

CHAPTER 1

INTRODUCTION

Interest in estimating the size of populations has had a long history. The crudest methods date back at least to the 17th century and probably long before that. Applied capture-recapture methods with some theoretical basis began to appear in the 1930s and 1940s. The period since then has seen many developments in methods for estimating population size under a wide variety of assumptions and situations. Generally, modern methods can be classified into two groups: capture-recapture and removal methods.

Just what is a capture-recapture study? We will describe a simple example before we discuss more realistic cases (Chapter 3). Suppose that we wish to estimate the size N of a population in which there is no birth, death, immigration, or emigration over the time period for which we plan to make the estimate. On a first visit, we catch a sample of 1000 animals, mark them so that we can recognize individual animals in the future, and return them to the population where the marked animals mix with unmarked animals. We denote the number of animals in this first sample as n_1 ; $n_1 = 1000$ in this example. On a second visit, we catch 500 animals (call this n_2), of which 450 are unmarked (call this u_2) and 50 ($n_2 - u_2$) are marked. In this example, the proportion of the population that is marked, called the "capture probability," is denoted by p and its estimate by \hat{p} . The estimate of p is $\hat{p} = (n_2 - u_2)/n_2$, or $50/500 = 0.10$. Because the number of marked animals in the population is 1000, an estimate of the total population is $\hat{N} = n_1/\hat{p}$, or $1000/0.10 = 10\,000$ animals. To improve the precision of \hat{N} , we can mark the 450 unmarked individuals, return them to the population, and resample. On the third visit we catch more animals (call this n_3), of which some are marked and some are not. This procedure can be continued indefinitely as long as the initial assumptions (no births, deaths, immigration, or emigration) hold. Full details of this and other capture-recapture models are given in Chapter 3.

In a removal study, in contrast to the capture-recapture study described above, animals are captured and removed from the population rather than being marked and released. On the second and subsequent visits, more animals (u_2, u_3, u_4, \dots) are captured and removed; continued sampling will catch progressively fewer animals on each occasion until eventually none will remain to be captured. The progressive decrease in the first few terms of the series u_1, u_2, u_3, \dots , is used to estimate N , the total number of animals. Alternatively, we can mark the captured animals and return them to the population. In this way, they are "removed" from the unmarked population without our having to remove them physically. This kind of removal allows us to view capture-recapture experiments as if they were removal experiments; the advantages of this method will be explained later. Details of removal models are given in Chapter 4.

Capture-recapture and removal sampling are useful methods in some situations. On the whole, however, their usefulness is much overrated in the biological literature. In this primer we explain the methods, the assumptions on which they are based, and their average performance.

We believe a summary of the literature on the state of the art will be helpful. *Cormack (1968, 1979)* and *Seber (1982)* give detailed reviews. Appendix C, the General Reading List, provides an index to the relevant sources. Typically, only special cases of models for capture-recapture and removal experiments have appeared, and these have often involved approximations and simplifications. With some important exceptions, little emphasis has been placed on testing assumptions within or between existing methods. Many methods presented in the literature are *ad hoc* (without a firm basis), and some are demonstrably incorrect. Rarely have new methods been compared with older methods based on the same assumptions.



Richard Cormack

Richard Cormack has been interested in capture-recapture theory, primarily open-population models, for the past 20 years. He was born and raised in Scotland and educated in England. He took his degrees at Cambridge intending to be a theoretical astronomer, but after graduating he elected to work in the field of mathematical statistics. He spent a year in the United States at the University of Washington, with Douglas Chapman. Cormack worked at the University of Aberdeen for 10 years and at the University of Edinburgh for 6 years before going to the University of Saint Andrews in eastern Scotland, where he holds a chair in statistics.

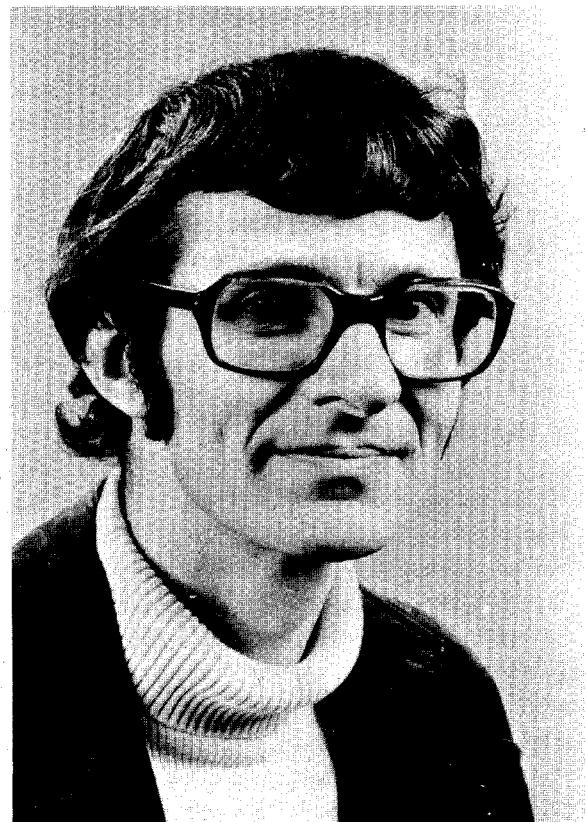
A review paper in 1968 on capture-recapture methods invited by the *Annual Review of Oceanography and Marine Biology* followed his paper in 1964 on the estimation of survival rates from capture-resighting data. More recently, he has published a series of papers relating primarily to open-population models. He was closely involved with the work of A.N. Arnason and A. D. Carothers while at Edinburgh. Cormack now is studying the use of log-linear methods for the analysis of capture-recapture data and feels this methodology is promising.

