Statistical Inference from Band Recovery Data
– A Handbook –

by

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Chapter 1. Introduction

1.1 Purpose and Scope of Handbook

This handbook was prepared as an aid to those engaged in the analysis of several kinds of bird banding and other animal tagging studies. A common objective in most of these studies is the estimation of parameters which will reflect population survival. Here we focus considerable attention on the estimation of survival rates and specifically concentrate on inference procedures (estimation and hypothesis tests) regarding time- and age-specific survival rates.

We focus on migratory bird banding studies because such studies motivated our research and the development of most of the techniques discussed in the following chapters. In addition, bird banding studies are relatively widely read and employ a common, simple terminology. We hope the consistent use of bird banding terminology and examples will aid rather than confuse people involved in other types of animal tagging experiments. We feel that the methods presented in this handbook are potentially applicable to a wide range of field studies in addition to bird banding studies: fish tagging; bat banding; marking studies of certain reptiles and amphibians, several marine and terrestrial mammals; and a wide variety of entomological investigations.

We examine animal banding or tagging studies where: (1) A number of animals are caught and banded (tag, mark) each time period (year, month, week) for k such equal time periods (often the time period is a year). Generally, each band or tag carries a unique number or code. (2) Records are kept of bands or tags reported from dead animals for each time period from each batch banded. Therefore, the recovery data conveniently form an array representing the number of bands or tags recovered in time period j from those animals originally banded in time period i.

We consider only bands from dead animals. However, the methods we discuss in the following chapters can often be used as a good approximation to the analysis of data from studies of banded animals recaptured alive and subsequently released again, if the recapture rate is low. This subject, which is discussed in Section 8.2, extends the usefulness of the methods described. The development of comprehensive, efficient inference methods for many common types of recapture studies is incomplete and, therefore, it may be appropriate to use the techniques presented here as useful approximations until more general and efficient methods are developed and made available.

Banding studies of exploited species of birds are typical of the types of field research covered in this handbook. For example, a large sample of birds such as adult male pintail *(Anas acuta)*, are banded in August each year for k consecutive years in one general area. Records are kept by the Bird Banding Laboratory on the number of bands reported from dead birds in the j^{th} year after banding. (For game bird data, it is common to analyze only recoveries from normal, wild birds that were shot during the legal hunting season.)

Several methods for the analysis of such data have been proposed in the literature over the last 4 decades. The early methods were unsophisticated and poorly developed and usually based on the deterministic life table concept taken from human demography. Only in recent years have the proper methods for analysis of these data been developed. Seber (1962) probably made the original contribution to the correct conceptualization of analysis procedures (although he drew from the results of Darroch [1959] and others). More recent papers of importance include **Jolly (1965), Robson and Youngs (1971), and Seber (1965, 1972). Cormack (1979) and Seber (1982) present detailed** reviews of the various methods for such data as well as analysis techniques for live recapture experiments.

This handbook covers the analysis of banding studies for one, two, or three identifiable age classes; it also presents methods for use when banding is done twice a year on the same population. In all, we discuss 14 models, each allowing different and testable assumptions. For each model we present optimal estimators of certain parameters, the most important of which are annual survival and recovery rates (other parameters include mean life span and average annual survival and recovery rates). Estimates of sampling variation (precision) are given for all parameter estimators. Confidence intervals on parameters are presented and, for models currently of practical value, goodness of fit tests are presented. Also, tests between models are presented which are useful for selection of the appropriate model and for pooling data sets. The last chapter is devoted to the subject of planning a banding study.

1.2 Basic Structure of Band Recovery Data

We will illustrate the basic nature of experimental banding data with a study from a midwestern State where adult male birds were banded in August each year in 1964-66. Banding was initiated in 1964 when 1,603 adults were banded. In August 1965, 1,595 birds were banded. Some banded birds from these two cohorts were killed during the hunting seasons of 1964 and 1965 and their bands were reported to the Banding Laboratory. After 2 years, the recovery data can be summarized in the following triangular array:

Year banded	Number banded	Recoveries by hunting season	
		1964	1965
1964	1,603	127	44
1965	1,595		62

The interpretation of this table is straightforward. Of the 1,603 birds banded and released before the 1964 hunting season, 127 bands were recovered from birds killed during the 1964 season. From survivors, of this original banded cohort of 1,603, alive at the start of the 1965 hunting season, 44 bands were recovered. Sixty-two bands were recovered during the 1965 hunting season from the 1,595 birds banded just before the 1965 season.

In 1966, 1,157 new birds were banded, and from this cohort 82 bands were recovered during the 1966 hunting season. The recovery data, through 1966, can now be summarized in the following triangular array:

Year banded	Number banded	Recoveries by hunting season		
		1964	1965	1966
1964	1,603	127	44	37
1965	1,595		62	76
1966	1,157			82

From the 1966 hunting season a total of 195(=37+76+82) bands were recovered from the three banded cohorts.

