss M_{bh} in Section 3.2.4. It is based on the following expression

$$\begin{aligned} E(u_i | M_i) &= p(N - M_i) \\ &= pN - pM_i \end{aligned} \quad (8)$$

where (8) can be described mathematically as follows. Given M_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 most applied, we have a linear regression of catch (u_i) versus cumulative catch (M_i).

The regression estimators of N and p are

$$\tilde{N} = \bar{M} + \bar{u}/\tilde{p} \quad (9)$$

$$\tilde{p} = \frac{-\sum_{i=1}^K u_i (M_i - \bar{M})}{\sum_{i=1}^K (M_i - \bar{M})^2}, \quad (10)$$

which are simple functions of the slope and intercept estimators in the linear regression.

3.2.3 M_h : THE HETEROGENEITY MODEL

This model allows heterogeneity but no trap response and assumes that each animal has its own unique capture probability (p_j , $j=1, \dots, N$) 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).

Under this model the vector of capture frequencies (f_1, f_2, \dots, f_K) composed of the numbers of animals captures 1, 2, \dots , K times, contains all the information for estimating N . In statistical parlance this is called a minimal sufficient statistic.

Difficulties exist in finding a satisfactory estimator for this model. Burnham originally tried modelling the capture probabilities as coming from a two parameter beta distribution (Johnson and Kotz 1970:37) and using M. L. estimation, but found it unsatisfactory.

A naive estimator of N is

$$\hat{N}_I = \sum_{i=1}^K f_i = M_{K+1} \quad (11)$$

which is simply the number of distinct animals seen in the whole experiment. This estimator is highly biased unless the capture probabilities are very high or the 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 Otis et al. (1978: 109). He also proposed an objective technique for choosing which one to use on a particular data set. The estimators all have the form

$$\hat{N}_{h\ell} = \sum_{i=1}^K a_{i\ell} f_i \quad (12)$$

where the $a_{i\ell}$ are constants which take on different values depending on the order (ℓ) of jackknife used. The naive initial estimator (11) is also of this form with $a_i = 1$ for all $i = 1, \dots, K$. An approximate variance estimator for $\hat{N}_{h\ell}$ in (12) is

$$\widehat{\text{Var}}(\hat{N}_{h\ell}) = \sum_{i=1}^K a_{i\ell}^2 f_i - \hat{N}_{j\ell} \quad (13)$$

Use of (12) and (13) for point and interval estimation is not without difficulties (Otis et al. 1978:37). However, this jackknife estimation procedure is the most robust method so far proposed for Model M_h .

3.2.4 M_{bh} : THE TRAP RESPONSE AND HETEROGENEITY MODEL

This model allows for 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. These probabilities are assumed to remain constant over all sampling times.

This model was first considered by me (Pollock 1974) and later it was developed further by Otis et al. (1978:40). They give an estimation procedure called the "generalized removal method". Here we describe their method

intuitively by generalizing the linear regression method at the end of Section 3.2.2.

If heterogeneity is operating (as well as trap response) there is no longer a linear relationship between catch (u_i) and cumulative catch (M_i) and thus (8) is no longer valid. In fact we now have

$$E(u_i | M_i) = \bar{p}_i(N - M_i) \quad (14)$$

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 gradually decrease 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 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 the 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 they are then we use the removal method (Section 3.2) which is a regression using all the sample points. If they are not then 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 be different.

Notice that while 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 will 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 there is no way any model can deal with this extreme situation. This has implications for study design which will be considered in Section 3.5.

3.2.5 TIME VARIATION IN CAPTURE PROBABILITIES

In addition to the four models (M_o , M_b , M_h , M_{bh}) just considered four others are possible by generalizing each to allow capture probabilities to vary over sampling times (M_t , M_{tb} , M_{th} , M_{tbh}). It should be emphasized that although these models are conceptually very important because they may be appropriate for a practical study, they do not usually permit estimation of population size. The exception of M_t , the classic Schnabel Model, which was discussed in Section 3.2.1. A summary of the 8 possible models and their assumptions is given in Table 1 to help the reader.