Statistical ecology remains his primary interest. He believes that the fascination of statistics resides in its capacity to help other scientists, and that this is best fulfilled by work with others. (Recent photograph by Peter Adamson.)

George Seber probably is best known to ecologists for his work on several open-population models and the two editions of his book, *Estimation of Animal Abundance and Related Parameters*. Of tremendous value to biologists and statisticians, his book draws together in a cohesive treatment the literature that had been scattered across various biological and statistical disciplines.

Seber became interested in capture-recapture models less by design than by accident, through his association with J. N. Darroch. His primary interest has been in statistical theory. He has found the quantitative aspects of ecology challenging and interesting from both practical and theoretical standpoints. He believes that mathematical models are important but that they must have a sound biological basis.

Seber took a B.Sc. degree and an M.Sc. degree in mathematics at Auckland University, New Zealand, and a Ph.D. degree from the University of Manchester, England. He served as a statistician at the London School of Economics, as professor of mathematics at Auckland University, and as Director of the Biometrics Unit at Otago University, New Zealand. He now is head of the Mathematics Department at Auckland University. (Recent photograph.)



George A. F. Seber

The results of computer simulations that compare methods or that examine the small-sample properties of a given method have been published only recently. Most estimation methods appear to be very sensitive to the breakdown of certain assumptions: they are not "robust." Little admission has been made of the fact that models developed under the closure assumptions are merely variations on the classic "ball and urn" model (*Feller 1950*). An analogy between this model and real animal populations has not been made, but few biologists seem to be aware of this lack. Finally, in the past decade or so, attention has been focused on the traditional assumption that all members in a population are equally catchable on all occasions. It is now recognized that this assumption rarely holds, and much work has been done in recent years to build models that allow the assumption to be relaxed.

Closure: An Important Assumption

Closure means that the size of a population is constant over the period of investigation: no recruitment (birth or immigration) or losses (death or emigration) occur. This is a strong assumption, and of course it is never completely true in a biological population. For greater generality, we define closure to mean that there are no unknown changes to the initial population. In practice, this means known losses (trap deaths, or deliberate removals) do not violate our definition of closure. If the study is designed properly, closure can be met, at least approximately.

Closure is a very important assumption because all previous capture-recapture and removal models are extensions of ball and urn models (*Feller 1950:45-47*). We subdivide the closure concept into two components:

- (1) "geographic" closure by a boundary, analogous to the sides of an urn, that limits the population.
- (2) "demographic" closure to birth, immigration, death, and emigration.

The distinction between geographic and demographic closure is important because open models (mentioned in Chapter 8) are open only to demographic closure: geographic closure is still a critical assumption.

Unless geographic closure is met, the area relating to the parameter N is not defined and N itself has no meaning. For example, geographic closure is met with fish in a small pond, mammals on a small island, or squirrels in an isolated woodlot. Geographic closure is violated when capture-recapture is done with a relatively small grid of traps in a very large field inhabited by small mammals. Similarly, geographic closure probably will be violated when fish are sampled in a large reservoir, unless the whole reservoir can be sampled properly.

The subject of geographic closure arises because models for capture-recapture and removal data are based on ball and urn studies, which assume a three-dimensional container (Figs. 1.1-1.3). In these studies, the samples are drawn from the urn, and the objects are marked and returned to the urn, which is shaken to mix the marked and unmarked objects randomly before the population is sampled again. The concept of geographic closure comes about when models for populations in three-dimensional containers are applied to two-dimensional areas. For example, a biologist may wish to sample a 2- by 3-km island to estimate the size of the meadow vole population. He typically will position a series of traps on a grid or lattice. Unless his grid is 2 by 3 km, he faces problems because he has not met the requirement for geographic closure. This subject is discussed in detail in Chapter 5; see especially Figs. 5.1-5.3.

Sometimes the assumption of demographic closure can be relaxed. *Seber (1973:70-71)* showed that natural mortality will not bias some estimators if it acts equally on marked and unmarked segments of the population. In such instances, the population estimate relates only to the population size at the beginning of the study. However, if both recruitment and mortality occur during the experiment and if both marked and unmarked animals are affected similarly by mortality, the estimate of N will be too high, on the average, for both initial and final population size (*Robson and Regier 1968*).