The analysis of this data could be accomplished by considering only the recovery data from the 1964-66 hunting seasons. The methods described in this handbook are free of "truncation" problems that are associated with many life table methods (i.e., analyzing the recoveries before all banded birds are dead). Although no bias results from the use of only the 1964-66 data, additional precision in the parameter estimates will be realized by using recovery data that are obtained after the 1966 hunting season. For example, if the recovery data from the 1967 and 1968 hunting seasons were also available, the analysis could be improved (greater precision) by considering the extended, nontriangular data array below:

Year banded	Number banded	Recoveries by hunting season				
		1964	1965	1966	1967	1968
1964	1,603	127	44	37	40	17
1965	1,595		62	76	44	28
1966	1,157			82	61	24

Experimental data, such as those shown above, could result from banding programs conducted during the winter (when birds are on the wintering grounds) or in late summer (when birds are still on the breeding grounds). Birds are generally not banded during the breeding seasons so as not to disturb them during this critical period. Banding during migration or during the hunting season should be avoided because of difficulties in interpretation and analysis of such data.

In general, banding studies will involve catching, banding, and releasing a sample from some population at regular intervals. (In bird banding studies, intervals are usually 1 calendar year.) We introduce the following terminology to facilitate developments of this chapter. For k banding occasions let $N_1, \ldots, N_k$ be the numbers banded and released back into the population. Equal time intervals between bandings are assumed. Let the band recovery data be represented by R_{ij} defined as

R_{ij} = the number of band recoveries in hunting season j from birds originally banded in year i.

In the example above $R_{11}=127$, $R_{12}=44$, $R_{23}=76$, etc. The general method we recommend for displaying data is shown below in this symbolic notation

Year banded	Number banded	Recoveries by hunting season				
		1	2	3,	...	,k
1	N_1	R_{11}	R_{12}	R_{13},	...	,R_{1k}
2	N_2		R_{22}	R_{23},	...	,R_{2k}
3	N_3			R_{33},	...	,R_{3k}
.	.				.	.
.	.				.	.
.	.				.	.
k	N_k					R_{kk}

We make the following definitions:

k = the number of years of banding
ℓ = the total number of years of recovery ($\ell \geqslant k$).

Often one has $k=\ell$ as in the triangular data array above. In general, however, band recoveries continue to be reported after the banding program has ceased. In the example above, the extended, nontriangular data array has $k=3$ and $\ell=5$.

For adults from one species and sex, there will be just one such recovery data array per study. Often, however, both young and adults are banded from the same species and population. Then there will be two such data arrays to consider for statistical analysis. Less often, three age classes are banded: young, subadults, and adults. Also, there may be birds of both sexes banded leading to yet more data arrays to consider. Models (14 in all) and data analysis procedures for all these situations are dealt with in chapters to follow.

1.3 Modeling Band Recovery Data

General Concepts

Explicitly-stated models are essential to any statistical inference problem; it is the model which hypothesizes the relationship between what we know (the data) and what we do not know but want to estimate, e.g., the relationship of band recovery data to the animal population under study. Because the detailed statistical analyses and their recommended interpretation are critically dependent upon the various models used, it is imperative that the reader understand the assumptions of these models. For this reason, in the following chapters, we have stressed the nature and assumptions of each model. This section gives an introduction to how these models are conceived and structured, and to the basic underlying assumptions.

When an animal is banded or tagged we cannot predict when, if ever, the band or tag will be recovered; thus the event "the band is recovered" must be conceptualized as a random event. The correct model to describe these events requires the use of probability statements, and consequently must be stochastic (probabilistic) as opposed to the older deterministic descriptions of such data.

For example, consider just the recoveries R_{11} from the first hunting season after banding N_1 birds. The appropriate model is a probabilistic one, which treats R_{11} as a random variable. If we let the parameter f_1 be the band recovery rate (i.e., the probability of a band recovery from any bird) for this first year, an appropriate model takes R_{11} as a binomial random variable with sample size N_1, and rate parameter f_1. In abbreviated form we say R_{11} is binomial (N_1,f_1). We note this model has both stochastic and structural components, with the structural component being represented by the average or expected value of R_{11}, symbolized as $\mathbf{E}(R_{11})=N_1f_1$. Let R_{12} be the number of bands recovered in the second hunting season from the N_1 banded birds. Let S_1 be the survival rate during this first year of the study (the calendar year between bandings). Let f_2 be the band recovery rate from birds alive at the time of banding in the second year of the study. Then the model structure for the expected number of recoveries in year 2 ($\mathbf{E}(R_{12})$) is $N_1S_1f_2$. A model for R_{12}, as a random variable, is the binomial (N_1,S_1f_2) model.

