Post-release Stratification and Migration Models in Band-recovery and Capture-recapture models

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© Carl James Schwarz

A Thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Abstract

In this Thesis, I examine two generalizations of band-recovery experiments used in the study of animal populations. First, it is well known that heterogeneity in survival or band-recovery rates among animals in a population can cause the usual estimates obtained from band-recovery studies to be biased. The usual remedy is to stratify the animals at the time of banding or release into more homogeneous groups. In some cases, the stratification can only take place after release, usually at recovery time. For example, animals may be stratified at recovery time on the basis of location of recovery (i.e., by area), or by type of recovery (e.g., by how killed). I develop mathematical models incorporating various assumptions about the survival and band-recovery rates in the sub-populations formed by the post-release stratification. For each model, the maximum likelihood estimates and the estimates of their variances and covariances are found. Procedures are developed to assess the goodness-of-fit of these models to a set of data and to determine which model is most appropriate for a set of data. The power function of these tests is developed so that the extent of heterogeneity present but largely undetectable can be assessed. A numerical example using real data is used to illustrate these results.

Second, since post-release stratification commonly is performed on the basis of area of recovery, the previous models are extended to model explicitly a seasonal migration process. For example, banding studies are often performed on ducks which migrate each year from their breeding sites in the northern United States and Canada to wintering areas in the southern United States. Three models, representing various assumptions about the fidelity of the animals to and from their migration sites are examined: the Complete-Fidelity Model where an animal is assumed to be faithful to both sites; the Partial-Fidelity Model where an animal is assumed to be faithful to the area of release but may choose a new migration site each year; and the Non-Fidelity Model where an animal is not assumed to be faithful to either site. In all models, the use of ordinary band-recovery data is shown to be inadequate for inference about the survival, migration, and band-recovery parameters since they are confounded. A modification to the experimental design involving live resightings of animals in the wintering areas is shown to allow complete inference about all parameters in each model. Maximum likelihood estimates and their covariances are determined along with procedures for testing model goodness-of-fit and for testing various assumptions about the homogeneity of the parameters over time or among sub-populations. Simulated data are used to illustrate these results. A fourth model, called the Internal-Transfer Model is developed to examine migration among the areas of release only; in this model, the recovery and release areas are not distinct. Ordinary band-recovery data is, in theory, adequate for this model, but, in practice, not useful since the near non-identifiability of the parameters leads to high sampling variances and covariances among the estimates. Live resightings are again shown to improve inferential procedures. A numerical example, using simulated data illustrates the use of this model.

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The material in Chapter 2 is based upon work by Dr. K. P. Burnham who originally presented the estimators for Models 3 and 2a, the test of Model 2a vs. Model 3, and the goodness-of-fit to Model 3 in correspondence between himself and Dr. Lyman McDonald. I considered the remaining models in the hierarchy (Models 1 and 2b) and: developed the estimation procedures for these two models; developed the testing procedures of Model 1 vs. 2a, Model 1 vs. 2b, and Model 2b vs. Model 3; developed the power results for all four models; and considered the implications of fidelity to the post-strata. The results of Chapter 2 have been submitted to *Biometrics* as:

Schwarz, C.J., Burnham, K.P., and Arnason, A.N. (1988). Post-release stratification in band-recovery models.

I would like to thank Dr. K. Burnham for copies of his notes and correspondence and for his suggestions on revisions to Chapter 2. I would also like to thank Dr. J. Nichols for providing the data used in the example.

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1.1 GENERAL OVERVIEW AND MOTIVATION

The use of capture-recapture data to study animal populations is well known (e.g., Seber, 1982, 1986). In these experiments, a group of animals are first captured over a short period of time. They are fitted with a uniquely numbered tag or band (or are physically marked) and are released. A second group of animals is captured at the next sampling time. These animals may already be tagged (from the first sample time), or untagged. The number of the tag on each animal captured that is already tagged, and the number of untagged animals is recorded. The untagged animals are tagged, and all animals are released. This process may be repeated for several more sample times. Hence, capture-recapture experiments are characterized by:

- captures and releases occur at two or more sampling times;
- at each sampling time, the number on the tag of previously tagged animals is recorded; the untagged animals are counted and tagged; and the animals are released. All this occurs over a short period of time.