Finally, we remark that removal studies often invite failure of the closure assumption. The removal of a significant number of animals may create a "vacuum," and animals outside the area may move into the

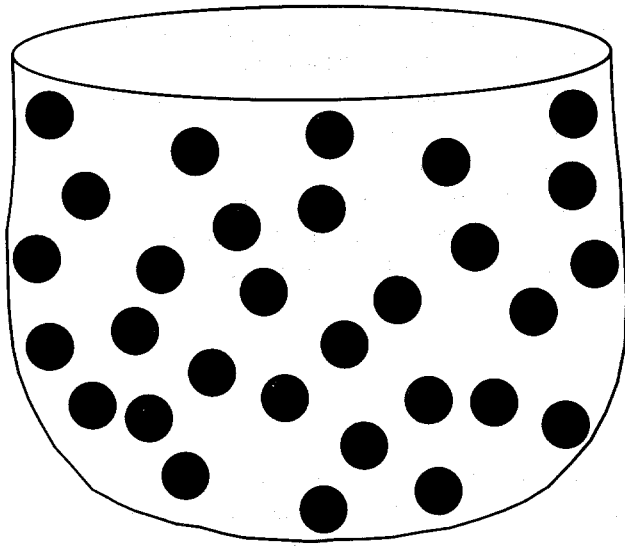


Fig. 1.1. The classic ball and urn experiment is the basis for the ball and urn model (Model M_0). Because balls neither die nor give birth, nor do they immigrate or emigrate, the demographic closure assumption is met. The sides of the glass urn limit the population boundaries, and, therefore, ensure geographic closure. N is well defined and here $N = 30$ balls.

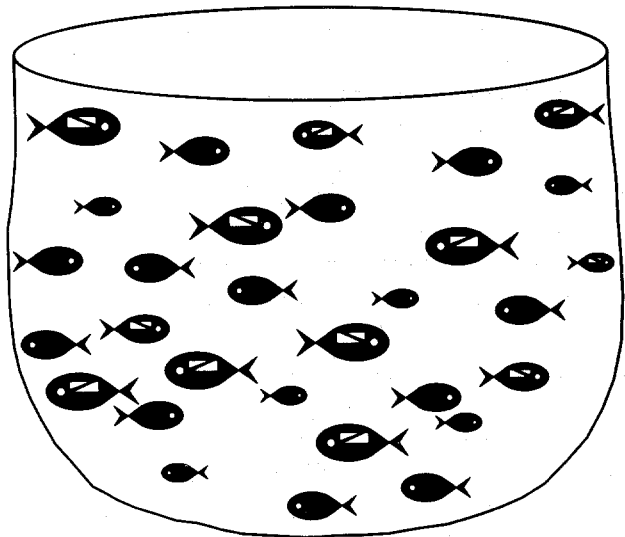


Fig. 1.2. A population of 30 adult fish, of which 12 are marked, in a glass container. Geographic closure is assured because the glass bowl confines the population. The bowl also prohibits immigration and emigration. If the length of a capture-recapture study is short (say 4 days), death can be assumed to be negligible; if it is not, dead fish will be noticed in the container. Any reproduction can be ignored on the basis of the small size of the young. Therefore, demographic closure is valid.

Although the closure assumption is met, the simplistic assumptions of Model M_0 are probably violated. Notice that the larger fish tend to be more prone to capture and, thus, to be marked. Therefore, we might expect Model M_h to be appropriate. (Models M_0 and M_h are discussed in this chapter and in Chapter 3.)

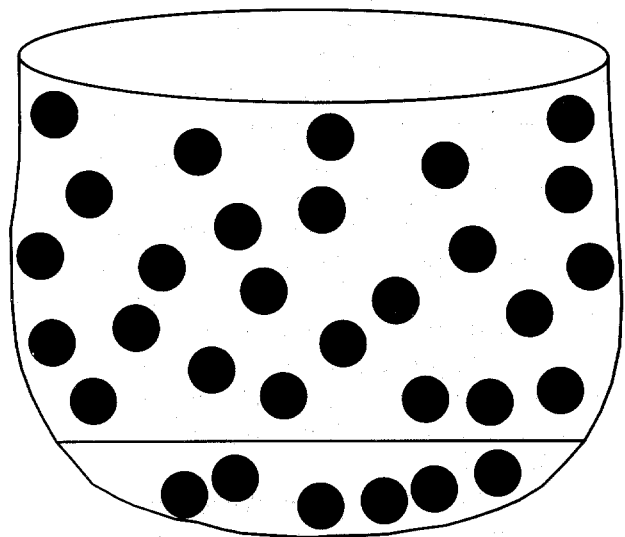


Fig. 1.3. A closed population of $N = 31$ individuals. The six individuals below the line are not subject to capture; that is, their capture probability p is zero. When such conditions exist, \hat{N} relates only to the catchable population, 25 in this example. Very large fish in a lake, old and wary coyotes, and mosquitoes distant from the nearest trap may be examples of individuals that are essentially untrappable.

trapping area and become subject to capture. In addition, the use of baited traps may induce movement of animals into the trapping area. If capture and marking methods induce mortality, demographic closure is violated. All these examples deal with violation of the closure assumption.