In practice we do not deal with just 1 year of recoveries from one banded cohort. As explained in the previous section, bandings will be made at approximately yearly intervals, for some period of years, and band recoveries obtained over several years from each banded cohort. The model used must relate to the entire study whether there is one or more array of recovery data (one or more age classes, and one or both sexes). There are three components to these models: (1) the model structure, which expresses the expected recoveries in terms of numbers banded and survival and recovery rate parameters; (2) the stochastic component which describes the sampling probability distribution of the recovery data (i.e., recognizing the recoveries are random variables and are from a sample); and (3) a component that is never explicity used. The third component is the assumption that the banded sample is representative of the larger population, hence inferences (such as survival rate estimates) apply to this population, not just the sample at hand. This last component can be broken into numerous assumptions, most of them not testable from the recovery data, and their validity generally depends upon the sampling design and field procedures used in banding.

In this section and throughout most of the handbook, when we refer to a model, we mean only the structural component. Only in Section 1.5 do we discuss the general sampling probability model for these types of data. The next two subsections should give the reader a better understanding of model structures and assumptions.

Model Structures

The structure of band recovery models is generally based on two types of parameters: an annual survival rate S and an annual band recovery rate f. These parameters have probability interpretations as follows: S = the probability that a bird alive when a given cohort is banded will survive 1 calendar year to the time of next banding, and f = the probability that a banded bird alive when a given cohort is banded will be shot and its band reported during the next hunting season.

We emphasize that the critical or key assumptions in constructing a model for the analysis of banding data relate to these survival and recovery rate parameters. For example, do the values of these parameters vary with the age or sex of the bird, its capture and banding history, or the calendar year? It is of biological importance to know if the survival rate for a particular species or population segment is age- or sex-specific. In an attempt both to answer these questions and to obtain estimates of the parameters, a series of models (hypotheses) have been developed, each with a different model structure. These models differ depending on the hypothesis concerning how S and f vary.

Consider the hypothesis (tentative assumption) that recovery and survival rates are constant (i.e., they do not vary by age of the bird or calendar year). This hypothesis leads to the following model structure representing the expected number of band recoveries:

		Expected recoveries by hunting season, $\mathbf{E}(R_{ij})$			
Year banded	Number banded	1	2	3	$\ell=4$
1	N_1	N_1f	N_1Sf	N_1SSf	N_1SSSf
2	N_2		N_2f	N_2Sf	$[N_2SSf]$
$k=3$	N_3			N_3f	N_3Sf

As above, our representation of a model will entail its structure only and be expressed in a form analogous to the recovery data themselves.

Consider the expression in brackets in the table above. This term represents the expected number of band recoveries the fourth year of the banding study, from the sample of N_2 birds banded in the second year of the study, $\mathbf{E}(R_{24}) = N_2SSf$. Its meaning is simple and logical. The expected number of survivors during year 2 of the study is N_2S. From the start of year 3, we expect a proportion S of these survivors to live to year 4 of the study. Hence, there are N_2SS survivors expected at the start of year 4. A proportion f of these survivors will, on the average, be shot and their bands reported. Thus the expected number of band recoveries in the fourth year of the study from the N_2 birds banded in year 2 is N_2SSf. In this particular model we are hypothesizing that S and f are constant from year to year and independent of age.

Now, let us specify, for illustrative purposes, that the underlying population parameters are:

$f = 0.10$ or a 10% annual recovery rate,
$S = 0.50$ or a 50% annual survival rate,

and that, in fact, f and S are indeed constant. We also specify (for the purpose of this example):

$$\left.\begin{array}{l} N_1 = 2{,}000 \\ N_2 = 400 \\ N_3 = 1{,}200 \end{array}\right\} \text{Number banded in the } i^{th} \text{ year.}$$

Then, on the average we would expect the following recovery data:

Year banded	Number banded	Expected recoveries by hunting season, $\mathbf{E}(R_{ij})$ 1	2	3	$\ell = 4$
1	2,000	200	100	50	25
2	400		40	20	[10]
$k = 3$	1,200			120	60

Return again to the value that is bracketed: $N_2SSf = 400 \times 0.50 \times 0.50 \times 0.10 = 10$ recoveries.

The expectations of the recovery data can be easily expressed for this simple model in terms of the two parameters S and f (for arbitrary values of k and ℓ, the number of years of banding and recovery, respectively):

$$\mathbf{E}(R_{ii}) = N_i f \qquad ,i = 1, \ldots, k,$$
$$\mathbf{E}(R_{ij}) = N_i S^{j-i} f \qquad ,i = 1, \ldots, k, \qquad j = i+1, \ldots, \ell \;.$$

These concepts could be made more general and realistic if, for instance, recovery and survival rates were hypothesized to vary each year. The model structure representing these tentative assumptions would be:

Year banded	Number banded	Expected recoveries by hunting seasion, $\mathbf{E}(R_{ij})$ 1	2	3	$\ell = 4$
1	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2S_3f_4$
2	N_2		N_2f_2	$N_2S_2f_3$	$[N_2S_2S_3f_4]$
$k = 3$	N_3			N_3f_3	$N_3S_3f_4$

Here, the parameters of the model are subscripted to indicate the dependence on calendar year (i.e., the parameters S and f are year-specific).