From this data, the population sizes at the sampling times, the combined mortality and emigration rates between sampling times, the combined immigration and birth rates between sampling times, and the probability of capture at a sampling time may be estimated.

A specialized form of capture-recapture experiments is the band-recovery experiment described in detail by Brownie *et al.* (1985). In fact, capture-recapture experiments may be reformulated and analyzed as a series of band-recovery experiments (Brownie and Pollock, 1985;

Burnham *et al.*, 1987). In these experiments, a group of animals are first captured over a short period of time; they are fitted with an individually numbered tag or band (or are physically marked); and they are released back to the population. Now, recaptures of banded animals may occur over the entire period between one release and the next release (usually a year later), and are typically obtained by exploitation (e.g., by hunting or by fishing). The exploiters are asked to report the time and location of any tagged or banded recovery to a central reporting site. At the next sampling time, a new set of animals is captured, banded, and released. Only information on newly banded animals is recorded at this time; recaptures of previously banded animals are ignored. Again, exploitation occurs over the next year, except that there are now two cohorts of animals (those released in year 1 and those released in year 2) which have bands. This sequence of capturing, banding, and releasing animals at a point in time (known as the banding time), and the recovery of bands from the entire time period between banding times may be repeated for several years. Hence, band-recovery experiments are characterized by:

- banding takes place at a point in time and only information on newly banded animals is recorded;
- the number of bands recovered and their locations is recorded from each cohort of releases for the entire period between banding times.

Band-recovery experiments differ from capture-recapture experiments in that:

- only information on newly banded animals released at each banding time is used; information on recaptures (at banding time) of previously banded animals is ignored.

· band recoveries come from (typically) dead animals and may occur over the entire period between banding times.

· a band is seen at most twice, at release and recovery.

Naturally, less information is obtained from these experiments; typically, estimates are only available for:

· the survival rates from banding time to banding time;

· the band-recovery rate, i.e., the overall probability that a band is recovered over the next year from an animal alive at banding time of that year.

Since information is not used on the ratio of the number of unbanded animals to previously banded animals in the sample taken at banding time, estimates of the population size and birth or immigration rates cannot be obtained.

One motivation for this Thesis is that the methodology presented in Brownie *et al.* (1985) for the analysis of band-recovery data makes the assumption (among others) that all animals are homogeneous with respect to survival and band-recovery rates. In some cases, it is doubtful that this occurs. Pollock and Raveling (1982) and Nichols *et al.* (1982) examined the effect of heterogeneity among animals on the bias of the estimates of survival and band-recovery rates and concluded that heterogeneity can cause substantial positive or negative bias, depending on the type of heterogeneity. If the animals can be divided into homogeneous strata at banding, then the biases will be reduced and stratum-specific estimates can be obtained and compared (Brownie *et al.*, 1985, Chapter 5). In some cases, stratification takes place only after releasing the banded animal, usually at recovery time. Examples of such post-release stratification events are: animals recovered in different areas (pin-tails as described by Anderson and Sterling, 1974); animals recovered by hunting and by live-trapping (Mardekian and McDonald, 1981); animals shot using steel or lead shot; or animals classified by sex or by age when this is difficult to do at banding time but may be done at recovery time (Pollock and Raveling, 1982). I examine the general question of post-release stratification in band-recovery experiments by constructing four stochastic models representing the possible heterogeneity of the survival or band-recovery rates, or both, among strata. These models are useful for cases (among others) where the post-release stratification is based upon unchanging attributes (such as sex) that are unknown at banding time, or for cases where the post-release stratification is based upon behavioral aspects of the animal such as movements to different areas. However, in the latter case, parameters explicitly modelling the movement process have not been defined; the gross band-recovery rate incorporates a hidden component for the movement of the animals to the area of recovery. In either case, proper post-release stratification can provide less biased estimates of the population parameters with little increase in experimental effort.