Many models have been developed for "open" populations. The concepts are discussed briefly in Chapter 8. Models for open populations are critically dependent on geographic closure for estimating population size, but they allow mortality + emigration and birth + immigration rates to be estimated.

Data

In capture-recapture studies, the same individuals are in the population on each trapping occasion, $j = 1, 2, \dots, t$, because of the closure assumption. (In removal studies, some individuals are removed on each sampling occasion.) Therefore, we can conceive of the individuals as being numbered from 1, 2, \dots , to the last individual, N ; that is, $i = 1, 2, \dots, N$. The capture and recapture history of each animal on each sampling occasion can be expressed conveniently in a simple table called the X matrix and denoted as $[X_{ij}]$. Let

$$[X_{ij}] = \begin{bmatrix} X_{11} & X_{12} & X_{13} & \dots & X_{1t} \\ X_{21} & X_{22} & X_{23} & \dots & X_{2t} \\ X_{31} & X_{32} & X_{33} & \dots & X_{3t} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ X_{M_{t+1}1} & X_{M_{t+1}2} & X_{M_{t+1}3} & \dots & X_{M_{t+1}t} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ X_{N1} & X_{N2} & X_{N3} & \dots & X_{Nt} \end{bmatrix}$$

$$\text{where } X_{ij} = \begin{cases} 1 & \text{if the } i^{\text{th}} \text{ animal is caught on the } j^{\text{th}} \text{ occasion} \\ 0 & \text{otherwise.} \end{cases}$$

Note that the first subscript denotes the row, and the second subscript denotes the column. For example, X_{31} represents the third row, first column.

The X matrix contains only zeros and ones indicating "not captured" and "captured," respectively. Each column details the history by sampling occasion, $j = 1, 2, \dots, t$. The first M_{t+1} rows relate to the capture and recapture history of each animal that was captured at least once during the study. The remainder of the X matrix contains all zeros, because these animals were never captured. In real studies, of course, one does not know how many remaining rows there should be.

The following is an example of an X matrix.

$$[X_{ij}] = \begin{matrix} & \begin{matrix} j = 1 & j = 2 & j = 3 & j = 4 = t \end{matrix} \\ \begin{matrix} i = 1 \\ i = 2 \\ i = 3 \\ i = 4 \\ i = 5 \\ i = 6 \\ i = 7 \\ i = 8 \\ i = 9 \end{matrix} & \begin{bmatrix} 1 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \end{matrix}$$

In this example, we see that animal 1 was captured on the first occasion and was recaptured on the fourth occasion. Animal 2 also was captured on the first occasion but was recaptured only on the third occasion. Animal 3 was captured on the second occasion and never was recaptured. Seven different animals were captured ($M_{t+1} = 7$) in this 4-day ($t = 4$) study. We can see that two animals were never captured ($N - M_{t+1} = 9 - 7 = 2$) because the two bottom rows, all zeros, indicate that these animals were never caught. Thus it is clear that only a portion of the X matrix is “observed” during a capture-recapture experiment. Of course, in a removal study there are no recaptures, so each row contains, at most, one nonzero entry.

The type of data we collect limits the parameters that we can estimate. In general, we can estimate population size (N), survival (S), and capture or recapture probability (p or c) from a capture-recapture study; however, $S \equiv 1$ for a closed population. In removal studies, only N and p can be estimated. In some studies, only data on marked animals, such as tag recoveries from dead animals, can be taken. In these studies, S and p can be estimated, but N cannot (see *Brownie et al. 1978*). These restrictions reflect inherent relations between the collected data and the parameters that can be estimated from them.

Parameters

If we assume population closure, only two parameters are of primary interest:

N = population size (a constant)

and

D = population density (animals per unit area).

Estimation of D is more difficult than estimation of N (see Chapter 5).

The capture probabilities are just as important as the N and D parameters, but are of less biological interest. The nature and number of capture probabilities depend on the assumptions being postulated (the model). For example, when we contrast capture-recapture studies with removal studies, we are interested in the initial capture and recapture probabilities, defined as

p = capture probability, the probability of first capture for an animal,

and

c = recapture probability, the probability that a marked animal will be recaptured.

In “trap happy” populations, we have $p < c$, whereas in “trap shy” populations, we have $p > c$. When there is no behavioral response to trapping, we have $p = c$. As detailed in Chapter 2, we denote estimators of these parameters by the symbol, $\hat{}$ called a *caret* or a *hat*. Examples are \hat{N} , \hat{D} , \hat{p} , and \hat{c} .

Estimators of p and c are important because of their close bond with \hat{N} . In other words, if p or c are estimated poorly and thus show large bias, then \hat{N} will be affected adversely.

Statistics

Statistics are entities computed from the data—for example, the X matrix in the context of these sampling studies. Statistics that are used frequently in capture-recapture and removal are defined and discussed below.

n_j = the number of animals captured in the j^{th} sample, $j = 1, 2, \dots, t$.

n = the total number of captures during the study.

u_j = the number of new (unmarked) animals captured in the j^{th} sample, $j = 1, 2, \dots, t$. Note that u_1 always equals n_1 .

f_j = the capture frequencies = the number of individuals captured exactly j times in t days of trapping, $j = 1, 2, \dots, t$. For example, f_3 = number of animals captured three times during the t days of trapping. The term f_0 is used for the number of individuals never captured; obviously, f_0 is not observable.