Again, for purposes of example, let us specify that the underlying population parameters are:

Year	Recovery rates	Survival rates
1	$f_1 = 0.05$ or 5%	$S_1 = 0.50$ or 50%
2	$f_2 = 0.10$ or 10%	$S_2 = 0.50$ or 50%
3	$f_3 = 0.06$ or 6%	$S_3 = 0.70$ or 70%
4	$f_4 = 0.05$ or 5%	

Given the above, on the average we would expect the following recovery data (the number banded will remain the same as the previous example):

Year banded	Number banded	Expected recoveries by hunting season, $\mathbf{E}(R_{ij})$ 1	2	3	$\ell=4$
1	2,000	100	100	30	18
2	400		40	12	[7]
$k=3$	1,200			72	42

Here, for example, the term in brackets is $N_2S_2S_3f_4 = 400 \times 0.50 \times 0.70 \times 0.05 = 7$ recoveries. Notice that the expected number of recoveries is quite different under the two models. In general, the expectations under the assumptions that recovery and survival rates are time-specific can be expressed in terms of these parameters as:

$$\mathbf{E}(R_{ii}) = N_i f_i \qquad ,i = 1, \ldots ,k ,$$
$$\mathbf{E}(R_{ij}) = N_i S_i \cdots S_{j-1} f_j \qquad ,i = 1, \ldots ,k, \qquad j = i+1, \ldots ,\ell.$$

In this case, the parameters $S_1, \ldots ,S_{k-1}$ and $f_1, \ldots ,f_k$ are estimable whether $\ell = k$ or not. If, however, $\ell > k$ the parameters $S_k, \ldots ,S_\ell$ and $f_{k+1}, \ldots ,f_\ell$ are not separately estimable; only the products such as $S_k f_{k+1}$, $S_k S_{k+1} f_{k+2}, \ldots$, $S_k \cdots S_{\ell-1} f$ are estimable. This subject is discussed in Section 2.2 of Chapter 2.

The above examples show the relationships among the specific hypotheses about survival and recovery rates, model structures representing these hypotheses, and the values that would be expected on the average under such a model. Of course, the actual recovery data will vary somewhat from the expected or average values because survival and band reporting are random events. In practice, the biologist has only the observed data (plus some knowledge of the biology of the species), but usually does not have *a priori* knowledge of the underlying process and, therefore, does not know what model is most appropriate.

Assumptions

As mentioned above, there are numerous assumptions involved in making inferences from banding data; important ones are listed below.

Assumptions relating to study planning, field procedures, and type of species:

(1) The sample is representative of the target population;
(2) age and sex of individuals are correctly determined;
(3) there is no band loss;
(4) survival rates are not affected by the banding or tagging itself; and
(5) the year (hunting season) of band recoveries is correctly tabulated.

Assumptions relating to the stochastic model component:

(6) The fate of each banded animal is independent of (not correlated with) the fate of other banded individuals;
(7) the fate of a given banded animal (i.e., band recovery in year 1, 2,... after banding) is a multinomial random variable.

Assumptions relating to model structure:

(8) All banded individuals of an identifiable class (e.g., by species, age, sex) in the sample have the same annual survival and recovery rates (except model H_3 of Chapter 3); and
(9) annual survival and recovery rates may vary by calendar year, and/or by age and sex of individuals (variation of survival and recovery rates by area [population] is also possible).

In practice, assumption 9 is a series of very specific assumptions which can be investigated and tested in detail from the recovery data themselves. These assumptions specify the exact model structure, they constitute the focus of this handbook, and in the usual type of banding study they are the only testable assumptions.

It is beyond the scope of this handbook to discuss field procedures in detail because they will vary by species and study. Sections 9.1 and 9.2 offer some guidelines on this subject. Obtaining a representative sample is important; in studying populations. This is always of potential concern (see Weatherhead and Ankney 1984, 1985 and Burnham and Nichols 1985). Recently, Pollock and Raveling (1982) and Nichols et al. (1982) presented valuable information on these assumptions (see Appendix C). Nelson et al. (1980) examines the effect of band loss (assumption 3)

on survival estimators and Anderson and Burnham (1980) investigate the effect of delayed reporting of bands (assumption 5) on these methods (both of these papers appear in Appendix C).