A second, and primary, motivation of this Thesis, is to explore the use of band-recovery data in studying animal movements. This entails generalizing the previous models on post-release stratification on the basis of area of recovery by explicitly including parameters describing the movement process. Not only is this of theoretical interest, but many types of wildlife undergo large scale movements and it is important to understand the patterns of movement so that scarce resources may be allocated in order to maintain or to increase populations, or to control exploitation. For example, an understanding of the relative contribution of breeding stocks to exploited populations assists wildlife managers in deciding which breeding habitats require protection or upgrading. An understanding of the movement patterns of sub-populations assists the manager in setting quotas on exploitation and in setting the opening and closing dates of the exploitation season in order to protect segments of the population.

These movement patterns of animal populations can take several forms:

- seasonal migrations, where there are well defined areas that are inhabited by the animals at different times of the year;
- dispersals, where animals move to new permanent habitats from a central point (such as a breeding area);
- diffusions, where the habitat gradually expands or contracts as animals move out from or in from the boundaries of the current habitat.

The seasonal migration patterns are the most difficult to quantify and are a source of problems to wildlife managers since the migration routes may be long and the different habitats may be in different countries, inhibiting co-operation in managing the species. Consequently, the majority of this Thesis examines the use of band-recovery data to study the seasonal migration patterns.

Typically, individually distinguishable bands are applied to the animal (or individually distinguishable marks are applied directly to the animal) in the breeding areas, e.g., bands applied to ducks in the Prairie pot-hole region (Anderson and Henny, 1972, and others in the series). Since the banding effort is under the control of the experimenter, the banded animals may be stratified at the time of banding by such attributes as: area of banding; type of banding; sex, age, or any other attribute of the animal that is known at the time of banding; or an applied treatment group (Burnham *et al.*, 1987). I refer to these strata as 'pre-strata' for convenience. Interest lies in comparing the movements of animals from one pre-stratum with the movements of the animals from another pre-stratum. The band applied to the animal should allow identification of the pre-stratum at a later date.

As or after the animals migrate, they may be exploited (e.g. by hunting or fishing), and the exploiters are asked to report any band from a harvested animal, along with the location of the recovery, to a central reporting site. The recoveries can also be stratified, usually by attributes such as: flyways, wintering areas, or any other attribute that is unknown at the time of banding but is known at recovery time. I refer to these strata as 'post-strata' for convenience. I also use the term 'habitat' as a synonym for pre- or post-stratum, even though this implies that the strata are geographical areas, rather than strata based upon attributes (e.g., sex). While the models discussed in this Thesis are applicable to attribute-based definitions of the strata, the models are primarily intended for situations involving physical migration and in assessing the contribution of animals from the pre-strata to the population in each post-stratum.

Various sets of assumptions (scenarios) can be made about the mechanisms of migration. Ideally, a single general model that contains all these scenarios as special cases should be constructed. However, this 'super'-model would have a very large number of parameters, would require a large amount of data in a complex form that is not easily obtained, and would be too complicated for general use. Instead, I have chosen to explain three migration models from this general family that form a hierarchical chain within the 'super'-model, that are biologically plausible for many species, that do not require complex data structures, and that are easier to use than this 'super'-model. These are:

- Complete-Fidelity Models where annual migrations occur between pre-strata (e.g., breeding areas) and post-strata (e.g., wintering areas), and animals have complete fidelity to both areas. For example, some species of birds home precisely to both their breeding sites and wintering sites each year. Banding takes place in the pre-strata. Recoveries occur in the post-strata. Interest lies on the migration patterns from pre-strata to post-strata.
- Partial-Fidelity Models where annual migrations occur between pre-strata (e.g., breeding areas) and post-strata (e.g., wintering areas), and animals are faithful to their pre-strata only. For example, some species of birds home precisely each year to areas where they were reared or had previously nested, but choose their

wintering areas based upon environmental conditions present during migration. Banding takes place in pre-strata. Recoveries occur in the post-strata. Interest lies in the migration patterns from the pre-strata to the post-strata. (This and the previous model are also applicable if the animals are pre-stratified by, for example, sex, and interest lies on the different migration patterns to wintering areas by the different sexes. In these cases, the animal is "faithful" to its sex at banding, rather than the breeding area at banding. Clearly sex cannot be a post-stratification factor in the Partial-Fidelity Model.)