(Table 1 to appear here)

3.2.6 MODEL SELECTION

Otis et al. (1978)³ present an important method of choosing a model from the 8 possible (M_o , M_t , M_b , M_{bt} , ..., M_{tbh}) based on a series of goodness of fit tests. This complex procedure may often need to be used but with caution (see also Chapman 1980) because the tests are not independent and often have low power. If possible biological information should be used to reduce the number of models considered in a study. For example there may be very strong evidence based on the behavior of the animal concerned that trap response is unlikely with the trapping method used. In this case any models which allow trap response could be eliminated from consideration (M_b , M_{bh} , M_{tbh}).

3.2.7 SOME ALTERNATIVE APPROACHES

Regression Methods: Tanaka (1951) and Marten (1970) have suggested different generalizations of the basic Schnabel Model (M_t) to allow "unequal

³Otis et al. (1978) also provide a very detailed computer program CAPTURE.

catchability." Unfortunately these methods (based on regression techniques) are rather ad hoc and do not distinguish between heterogeneity and trap response. I see no compelling reason for using either method.

Frequency of Capture Methods: Several authors (Craig 1953, Tanton 1953 and Eberhardt 1969) have suggested methods of allowing for unequal catchability (again with heterogeneity and trap response not being distinguished) based on frequency of capture methods. When heterogeneity alone is operating (M_h , Section 3.2.3) we have seen that the frequencies of capture contain all of the information for estimation of N so that these methods then have some theoretical justification. If trap response or time variation in capture probabilities is present, I suspect the methods will not be very useful.

3.3 THE CLOSURE ASSUMPTION

This assumption that the population must be static over the sampling period is very important to the models proposed thus far. It allows a substantial weakening of the other major assumption of equal catchability of animals. As we shall see in Section 4, it is very difficult to allow for unequal catchability when we have the additional complexity of open population models.

3.3.1 TESTING FOR CLOSURE

Pollock et al. (1974), assuming M_t as the basic model, derive a sequence of tests for closure versus the alternatives of deletions only, additions only, and both deletions and additions. Burnham (1974) derives a general closure test with Model M_h as the null hypothesis (see also Otis et al. 1978: 66). The problems of these tests are:

- (i) they have low power for detecting departures from closure, and
- (ii) there is difficulty in distinguishing closure from unequal catchability.

We shall consider the closure assumption further when we discuss study design in Section 3.5. The biologist must consider critically the reality of the closure assumption for his specific study.

3.3.2 A MODEL ALLOWING "WANDERERS"

In many short term studies particularly on birds and small mammals the closure assumption is a problem. Although the study may be short enough for no births or deaths to be occurring it is often extremely difficult to prevent migration. Manly (1977) develops a model based on some ideas of Mac Arthur and Mac Arthur (1974) which is a generalization of the Trap Response Model (M_b). This model allows a proportion of the population to be permanent "residents" of the study area. These "residents" may be subject to trap response but not heterogeneity or time variation of their first capture probabilities. The remainder of the population are "wanderers" who are only in the population a short time. The arrival times of the "wanderers" are assumed to be uniformly distributed over the whole sampling period.

Manly (1977) illustrates his model with some data on birds caught in mist nets by Terborgh and Faaborg (1973) in Puerto Rico. Estimators and their standard errors are given for

- (i) the proportion of "residents" in the population,
- (ii) the number of "residents" in the population,
- and (iii) the rate of capture of "residents."

The model is appealing and should be investigated further as should the more general problem of trying to separate migration from births and deaths as violations of closure. There are some potential problems with the model, however, which are

- (i) possible heterogeneity or time variation of the first capture probabilities of the "residents" and
- (ii) possible trends in the arrival times of the "wanderers."

Manly (1977:407) mentions that this second problem could be serious. There is also the point that the whole conceptual framework of the model depends on there being two extreme groups of animals which are "residents" and short term "wanderers." How long does a wandering animal have to be in the population to become a resident which then emigrates?

3.4 THE ZERO BAND LOSS ASSUMPTION

If animals lose their tags, the number of recaptures will be too small resulting in a potentially serious underestimation of the population size. Seber (1973:93) gives a good review on methods of marking animals, failure of the assumption, and a method to estimate and adjust for mark loss using a double banding scheme. See also Caughley (1977:139). It is important to realize that tag loss will cause a decrease in precision of estimators even when it can be estimated and adjusted for (Pollock 1981).