Based on assumptions 6, 7, and 8, we model the recovery data from any banded cohort as multinomially distributed random variables. This distribution is the basis for deriving sampling variances, and covariances of estimators, tests for goodness of fit, and tests between models. We believe these tests do not critically depend upon this presumed sampling distribution; hence, some degree of failure of this assumption (which occurs if assumption 6 is not true) does not destroy the usefulness of the methods presented here. Assumption 7 is shown to be mathematically true in Section 1.5. Assumption 8 is important but it is generally not testable if there is no method even in principle, to further partition the identified class of animals. However, the test between models H_1 and H_3 (Chapter 3) is a case where assumption 8 is testable.

Given assumptions 1 through 8, we have a model in which the only unknown is the structure of the expected band recoveries as a function of annual survival and recovery rates, i.e., $\mathbf{E}(R_{ij}) = N \times$ (a function of annual survival and recovery rates). In subsequent chapters when we discuss model assumptions, we mean those distinct, detailed assumptions which specify a model structure for expected band recoveries in terms of variations in S and f (survival and recovery rates) with respect to time (calendar year), area, age, or sex.

The reader should be aware of one more assumption. We have limited ourselves to instances of equal time periods (usually 1 year) between bandings, the most common situation. All the analysis methods presented herein assume equal time periods, and thus certain of these models and tests are not appropriate for use on data with unequal time periods between banding or tagging. This subject is discussed further in Section 8.5.

1.4 Data Analysis

Estimation with a Given Model

Given an explicit, biologically reasonable stochastic model representing a specific hypothesis about survival and band recovery rates, we are faced with estimating the parameters of the model. Fortunately, a well-developed theory for efficient estimation of parameters from such models exists. This theory of parameter estimation has had a long history; most of the initial developments and their early elaboration are credited to the famous statistician Sir Ronald A. Fisher. In the 1920's, Fisher published extensively on the method he called "Maximum Likelihood." This method forms one fundamental approach to statistical estimation and inference theory. For many practical models, Maximum Likelihood (ML) estimators are optimal in many respects (e.g., for a given model, no other method will produce consistent estimators with a smaller sampling variance). Most modern methods for estimating parameters from animal marking experiments are based on the ML method, and it is the basis for the estimation procedures in this handbook.

It is not necessary for the reader to understand the statistical theory underlying any of the data analysis methods presented in this handbook (e.g., parameter estimation, estimation of sampling variances and covariances, confidence interval construction, goodness of fit tests, or tests between models). All the general underlying statistical theory is fairly standard, and its properties are known. Thus we can assert that most of the data analyses methods presented here can not be improved upon. These methods make optimal use of the data under any given model. We give some minimal introduction to the relevant mathematical methods behind these models in Section 1.5 and in the Appendices. However, for the most part, the interested reader will have to consult the original references for the details of estimation and inference developments for each model.

Our strategy in the following chapters that discuss given models is to first present the model structure and the key assumptions on survival and recovery rates which yield this structure. Then, where possible, the formulae for parameter estimators are given; finally, the formulae are given for sampling variances and covariances of these estimators. The following type of notation is used: If X represents a parameter, then its ML estimator is denoted by $\hat{X}$. Theoretical sampling variances, covariances, etc., and their estimators are denoted as shown below:

Quantity	Theoretical	Estimated
variance	$\mathrm{VAR}(\hat{X})$	$\mathrm{var}(\hat{X})$
standard error	$\mathrm{SE}(\hat{X})$	$\mathrm{se}(\hat{X})$
covariance	$\mathrm{COV}(\hat{X},\hat{Y})$	$\mathrm{cov}(\hat{X},\hat{Y})$
correlation	$\mathrm{CORR}(\hat{X},\hat{Y})$	$\mathrm{corr}(\hat{X},\hat{Y})$

Often ML estimators are slightly biased. This is true with some estimators (mainly estimators of survival rates) under several models. We have developed adjusted estimators that are essentially free of this small sample statistical bias. The ML estimators that are adjusted for statistical bias are represented by a tilde (˜) over the parameter, e.g., $\tilde{X}$. Correspondingly, $\tilde{X}$ replaces $\hat{X}$ in formulae for sampling variances, covariances, and correlations, e.g., VAR($\tilde{X}$) and var($\tilde{X}$). (We do assume that the reader has had some basic statistics, and is familiar with concepts of estimation, bias, accuracy, sampling variation, models, etc. A useful reference on this subject is Overton 1969.)

As part of the analysis of recovery data under any given model we also usually give a goodness of fit test to judge whether the model is an acceptable fit to the data. These goodness of fit tests are meant to be used in the processes of selecting the appropriate model for any given data set.

Selecting the Best Model

The proper model must be used if sound inferences are to be made from the analysis of banding or tagging data. We want to adopt the simplest model which adequately fits the given data set. This philosophy follows the general principle in science of using the simplest acceptable model to describe a phenomenon (Occam's razor).