· Non-Fidelity Models where annual migrations occur between pre-strata and post-strata, and animals are faithful to neither area. For example, the animal may choose a different wintering area each year upon leaving the breeding area, and may return to a different breeding area each year upon leaving the wintering area. Banding takes place in the pre-strata. Recoveries occur in the post-strata. Interest lies in the migration patterns from the pre-strata to the post-strata.

In all cases, I demonstrate that ordinary band-recovery experiments do not yield information sufficient to estimate the migration rates. Modifications to the experimental design, involving live resightings, are shown to allow estimation of most of the parameters of interest.

A fourth model, the Internal-Transfer Model, is also considered. In this model the banding and recovery areas are not separately distinguished and animals migrate between or remain in the banding/recovery area. For example, animals may move among breeding areas from year-to-year. Banding takes place in the breeding areas. Recoveries also take place in the breeding areas next year. Any migration to and from wintering areas is ignored. The crucial distinction between this model and previous models is that the pre- and post-strata are not distinct.

Of interest to the manager are several biological quantities pertinent to the species being managed:

- survival rates - what fraction of animals survive from one year to the next for each pre-stratum;
- emigration rates - what fraction of the animals from a pre-stratum migrate to each of the post-strata;
- immigration rates - what fraction of the animals within a post-stratum have come from each pre-stratum;
- harvest-derivation rates - what fraction of the animals harvested (i.e., killed and retrieved) within a post-stratum have come from each pre-stratum.

A distinction is made between the immigration rates and the harvest-derivation rates since the pattern of exploitation may be different for different sub-populations due to such factors as the timing of arrivals, the opening and closing dates of the harvest, fitness of the animals, or other biological or behavioral aspects of the animals. In all models, the conditions necessary for estimation of these parameters are considered.

In the remainder of this Chapter, I will:

· briefly review the literature applicable to this Thesis;

· briefly summarize current methodology in ordinary band-recovery experiments and list the assumptions that are required for these models, as well as for all models in this Thesis;

· outline the methodology that is used to estimate the parameters in the models or to test among sub-models;

· describe in detail, with a numerical example, the concepts, terminology, and problems in using band-recovery data in studying animal movements.

The remainder of the thesis is organized as follows:

· In Chapter 2, I consider the general problem of post-release stratification in band-recovery experiments without attempting to model the migration process explicitly. The models and methodology in this chapter form the basis for the results in subsequent chapters.

· In Chapter 3, the Partial- and Complete-Fidelity Models are explored in detail. These are combined into one chapter since the results from both models are similar. Ordinary band-recovery data are found to be inadequate for inference and a modification to the experimental design using live resightings is shown to overcome this problem.

· In Chapter 4, the Non-Fidelity Model is explored. Ordinary band-recovery data are also inadequate for inference, and the use of live resightings also poses problems.

· In Chapter 5, the Internal-Transfer Model is explored. Ordinary band-recovery data are theoretically adequate for this model, but in practice, prove to be less satisfactory. Again, a modification to the experimental design using live resightings is described.

· Finally, in Chapter 6, considerations in using the models of this Thesis are discussed.

Each chapter is designed to be largely self-contained. This implies that there will be some duplication of the introductory material, but this has been kept to a minimum. The chapter format is similar for all chapters: a brief overview of the problem; a description of the notation used in the chapter; a discussion of the assumptions and the interpretation of the parameters; a discussion of the stochastic model (estimators, tests, power and bias are considered); a numerical example; and finally, a discussion of the results of the chapter. Figures and Tables are numbered using the Section of the Thesis where they are first introduced. References are collected into a common bibliography at the end of the Thesis.