3.5 STUDY DESIGN

Here we consider the design of short term studies where the objective is estimation of population size with perhaps a conversion to a density estimator. It is often difficult to define the exact area a population covers, although there is a large literature on the problem with most of it oriented towards small mammal studies, (Otis et al. 1978:67).

In this type of study many potentially useful models exist. I feel that 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. Traditional sample size calculations for a given precision are only partially useful because often the biologists must do a substantial amount of model selection after the study is completed.

3.5.1 CLOSURE

In many short-term studies, especially on birds, this assumption is difficult to satisfy because of movement. In some cases careful choice of study

area so that there are natural boundaries may reduce movement. Another method is to use a short sampling period for the whole study but this must be balanced against the need for as many samples as possible.

The model of Manly (1977) discussed in Section 3.3.2 deserves further study because it allows some movement through the area. Other methods which allow movement (but not births or mortality) would be valuable but little has been developed at this time.

3.5.2 TIME VARIATION

If closure can be approximately guaranteed, the next most important aspect of the design process is to try to achieve constant capture probabilities over time. This makes available a range of potentially useful models which allow heterogeneity and or trap response of the capture probabilities (M_o , M_b , M_h , M_{bh}).

The sampling times chosen should be as similar as is practically feasible. Effort, time of day, weather conditions and any other biologically important factors should be kept as constant as possible. There is once again a trade off in number of sampling periods. The capture probabilities will be easier to keep constant for a small number of periods but the models obviously give more precise estimators with more periods especially if heterogeneity is present (M_h , M_{bh}).

3.5.3 TRAP RESPONSE AND HETEROGENEITY

If closure and no time variation in capture probabilities can be guaranteed, then it is not strictly necessary to try to avoid trap response or heterogeneity. This is fortunate because in many practical studies it is not possible.

Trap response may often be severe. Manly (1977) states that it can be very serious in mist net studies. "Baiting" of traps will often induce trap

response but unfortunately the alternative may often be no captures! Sometimes use of resighting data (without capture) may avoid trap response.

Heterogeneity is likely to occur to some degree in almost all studies. Attempts to minimize it can be made by trying to ensure that all sections of the study area are sampled with equal intensity. Another approach is to try to stratify the data based on known sources of heterogeneity such as age or sex. Unfortunately sample sizes often are not adequate to do this.

3.5.4 BAND LOSS

Clearly one should attempt to avoid this problem by using a proven marking method. If a new method is being used, perhaps a pilot study should be considered or at the very least some attempt should be made to estimate mark loss through techniques like double banding (See also Section 3.4).

3.5.5 SAMPLE SIZE CONSIDERATIONS

Often sample sizes will be limited by practical problems but it is important for biologists to realize that small studies may be little better than none at all! Ideally one would like a study with approximately ten sampling periods and constant capture probabilities averaging at least 0.2 for the whole study. This enables reasonable identification of the correct model and good precision of the population size estimator under that model.

4. LONG-TERM STUDIES: OPEN-POPULATION MODELS

Often the biologist is interested in a long-term study where it is not feasible to assume a closed population. Open population models are now of interest and they allow estimation of "survival"⁴ rates and "birth"⁴ rates as well as the population size at the different sampling times. In Table 2 we give a summary of the models considered in this section.

⁴It should be emphasized that in capture-recapture studies it is not possible to separate births from immigration or deaths from emigration so that "survival" and "birth" rate estimators may include migrants.

(Table 2 to appear here)

4.1 THE JOLLY-SEBER MODEL

4.1.1 ASSUMPTIONS

The most important open population model is the Jolly-Seber (J-S) Model (after Jolly (1965) and Seber (1965)). The best reference for detailed study of this model is Seber (1973:196). A good intuitive introduction suitable for biologists is given by Cormack (1973).

This model makes the following assumptions (Seber 1973):

(i) Every animal in the population (marked or unmarked) has the same probability (p_i) of being caught in the i th sample ($i = 1, \dots, K$), given that it is alive and in the population when the sample is taken.

(ii) Every animal has the same probability (ϕ_i) of surviving from the i th to the $(i + 1)$ th sample, given that it is alive and in the population immediately after the i th release ($i = 1, \dots, K - 1$).

(iii) Marked animals do not lose their marks and all marks are reported on recovery.

(iv) The actual time spent sampling occupies a short period.