First we will examine the alternatives to this philosphy: models that are too simple and models that are too general. In using models of banding studies, we have found that overly simple and restrictive models are worse than overly general models. Here the simplified model, and the hypothesis (tentative set of assumptions) it represents, does not fit the observed data. Here we risk substantial bias (regardless of how large the sample size) in the estimates of parameters and/or their sampling variances and covariances. Worse yet, the estimates of sampling variances are almost always too small. Consequently, the investigator has a false sense of security because he/she believes the estimates are very precise. This bias can lead to apparently significant differences if, for example, survival rates are compared between two geographic areas, where actually no differences can properly be shown. Use of a model that is too simple is almost always nonconservative. The composite dynamic method has been used in the analysis of bird banding data for 35 years but few investigators had ever bothered to see if this "model" fit the data being analyzed. These assumptions were recently tested for waterfowl (Burnham and Anderson 1979) and nongame birds (Anderson et al. 1981) and were soundly rejected. These facts further emphasize the need for proper testing procedures to aid the selection of an adequate set of models.

The second alternative is the use of a model that is too general, a model that allows more parameters than are necessary. Here, the point estimators of parameters are inefficient, although they are unbiased. The estimated sampling variances and covariances are large, indicating that precision has been sacrificed. Testing procedures tend to be conservative, failing to detect significant differences that, in fact, exist.

We are recommending two types of procedures to statistically test various models and to select the proper one. The first test is a goodness of fit test. Here the null hypothesis is that the model fits the data, while the alternative hypothesis is a general one – the model does not fit the data. If the null hypothesis is rejected for a particular data set, that model should no longer be considered. The second test is more specific and tests one model against another. Here the alternative is specific. The null hypothesis is that the simplest model, the one with the fewest parameters, fits. Again, if the null hypothesis is rejected, the simple model should not be considered further in the analysis of a particular data set.

Choice of a "proper" and "adequate" model is somewhat relative since other models may also be "good." For example, Model H_1 (given in Chapter 3 and used for the analysis of banding of both young and adults) is often a good model of a bird population with age-specific parameters. Results of the goodness of fit test usually fail to reject H_1 whereas simpler models are often rejected, and more general models are often shown to be unnecessary for a particular data set. However, although Model H_1 might be adequate for the analysis of the data set, there may be other models that are equally appropriate. For example, Johnson (1974) developed a model similar to H_1, but containing fewer parameters because of two restrictions. In many situations, both models would be satisfactory and we have little preference as to which of the two is better except that Johnson's has fewer parameters. (Note: we do not discuss Johnson's model in this handbook because it is not fully developed; Model H_1 is fully developed, complete with intensive testing features and a comprehensive computer code).

Computer Algorithms

We have developed two large computer programs to alleviate the tedious task of computing the estimators, test statistics, etc., presented in this handbook. Program ESTIMATE is for age-independent populations and is discussed in Chapter 2. Program BROWNIE was written for several age-dependent models and to test for sex-specific parameters in adult recovery data. Output from BROWNIE is discussed in Chapters 3, 4, and 5. The use of programs ESTIMATE and BROWNIE is discussed in Chapter 6.

1.5 Mathematical Overview

This section can be omitted by the reader with little knowledge or interest in mathematical statistics.

Model Conceptualization

Consider a study where banding is done for k consecutive years, and recoveries are accumulated for $\ell \geq k$ years. For a given bird banded in year i, exactly one of $\ell - i + 2$ discrete events regarding the band will occur. Either the band is recovered in one of the $\ell - i + 1$ years after banding, or it is never recovered. For recovery to occur in year j the bird must survive until the start of year j, then be shot during that year, and the band must be reported to the Bird Banding Laboratory. To represent these outcomes, define an indicator random variable for a bird banded in year i $(i = 1, \ldots, k)$ as

$$X_{ij} = \begin{cases} 1 \text{ if the band is recovered in year } j,\ j = i, \ldots, \ell, \\ 0 \text{ otherwise.} \end{cases}$$

For notational convenience, define $X_{i,\ell+1} = 1 - \sum_{j=i}^{\ell} X_{ij}$. Hence, $X_{i,\ell+1}$ is 1 if and only if the band is never recovered. Finally define the vector valued random variable $\underline{X}_i = (X_{ii}, \ldots, X_{i,\ell+1})$.

The random variable $\underline{X}_i$ has the classic multinominal probability distribution with $\ell - i + 2$ cells (Johnson and and Kotz 1969). Let $P\{X_{ij} = 1\} = \pi_{ij}$ be the probability the band is recovered in year $j, j = i, \ldots, \ell$. Then $\pi_{i,\ell+1} = 1 - \sum_{j=i}^{\ell} \pi_{ij}$ is the probability the band is never recovered. The probability of any of the $\ell - i + 2$ possible outcomes is represented as $P\{\underline{X}_i\} = \prod_{j=i}^{\ell+1} (\pi_{ij})^{X_{ij}}$.