1.2 **LITERATURE REVIEW**

The use of capture-recapture and band-recovery methods to estimate animal abundance and other related parameters is well known (Seber, 1982, 1986). In particular, Brownie *et al.* (1985) presented comprehensive methodology on the analysis of band-recovery experiments. Although models for capture-recapture and band-recovery experiments have tended to be developed independently of each other, there is a growing recognition that the methodology used in band-recovery studies is directly applicable to the analysis of capture-recapture data

(Brownie and Robson, 1983; Brownie and Pollock, 1985; Brownie *et al.*, 1985, Section 8.2; Burnham *et al.*, 1987, Section 1.3; Burnham, 1987).

Much work has been done on assessing the robustness of the estimators to failures of the assumptions in both types of experiments:

· Gilbert (1973), Carothers (1973), Arnason and Mills (1981), Seber (1982, pp. 506-509), Nichols and Pollock (1983), Nichols, Hines and Pollock (1984), Arnason and Mills (1987) studied the effect of trap response, handling effects, tag loss, and heterogeneity of capture and survival parameters among animals in capture-recapture experiments. Usually, heterogeneity causes population estimates and survival estimates to be biased downward; temporary trap response may cause biases in either direction; permanent trap response (trap happiness) causes population estimates to be biased downward; and handling effects cause population estimates to be biased upwards, but can bias survival estimates in either direction.

· Anderson and Burnham (1980), Nelson, Anderson, and Burnham (1980), Conroy and Williams (1981), Nichols *et al.* (1982), Pollock and Ravelling (1982), Burnham and Nichols (1985), and Weatherhead and Ankney (1984, 1985) investigated the effects of band loss, delayed reporting, and heterogeneity in the survival and band-recovery rates in band-recovery experiments. In general, estimates of survival are robust to the degree of band loss, delayed reporting, and heterogeneity of band-recovery rates commonly found in real studies. However, they are not as robust to heterogeneity in the survival rate among animals, and estimates of the average survival rate can be biased in either direction.

The usual remedy for heterogeneity is stratification based upon a characteristic related to the parameter being estimated. This allows a less biased estimate of the parameter with little increase in experimental effort. As well, tests can be developed to examine the heterogeneity of the parameter values among the sub-populations. Methods for analysis of capture-recapture and band-recovery data based upon pre-sampling stratification are well developed:

· Schaeffer (1951), Chapman and Junge (1956), Darroch (1961), Arnason (1972, 1973), and Seber (1982, p. 555) discussed stratification in capture-recapture studies based upon geographical area and discussed methods to estimate, primarily, the population size;

· Pollock (1975) discussed stratification in capture-recapture studies based upon previous capture history and developed tests to examine if the previous capture history is related to subsequent survival or recapture rates;

· Pollock (1981) discussed stratification in capture-recapture models based upon the age of the animal at the first capture time and where subsequent recapture and survival rates are age dependent;

· Brownie *et al.* (1985, Section 8.6) discussed stratification in band-recovery models based upon fixed attributes (e.g., sex or area of release) that are known at the time of banding, and developed tests to examine if these groups have the same band-recovery and survival rates. They also developed models allowing for age-dependent survival and band-recovery rates where the age is determined at the time of banding;

· Burnham *et al.* (1987) discussed stratification based upon experimental treatment of animals and developed methods to assess the magnitude of the treatment effect on subsequent survival or recovery/recapture rates.

In some cases, stratification can only be done after sampling has taken place - this is generally referred to as post-stratification (Holt and Smith, 1979). Chapter 2 of this Thesis develops models for such post-stratification in band-recovery models; by using the relationship between band-recovery and capture-recapture models, these models can also be applied to capture-recapture studies.

Since one type of post-stratification is by area of recapture or recovery, the use of capture-recapture or band-recovery experiments to study animal movements is not unexpected, but suffers from some unique problems. The use of capture-recapture experiments to estimate migration patterns is more developed than the use of band-recovery studies since some of these problems are more easily resolved.