M_{t+1} = the number of different individuals caught during the experiment. Recall that t is fixed for a given experiment; this term is merely the number of nonzero rows in the X matrix.

M_j = the number of marked animals in the population at the time of the j^{th} sample, $j = 2, 3, \dots, t$. Note that $M_1 \equiv 0$.

M = sum of the M_j , not including M_{t+1} .

m_j = the number of marked animals captured in the j^{th} sample, $j = 2, \dots, t$. Note that $u_j = n_j - m_j$ and that $m_1 \equiv 0$.

m = sum of the m_j .

The dot notation indicates the summation.

The statistics n_j , u_j , f_j , M_j , and m_j may be computed directly from the X matrix; see *Otis et al. (1978:15)* for additional details.

Fundamental Assumptions

Every modern estimation method is based on a set of well-defined, explicit assumptions. There are three general assumptions for *all* capture-recapture studies.

(1) The population is closed. (Open models allow this assumption to be relaxed, except that geographic closure is still required.)

(2) Animals do not lose their marks during the experiment.

(3) All marks are noted and recorded correctly at each sampling occasion j .

There are two corresponding assumptions for all removal studies.

(1) The population is closed. (However, see remarks at the end of the *Closure* section in this chapter.)

(2) The number of unmarked animals is counted and recorded correctly at each sampling occasion j .

The crucial assumption for a model relates to the capture probabilities of the various population members. The modeling of capture probabilities is the key problem in both capture-recapture and removal studies. For example, the earliest assumption was that each animal has a constant and equal probability of capture on each trapping occasion and that capture and marking do not affect subsequent catchability of the animal. This assumption, related directly to the original ball and urn model (Model M_0), is unrealistic in capture studies of animal populations. It is now widely recognized that this assumption usually is not met (*Young et al. 1952, Geis 1955, Huber 1962, Swinebrood 1964*). *Edwards and Eberhardt (1967)*, *Nixon et al. (1967)*, and *Carothers (1973a)* provide clear evidence that accurate population estimation usually requires models that provide for unequal probabilities of capture. The effects of unequal capture probabilities on estimates derived from models that assume equal catchabilities have been studied through computer simulation by *Burnham and Overton (1969)*, *Manly (1970)*, *Gilbert (1973)*, and *Carothers (1973b)*. The estimators they studied generally were biased significantly when this assumption was violated.

Capture-Recapture Models

Otis *et al.* (1978) have presented several methods that allow various relaxations of the assumption of equal catchability. Much of this work started with the results of Burnham (1972) and Pollock (1974). Following Pollock (1974), we consider a sequence of models (assumptions) allowing for three major sources of variation in capture probabilities:

- (1) Model M_t assumes that capture probabilities vary by time or trapping occasion.
- (2) Model M_b assumes that capture probabilities vary by behavioral responses to capture.
- (3) Model M_h assumes that capture probabilities vary by individual animal (h = heterogeneity among animals).

The assumptions regarding unequal capture probabilities must be embodied explicitly in probability models that describe capture studies. We agree with Carothers (1973b:146) that equal catchability is an unattainable ideal in natural populations (*cf.* Seber 1973:81-84). Therefore, we discuss the three simplest ways to relax this assumption.

Model M_t allows capture probabilities to vary by time; that is, to differ on each trapping occasion. This situation may be common even though the number of traps is fixed during the course of a study. For example, a cold rainy period during the study might reduce the probability of capture during this time. If the trapping effort were to vary, Model M_t might be appropriate. Also, if different capture methods were to be used on each occasion, this model could be appropriate.

Model M_b allows capture probabilities to vary by behavioral response, or "capture history," and deals with situations in which animals become trap happy or trap shy. Carothers (1973a) referred to this response as a "contagion of catchability." This variation implies that an animal's behavior tends to be altered after its initial capture. For example, if an animal is frightened or hurt during initial capture and marking, it probably will not enter a trap again.

Model M_h allows capture probabilities to vary by individual animal. This situation has been modeled only with great difficulty and requires that additional assumptions be made about the statistical distribution of the capture probability p . Individual heterogeneity of capture probability may arise in many ways. Perhaps accessibility to traps (as influenced by individual home ranges), social dominance, or differences in age or sex can cause such an unequal probability structure. This important type of variation has been treated rigorously by Burnham (1972) and Burnham and Overton (1978, 1979); their nonparametric approach is presented in Chapter 3.

In addition to Models M_t , M_b , and M_h , we consider all possible combinations of these three types of unequal capture probabilities; that is, Models M_{tb} , M_{th} , M_{bh} , and M_{tbb} . We also treat Model M_o , the "null" case in which capture probability is constant with respect to all factors. Model M_o corresponds to the assumption of equal catchability. For simplicity, we denote estimators of population size for a specific model by using the same subscript notation. For example, \hat{N}_o denotes the estimator derived from Model M_o , \hat{N}_t denotes the estimator derived from Model M_t , and \hat{N}_{bh} denotes the estimator derived from Model M_{bh} .