A general structure on the π_{ij} cell probabilities can be used without loss of generality. A band can be recovered in year j only if the bird survived and retained its band until the start of year j. Then it must be shot and the band reported to the Bird Banding Laboratory. Consequently, define the following conditional annual survival, band retention, and recovery rates:

S_{ji} = probability of surviving year j, given the bird was alive at the start of year j and was banded at the start of year $i \leq j$;

θ_{ji} = probability of band retention in year j given the bird still has the band at the start of year j and was banded in year i; and

f_{ji} = probability that a bird alive at the start of year j, which was banded in year i, is shot in year j and its band reported to the Banding Laboratory.

Now a general structural representation for any π_{ij} is

$$\pi_{ij} = \begin{cases} f_{ii} & , j = i \\ \left[\prod_{h=i}^{j-1} (S_{hi}\theta_{hi})\right] f_{ji} & , j > i. \end{cases}$$

It should be clear that survival rates are confounded with band retention rates. This is indeed true; no useful models can be developed for band recovery data unless we assume there is no band loss, i.e., $\theta_{hi} \equiv 1$. We do make this assumption; it is implicit in all the models presented in this handbook. Given that no band loss occurs, the general structural representation for π_{ij} is

$$\pi_{ij} = \begin{cases} f_{ii} & , j = i \\ \left[\prod_{h=i}^{j-1} S_{hi}\right] f_{ji} & , j > i. \end{cases} \tag{1.5.1}$$

Now assume N_i birds from the same population are banded and released in year i. We make two more assumptions to obtain a general model structure for banding studies. First, assume all these N_i birds suffer statistically independent fates. Second, assume that all the N_i banded birds have the same annual survival and recovery probabilities. From a practical standpoint this second assumption is unavoidable if the N_i birds cannot be partitioned, even in principle, into subgroups whose survival and recovery parameters might differ. Thus, with a banded sample from one species, age, sex, and area obtained at one brief time interval this second assumption is acceptable.

Define new summary random variables (for k years of banding)

$$R_{ij} = \text{all recoveries in year } j \text{ of birds banded in year } i, j=i,\ldots,\ell, i=1,\ldots,k.$$

If we use m to index the variables $\underline{X}_i$ over the N_i birds, then the raw data are $\underline{X}_{i,m}$, $m=1,\ldots,N_i$, $i=1,\ldots,k$. But for each i, $\underline{X}_{i,1},\ldots,\underline{X}_{i,Ni}$ are identically and independently distributed as multinomial random variables; hence, their sum

$$(R_{ii},\ldots,R_{i,\ell+1}) = \sum_{m=1}^{N_i} \underline{X}_{i,m}$$

is a sufficient statistic with the multinomial distribution Mult$(N_i; \pi_{ii},\ldots,\pi_{i,\ell+1})$. Consequently,

$$P\{R_{ii},\ldots,R_{i\ell}\} = \binom{N_i}{R_{ii},\ldots,R_{i\ell},R_{i,\ell+1}} \prod_{j=i}^{\ell+1} [\pi_{ij}]^{R_{ij}},$$

where $R_{i,\ell+1} = N_i - \sum_{j=i}^{\ell} R_{ij}$ and the π_{ij} have the general structure displayed in formula (1.5.1).

The above development shows we can reduce our data to the recovery frequencies $\{R_{ij}\}$ which may be conveniently displayed in an array as:

Year banded	Number banded	Recoveries by hunting season						
		1	2	3	,...,	k	,...,	ℓ
1	N_1	R_{11}	R_{12}	R_{13}	...,	R_{1k},	...,	$R_{1\ell}$
2	N_2		R_{22}	R_{23}	...,	R_{2k},	...,	$R_{2\ell}$
3	N_3			R_{33}	...,	R_{3k},	...,	$R_{3\ell}$
.	.				.	.		.
.	.				.	.		.
.	.				.	.		.
k	N_k					R_{kk},	...,	$R_{k\ell}$

where if $\ell = k$ the above array of recoveries is triangular. The number of bands never recovered for a given cohort is $N_i - R_{i.}$ where $R_{i.} = \sum_{j=1}^{\ell} R_{ij}$, hence, their number need not be displayed.