Assumption (i) is the equal catchability assumption discussed in the short-term studies except that now it applies only to live animals. Also we now assume equal survival rates for all animals (ii). These two assumptions and some alternatives to them will be discussed further in later sections. Clearly the Zero Band Loss Assumption (iii) is still important. Assumption (iv) is necessary because this is an open population model and otherwise it does not make logical sense to estimate parameters at a particular sampling time.

4.1.2 PARAMETER ESTIMATION

Here an intuitive discussion of parameter estimation will be given.

Suppose to begin with that we pretend 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 $M_1 = 0$).

Obviously an intuitive estimator of N_i , the population size at time i , is the Petersen estimator discussed in Section 3.1. If the model assumptions are valid then

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

which gives

$$\hat{N}_i = \frac{n_i M_i}{m_i}, \quad (14)$$

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

An estimator of the survival rate from sample i to sample $(i+1)$ is M_{i+1} , which is the total number of marked animals in the population just before the $(i+1)$ th sample, divided by the total number of marked animals released after sample i which is $M_i - m_i + R_i$. Note that R_i is the number of the n_i animals captured that are released.

$$\hat{\phi}_i = \frac{M_{i+1}}{(M_i - m_i + R_i)} \quad (15)$$

An intuitive estimator of the recruitment in time interval i to $(i+1)$ is

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + R_i). \quad (16)$$

This is simply the estimated difference between the population size at time $(i+1)$ (which is N_{i+1}) and the expected number of survivors from time i to time $(i+1)$ (which is $\phi_i (N_i - n_i + R_i)$).

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 two ratios

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

which are the future recovery rates of the two distinct groups of marked animals:

(i) $(M_i - m_i)$ are the marked animals not seen at i and (ii) R_i are the marked animals seen at i and then released for possible recapture. Note that Z_i and r_i are the members of $(M_i - m_i)$ and R_i which are captured again at least once.

The estimator of M_i is thus given by

$$\hat{M}_i = m_i + \frac{R_i Z_i}{r_i} \quad (17)$$

and is defined only for $i = 2, \dots, K - 1$. It follows that \hat{N}_i in (14) is defined for $i = 2, \dots, K - 1$; $\hat{\phi}_i$ in (15) for $i = 1, \dots, K - 2$; and \hat{B}_i in (16) for $i = 2, \dots, K - 2$. A summary of these parameter estimators and their approximate large sample variances are given in Seber (1973:205), which should also be consulted for some detailed examples. Cormack (1964) presents a model for recaptures of marked animals by resighting without capture, which is actually a special case of the J-S Model. For that model it is possible to estimate survival rates but not population size.

4.1.3 CONSTANT SURVIVAL AND/OR CONSTANT CAPTURE PROBABILITIES

A very important new development is the work of Jolly (1979, 1980). He restricts the large number of parameters by assuming a constant survival rate and/or a constant capture rate over the whole study. If these assumptions are realistic, as they often are, then he shows that there can be large gains in precision of estimators. Crosbie (1979) has also considered these models and

has developed a computer package to facilitate their use.

4.1.4 UNEQUAL SURVIVAL AND CATCHABILITY

With the added complexity of an open population model, it is difficult to build alternative models to the same degree as in the closed population case. We also have the added complexity of possible heterogeneity and trap response of the survival probabilities of different animals.

Trap Response: Robson (1969) and Pollock (1975) have shown that it is possible to generalize the J-S model to allow for a trap response in survival and capture probabilities which lasts for a short time (typically only one period after initial capture). The estimators still have a similar intuitive form to the original J-S estimators. Tests for this type of temporary trap response are also given and involve contingency table chi-square tests.

Permanent trap response can have a very large influence on the J-S estimators. If animals are "trap shy" there will be too few recaptures resulting in overestimation of population size whereas underestimation will result from "trap happy" animals. Survival and birth rate estimators can also be severely affected.

Heterogeneity: Carrothers (1973) and Gilbert (1973) have used simulation to study the influence of heterogeneity of capture probabilities on the J-S estimators. Serious negative bias of population size estimators can result, but survival estimators, although negatively biased, are much less affected. This has implications for the design of long-term studies which will be discussed in Section 4.4.