Removal Models

Removal models are discussed in Otis *et al.* (1978:44-50). The simplest removal model we discuss here was proposed by Moran (1951) and Zippin (1956, 1958). It is closely related to Model M_b for capture-recapture studies. We assume that effort is constant during the study and formulate a sequence of removal models: Models M_{R1} , M_{R2} , M_{R3} , In this primer, we do not discuss the models in which effort is deliberately varied; however, a good review of such catch-effort methods can be found in Seber (1973:296-347).

In removal studies, the collected data are the numbers of unmarked animals u_j captured at each sampling occasion j , $j = 1, 2, \dots, t$. After the animals are captured, they are "removed" from the



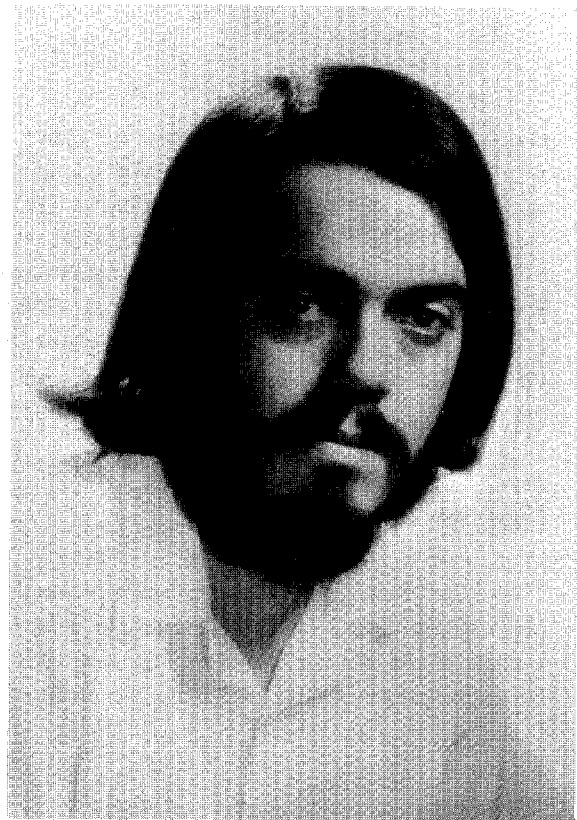
Kenneth P. Burnham

Kenneth Burnham has made a number of important contributions to estimation and testing theory for closed animal population models. He began his education with a B.S. degree in biology at Portland State College, and subsequently took M.S. and Ph.D. degrees in mathematical statistics at Oregon State University under W. S. Overton. His M.S. degree, in the late 1960s, dealt with simulation studies of the robustness of existing estimators of population size. He found that unequal probability of capture (heterogeneity) caused serious bias in the existing estimators. In his Ph.D. work he explored ML estimation for a generalized model for heterogeneity. Having found that it had unacceptable estimators of parameters, he derived a very nontraditional estimator based on the theory of the generalized jackknife. While working in Alaska with C. Cushwa on a rabbit population study, he developed a method to estimate density from capture-recapture sampling. This method allows a parameter to account explicitly for "edge effect"—a problem that has plagued biologists for several decades.

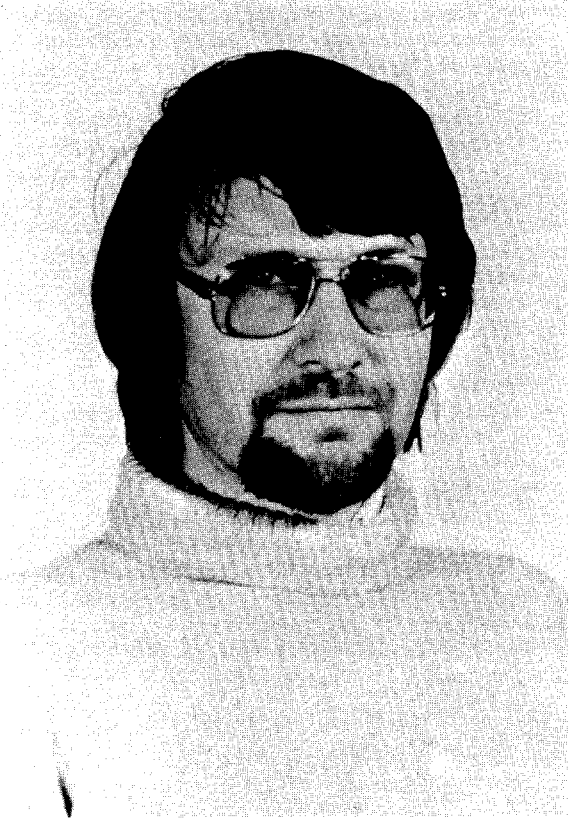
Burnham has worked as a statistician for the U.S. Fish and Wildlife Service since 1973. He believes that more work is needed on the tests of model assumptions, on model selection, and on the derivation of robust estimators. He sees the role of easy-to-use computer algorithms as becoming increasingly important and thinks that practical theory can be advanced as biologists and statisticians work together more closely. (Early 1970s photograph.)