Bearing in mind that each set of recovery data $(R_{ii},\ldots,R_{i\ell})$ are independent multinomial random variables for $i=1,\ldots,k$; the statistical model for these data is completely specified by displaying the cell probabilities π_{ij} as:

Year banded	Number banded	Model structure, by year of recovery						
		1	2	3	,...,	k	,...,	ℓ
1	N_1	π_{11}	π_{12}	π_{13},	...,	π_{1k},	...,	$\pi_{1\ell}$
2	N_2		π_{22}	π_{23},	...,	π_{2k},	...,	$\pi_{2\ell}$
3	N_3			π_{33},	...,	π_{3k},	...,	$\pi_{3\ell}$
.	.				.	.		.
.	.				.	.		.
.	.				.	.		.
k	N_k					π_{kk},	...,	$\pi_{k\ell}$.

The representation $\pi_{ij}=\left(\prod_{h=1}^{j-1} S_{hi}\right)f_{hi}$ is too general to be useful; none of the individual survival or recovery rates are estimable. In order to obtain meaningful, useful models we must make additional assumptions about the nature of the annual survival probabilities and about the annual recovery probabilities. For example, if we band only adults, then perhaps the survival rate is age-independent. This implies S_{hi} need not depend upon the year of banding; rather, adult survival may depend only upon environmental conditions in each year. This implies assuming $S_{hi}\equiv S_h$ independent of the year the bird was banded. Similarly, adult recovery rates may be independent of the year of banding, which implies assuming $f_{hi}\equiv f_h$. Given these assumptions of age-independent survival and recovery rates, the model structure is given by

$$\pi_{ij}=\begin{cases} f_i & ,j=i \\ S_i\cdots S_{j-1}f_j & ,j>i. \end{cases}$$

This model is displayed in array form below:

Year banded	Number banded	Model structure, by year of recovery						
		1	2	3	,...,	k	,...,	ℓ
1	N_1	f_1	S_1f_2	$S_1S_2f_3$,	...,	$S_1S_2\cdots S_{k-1}f_k$,	...,	$S_1S_2\cdots S_{\ell-1}f_\ell$
2	N_2		f_2	S_2f_3,	...,	$S_2\cdots S_{k-1}f_k$,	...,	$S_2\cdots S_{\ell-1}f_\ell$
3	N_3			f_3,	...,	$S_3\cdots S_{k-1}f_k$,	...,	$S_3\cdots S_{\ell-1}f_\ell$
.	.				.	.		.
.	.				.	.		.
.	.				.	.		.
k	N_k					f_k,	...,	$S_k\cdots S_{\ell-1}f_\ell$

Analysis of adult banding data based on the above model (which we call Model 1 here) has been thoroughly developed by Seber (1970) and Robson and Youngs (1971).

The above discusses only one data set. Often birds will be identified as to sex or age, giving rise to multiple data sets that may have some survival or recovery rates in common. The modeling problem in these cases is to specify what parameters may be the same or different across ages and/or sexes. The theory of the problem is not fundamentally altered, just made more complex because of additional parameters and data.

The Likelihood Function

The recoveries from any given banded cohort in the data matrix $\{R_{ij}\}$ are modeled as multinomial random variables. From this fact we can write the joint probability function of the data as

$$P(\{R_{ij}\}\,|\,\underline{S},\underline{f},\underline{N})=\prod_{i=1}^{k}\left\{\binom{N_i}{R_{ii},\ldots,R_{i\ell},R_{i,\ell+1}}\prod_{j=i}^{\ell+1}[\pi_{ij}]^{R_{ij}}\right\}, \tag{1.5.2}$$

where

$$R_{i,\ell+1}=N_i-\sum_{j=i}^{\ell}R_{ij}\equiv N_i-R_{i\cdot}$$

$$\pi_{i,\ell+1}=1-\sum_{j=i}^{\ell}\pi_{ij},$$

$$\pi_{ij}=\left(\prod_{h=i}^{j-1}S_{hi}\right)f_{hi}\qquad ,j=i,\ldots,\ell,\ i=1,\ldots,k,$$

and $\underline{S}$, f are the vectors of parameters. For any given model used in this handbook the actual likelihood function can easily be derived from the above symbolic representation. For example, assuming $S_{hi} \equiv S$, and $f_{hi} \equiv f$ we have

$$\pi_{ij} = S^{(j-i)} f \quad , j = i, \ldots, \ell \quad , i = 1, \ldots, k$$

and

$$\pi_{i,\ell+1} = 1 - \left(\frac{1 - S^{\ell-i+1}}{1 - S}\right) f.$$

Therefore, the likelihood is

$$\mathcal{L}(S,f) = \left[\prod_{i=1}^{k} \left(1 - \left(\frac{1 - S^{\ell-i+1}}{1 - S}\right) f\right)^{N_i - R_{i.}} \right] f^T S^Q,$$

where

$$T = \sum_{i=1}^{k} \sum_{j=i}^{\ell} R_{ij}, \text{ and } Q = \sum_{i=1}^{k} \sum_{j=i}^{\ell} (j-i) R_{ij}.$$