Heterogeneity of survival probabilities over animals has not been considered in any detail in the literature although it obviously occurs in practice. Cormack (1972) states that the J-S estimators will be little affected by this type of heterogeneity. Based on some recent work, Pollock and Raveling (1981)

agree with this assessment if an animal's survival probability is independent of its capture probability. In many practical studies with live recaptures this is probably a reasonable assumption. However, in band recovery studies, in which animals are recovered dead, an animal's survival probability is clearly negatively related to its recovery probability. In this situation a negative bias on survival estimators results. Band recovery models will be considered briefly in Section 4.3.

4.1.5 AGE-DEPENDENT SURVIVAL RATES

A special type of heterogeneity of survival probabilities occurs when survival is a function of the age of the animal. Manly and Parr (1968) give a method of allowing for this when capture probabilities are assumed to be independent of age. The method is described in simple terms suitable for a biological audience and includes a worked example (see also Seber 1973:233).

4.1.6 COMPUTER PROGRAMS

Unless the number of samples is small computation of the J-S estimators and their variances becomes time consuming. Some computer programs are available. Two simple programs are given by Davies (1971) and White (1971). For those who do many capture-recapture studies and desire to try a range of options on their data, a detailed program package called POPAN-2 is recommended. It was developed by Arnason and Baniuk (1978) and the manual provides a lot of information on data management. It contains a particularly valuable section on methods of combining samples when capture probabilities are low (which is a common practical problem). The authors state that POPAN-2 is not really suitable for "one-shot" users, but they also validly point out that a biologist should be cautious about embarking on such a "one-shot" study anyway.

4.2 GENERALIZATION TO MULTIPLE DISTINCT AGE CLASSES

For some species (especially of birds) several clearly identifiable age

classes occur that are likely to have different survival rates and perhaps also different capture rates. I have shown that it is possible to generalize the J-S Model to allow these different age classes to have different survival and capture probabilities (Pollock 1981). The estimators take a form similar to those under the J-S Model and it is possible to test if the survival and capture probabilities are age dependent using a series of contingency table chi-square tests. The model was found to be useful for some resighting data on neck-collared Giant Canada Geese (Branta canadensis maxima) where both young and adults (age one year or more) were neck-collared.

In this model (Pollock 1981) we assume one capture period each "year"^{5, 6} for K "years." There are $(\ell + 1)$ distinguishable age classes of animals 0, 1, ..., ℓ which therefore move forward one class each "year." We further assume that each age class has a different capture rate in the i th sample and a different survival rate from the i th to the $(i + 1)$ th sample ($i = 1, \dots, K$). Also immigration or emigration can occur for each age class of the population, but births can occur only into the zero age group. Thus when referring to survival, we really mean those animals which have not died or emigrated. Similarly, when referring to additions, we really mean births and immigration for the young animals ($V = 0$) but only immigration for the older animals ($V = 1, \dots, \ell$).

The author believes that this extension of the J-S Model will be useful to biologists. In most applications, the number of age classes will only be two or three because that is all that can be identified in the field.

⁵We use "year" to represent the period of time an animal remains in an age class. This will not necessarily represent a calendar year.

⁶It is not necessary to restrict oneself to one capture period per year. Stokes (personal communication) has investigated a model with several periods per year for use on American Woodcock (Philohela minor) data.

The number of age classes should be kept as small as biologically reasonable so that sufficient numbers of each class can be marked to give reasonable precision to the estimators of population parameters. Restrictions on this general model such as assuming that each age class has a constant survival rate over the whole study, could also be considered to increase precision of estimators. Unfortunately these restricted models do not give rise to simple intuitive estimators.

4.3 BAND RECOVERY MODELS

The Band Recovery Models in current use (Brownie et al. 1978) are closely related to the J-S Model and its generalization to allow for age-dependence (Section 4.2) but now there are 100 per cent "losses on capture." However the biological issues involved are beyond this review, which is intended to concentrate on live recapture studies.

Important references are Seber (1973:239) and Brownie et al. (1978) which is written for biologists. The assumptions behind band recovery models are reviewed by Pollock and Raveling (1981). They are particularly interested in the effect of potential heterogeneity of survival probabilities.

4.4 DESIGN OF LONG-TERM STUDIES

Very little has been done on the design of capture-recapture studies that use open population models. Seber (1973:204) gives an ad hoc rule of thumb that m_i , the number marked in each sample, and r_i , the number of animals released from the i th sample that are recovered should be at least 10 for all values of i .