Kenneth Pollock has made major state-of-the-art contributions to the estimation theory for both open and closed capture-recapture models. He was among the first to delve into the problems implicit in the assumption of equal catchability in closed populations. Early in his graduate work, he focused on model-building, estimation, and tests of assumptions for closed-population models. His findings provided an important part of the basis for the monograph by Otis *et al.* (1978). His recent work has turned to open models, using the multiple hypergeometric approach. He has derived ML estimators for a series of such models for both age-independent and age-dependent populations.

Pollock was born in 1948 in Australia and received a B.S. degree in agriculture from the University of Sydney. He took M.S. and Ph.D. degrees from Cornell University working primarily with D.S. Robson in the Biometrics Unit. Since receiving a Ph.D. in 1974 he has held several professional positions including faculty appointments at the University of Reading and University of California at Davis; he is now with the Department of Experimental Statistics at North Carolina State University. His interests include building realistic statistical models and deriving statistical procedures that are robust to model failure. (Recent photograph.)



Kenneth H. Pollock



Andrew D. Carothers

Andrew Carothers has made contributions to the theory of both open- and closed-population models. Born in Nairobi, Kenya, he took a B.S. degree in Mathematics at the University of Bristol, and, in 1969, an M.S. in Biometry at the University of Reading after teaching for several years in East Africa. He spent 3 years working on capture-recapture theory at the University of Edinburgh in association with R. M. Cormack, G. M. Jolly, and A. N. Arnason. His work focused on the testing of model assumptions and the robustness of estimators, especially in relation to the assumptions of equal catchability. Since 1972, he has worked primarily on the applications of statistics in genetics.

Carothers feels that more emphasis should be given to the power of tests in capture studies and to the relation between test statistics and biased estimators, because he believes there are cases where a model assumption is rejected by a significance test even though the model is still quite useful. (Recent photograph.)

population. Physical removal is the most common application; for example, the fish are transplanted to another pond, or the animals are kept in a holding area until the study is completed. Another possibility is to remove the animals by marking them in some manner; in this instance, the marked animals thus are "removed" from the unmarked population of interest.

Model M_{R1} , the first removal model, assumes that the capture probability is constant for all trapping periods; that is, $p_1 = p_2 = p_3 = \dots = p_t$. (The R stands for removal.) Model M_{R2} allows the animals caught on the first occasion to have a higher capture probability than on all subsequent occasions; that is, $p_1 > p_2 = p_3 = \dots = p_t$. Model M_{R3} allows $p_1 > p_2 > p_3 = p_4 = \dots = p_t$ and so on. These models are developed in detail in Chapters 3 and 4.

Program CAPTURE

Most of the computations necessary in the analysis methods presented here are nearly impossible to perform without a computer. They include computations for estimators of parameters, sampling variances and covariances, test statistics, and model selection. Our philosophy has been to let the computer program CAPTURE do the arithmetic, leaving the biologist free to concentrate on the full

interpretation of results. The computer is far more accurate than a hand calculator, but it requires some adjustments. For example, because most computer printers cannot print lower-case letters and subscripts, the symbol n_j appears on the computer output as N(J), and the estimators \hat{c} and \hat{p} appear as C-HAT and P-HAT, respectively.

Program input follows a simple, free-format style for easy use. A variety of options is available. We advise users to enter the full X matrix to allow a very complete analysis. Alternatively, the user can enter only certain summary statistics, for example, n_1, n_2, \dots, n_t , and M_{t+1} for Model M_1 .

The documentation for program CAPTURE is found in *White et al. (1978)*, available without cost from the Utah Cooperative Wildlife Research Unit, Utah State University, Logan, UT 84322. An abbreviated version is presented in Appendix A.

Questions and Exercises

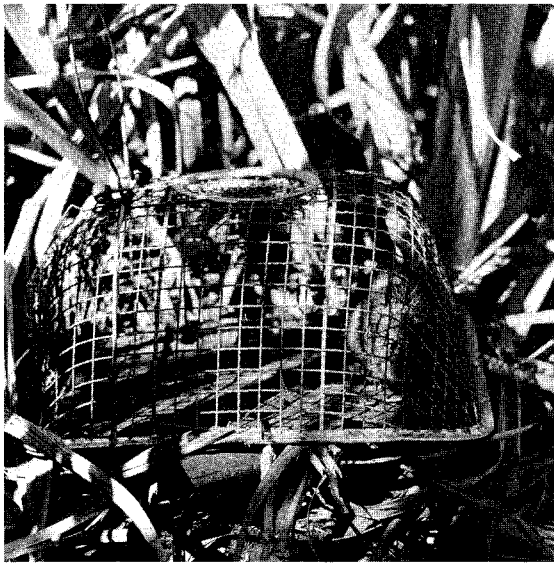
1. Is Model M_{tth} the most general model?
2. Can summary statistics, such as m_j, u_j, M_j, M_{t+1} , and m_j , be computed from the X matrix?
3. Is Model M_0 generally useful for estimating N in biological populations?
4. Is the closure assumption relatively unimportant? Why? Why not?
5. Consider the following data (X matrix) from a capture-recapture study.