Manly (1971) found that studies with small capture probabilities suffer from a problem in estimation of variances. Underestimates of parameters appear to be more accurate than they really are. This is because the parameter estimate is substituted in the variance formula to obtain a variance estimate.

Jolly (1965) pointed out that recaptures enter into the estimates in two distinct ways. First as the proportion of marked animals in the i th sample and second as the ratio of future recaptures. This has design implications as Jolly (1965) realizes: "It might well, therefore, be advantageous to have a separate organization for recording future recaptures, Z_i and r_i , from that for releasing animals. Since it is necessary to distinguish only two classes of marked animals in the future recaptures with respect to each time i , a very simple code of marks might be used in specific situations, thus enabling untrained persons over a wide area to recapture, or possibly merely to observe, marked animals. Such a recapture system could proceed continuously, since the time at which an animal is recaptured is of no importance. Releases, on the other hand, would only be made at the particular times for which estimates \hat{M}_i were required, the marking and releasing being done by more experienced staff."

Another method of increasing precision might be to use equally spaced sampling periods with the sampling periods being as similar as possible. The reason is that it may then be feasible to assume constant survival and/or capture rates over time and to use the restricted models of Jolly (1979, 1980), which were discussed in Section 4.1.3.

Any method of reducing heterogeneity and trap response of capture probabilities here is extremely important because it is not possible to allow for them to the same degree as in closed population models. One design which has great potential especially for some bird species is to mark individuals so that they can be identified without capture. As usually only marked birds are considered for resighting, this design allows only estimation of survival rates. It does mean, however, that there is no problem with trap response and also it is known that heterogeneity does not have much influence on survival estimators (Carrothers 1973). Cormack (1964) discusses an example of this

type on the Fulmar (Fulmarus glacialis) and Pollock (1981) gives an example on Giant Canada Geese (Branta canadensis maxima) where two age classes are neck-collared. The problems with this design are:

(i) There is no estimator of population size unless the experimenter can in some way estimate the proportion of marked to total animals.

(ii) Marking schemes must be clearly visible and permanent. This can be a big problem in studies which use neck collars.

(iii) Some marking schemes that are very visible may alter the survival rate of the animal.

5. GENERAL DISCUSSION

In this review a sharp distinction between short-term and long-term studies has been drawn. This is somewhat artificial. 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 of Section 3 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.

One problem which comes up again and again is the shortage of models and techniques allowing for local movement. Cormack (1979) asserts that this may be the most important area for future research.

An approach to capture-recapture problems which has some potential is the use of log linear models originally proposed by Fienberg (1972). Cormack (1981) has shown how this approach can be used practically for open and closed populations. Unfortunately this approach does not allow for heterogeneity or permanent trap response.

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TABLE 1
CLOSED POPULATION MODELS

Model	Section	Unequal Catchability due to			Estimator Available	References ¹
		Trap Response	Heterogeneity	Time		
M_o	3.2.1				Yes	Darroch (1958)
M_b^2	3.2.2	x			Yes	Zippin (1956)
M_h	3.2.3		x		Yes	Burnham and Overton (1978, 1979)
M_{bh}	3.2.4	x	x		Yes	
M_t	3.2.1			x	Yes	Schnabel (1938) Darroch (1958)
M_{tb}	3.2.5	x		x	No	
M_{th}	3.2.5		x	x	No	
M_{tbh}	3.2.5	x	x	x	No	

¹Otis et al. (1978) is the definitive reference for biologists on all 8 models.

²Manly (1977) has developed an extension of M_b to allow for short-term "wanderers" through the study area. (Section 3.3.2).

TABLE 2

OPEN POPULATION MODELS

Model	Section	Assumptions	References
Jolly-Seber ¹	4.1	Equal capture and survival probabilities for all animals at each sampling time	Jolly (1965) Seber (1965) Seber (1973)
Manly-Parr	4.1.5	Equal capture probabilities but survival probabilities may vary with age of animal.	Manly and Parr (1968) Seber (1973)
Age-Dependent	4.2	Identifiable age classes exist which may have different survival and capture probabilities	Pollock (1981)

¹Jolly (1979, 1980) and Crosbie (1979) have considered some restricted versions of the Jolly-Seber model which could be very important to biologists (Section 4.1.3).