	j = 1	j = 2	j = 3	j = 4	j = 5	j = 6	j = 7
i = 1	1	0	0	0	1	0	0
i = 2	1	1	1	1	1	1	1
i = 3	1	0	1	0	0	0	0
i = 4	0	1	0	1	0	0	0
i = 5	0	1	0	0	0	1	0
i = 6	0	1	0	0	0	0	0
i = 7	0	1	1	1	1	1	1

- (a) What is t (the number of trapping occasions)?
- (b) What is n_j for $j = 1, 2, \dots, t$?
- (c) What is u_j for $j = 1, 2$?
- (d) What is noticeable from the data on animals 2 and 7?
- (e) What is M_{t+1} ?
- (f) What is M_1 ?
6. Does Model M_0 allow some animals to be trap happy and others in the same population to be trap shy?
7. Can survival rates be estimated under the closure assumption?
8. Assume a fishery biologist must determine the *exact* numbers of fish in a small pond. Would you advise him to use capture-recapture sampling? Removal sampling? What?
9. Why must biologists be concerned about the capture probabilities?
10. Do you think that capture-recapture studies are easy to conduct, require only a few traps (say, 25 to 50), and are easy to analyze?
11. Why not always use a very general model that will not require concern about assumptions involving the type and significance of various types of unequal catchability?
12. Consider the following X matrix from a capture-recapture study. Only the observed portion is shown; animals that were never captured are not shown. Zero entries are left blank.

	$j = 1$	$j = 2$	$j = 3$
$i = 1$	1		1
$i = 2$	1	1	1
$i = 3$	1		
$i = 4$	1		1
$i = 5$	1	1	1
$i = 6$	1		
$i = 7$	1		
$i = 8$		1	
$i = 9$		1	1
$i = 10$		1	1
$i = 11$		1	
$i = 12$		1	
$i = 13$		1	
$i = 14$		1	
$i = 15$		1	1
$i = 16$		1	
$i = 17$			1
$i = 18$			1
$i = 19$			1
$i = 20$			1

- What is t ?
- What is M_{t+1} ?
- What are n_1 , n_2 , and n_3 ?
- What is n ?
- What are u_1 , u_2 , and u_3 ?
- What are f_1 , f_2 , and f_3 ?
- What are M_1 , M_2 , M_3 , and M_4 ?
- What is M ?
- What are m_1 , m_2 , and m_3 ?
- What is m ?



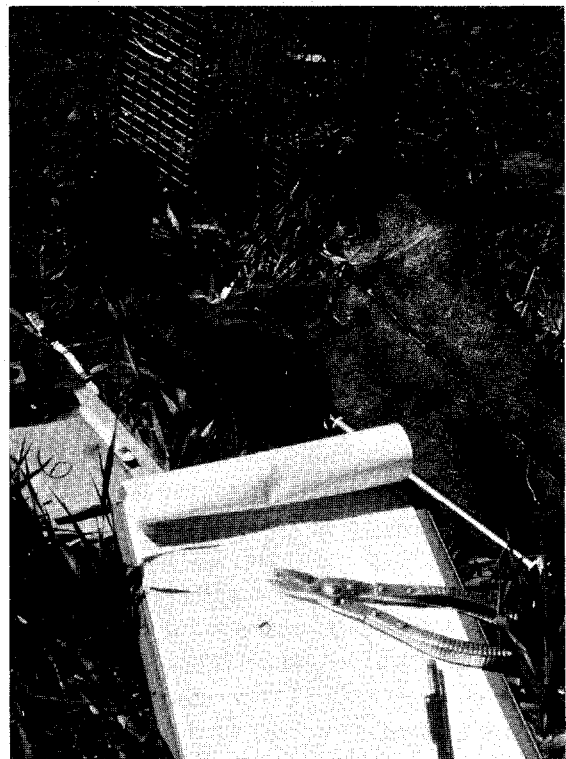
This cotton rat has been captured in a wire mesh Japanese live trap. (Photograph courtesy of Lynn Lefebvre.)



This Richardson's ground squirrel has been captured in a wire live trap. (Photograph courtesy of Kathy A. Fagerstone.)



This Indiana bat (*Myotis sodalis*) has been tagged on the wing with a celluloid ring. Bats tend to show fidelity to roost sites, so that they can be mist-netted in the vicinity of the roost with a good chance the closure assumption will be met. (Photograph courtesy of Richard Clawson.)



The equipment shown is commonly used in capture-recapture studies. The data sheet is in a waterproof notebook, and a pencil, ear tag, and ear tag pliers lie on top of the data sheet. A spring scale lies beside the clipboard. Additional tags are in the envelope. Other miscellaneous equipment and a live trap are in the background. (Photograph courtesy of Kathy A. Fagerstone.)