Schaeffer (1951) used a capture-recapture experiment to study migrating salmon. In this case, stratification was by both the week of release and the week of recapture, and interest focussed primarily upon the estimation of the total salmon run, rather than on the destinations of the salmon. Macdonald and Smith (1980) also considered this problem using a slightly different approach. Junge and Bayliff (1955) used marking to estimate the contribution of salmon production areas to a fishery and outlined the assumptions necessary for such estimates to be valid, namely, that the probability of recovery of a marked fish is independent of where the fish originated, and that surviving fish from one production area return only to their area of release (fidelity to their area of release). These assumptions are required in order that estimates of the production population sizes can be computed and then the proper 'weights' can be attached to a recovered fish so that it is 'representative' of its population.

Chapman and Junge (1956) discussed these assumptions and proposed moment estimators of the total population sizes and the migration rates among two sets of strata under various assumptions. Beverton and Holt (1957) outlined a deterministic approach with releases only in one stratum. The first approach using the likelihood function was by Darroch (1961). He examined a two-sample experiment where the releases at the first sampling time occurred in one set of strata and recoveries at the second sampling time occurred in a different set of strata. He derived estimators of the total population size and of the net movement/survival rates from the first set of strata to the second set of strata. These methods could be used to estimate the seasonal migration rates between two sets of strata; however, since only two sampling times are used, it is not necessary to consider the effects of fidelity.

There appears to have been no work on estimating seasonal migration rates between two different sets of strata using capture-recapture methods with more than two sample times. Capture-recapture results are available, however, when the two sets of strata are identical. Iwao (1963) developped a three-sample model to estimate net migration rates of insects between two fields. Rather than estimating the migration rates from the breeding areas to the wintering areas, this and subsequent papers examined the migration rates among areas from one sample time to the next. Arnason (1972) demonstrated that Iwao made an implicit assumption that animals are free to migrate between times 1 and 2, but may not migrate again between times 2 and 3, i.e., animals are completely faithful to their stratum between times 2 and 3. Arnason (1972, 1973) relaxed this assumption and considered moment estimators of the population sizes and migration rates among the strata. This was generalized by Seber (1982, p. 555) to cases of more than three sampling times by grouping the sampling times into sets of three times and applying the methods of Arnason (1972, 1973) to each set.

The use of band-recovery data to study animal movements is less well developed. The problems with such experiments in studying migration are well known (Crissey, 1955): not all bands on killed (recaptured) animals are reported; and the recovery effort may be different for different sub-populations. (In capture-recapture studies, it was assumed that all marked animals in a recapture sample had the same probability of capture and that are all reported.) These problems make it difficult to determine the proper 'weights' to be attached to a recovered band so that it is 'representative' of its population at banding. For this reason, the use of band-recovery data to describe animal movements has been primarily descriptive, e.g., Cooke *et al.* (1982) plot the recoveries from geese on a map to determine migration routes but do not estimate rates and Campbell (1986) plots the recoveries of lobsters to determine movement patterns but not rates. In some studies, these limitations have been recognized and interest focussed upon studying the distribution of exploited animals (those killed and retrieved) such as by Munro and Kimball (1982) who derive the exploitation rates for sub-populations and the relative contribution to the total harvest from sub-populations. It is a simple matter to test if the recovery distributions of two sub-populations are the same by comparing the centroids of the two sets of recovery locations (by latitude and by longitude) using the Mardia (1967) or Wheeler and Watson (1964) tests. As will be shown in Section 1.5, the recovery distributions may not reflect the actual migration distributions of the sub-populations.

Some studies have recognized the problems inherent in band-recovery studies and have modified the experimental design to account for these problems. For example Raveling (1978) and Rusch *et al.* (1985) studied the migration patterns of Canada Geese through a combination of band-recoveries, live resightings, and hunter surveys. They noted that the distribution of band-recoveries from hunters was unreliable for determining migration patterns, but the sighting data could be used to determine the migration patterns since they estimated that 90-95% of the banded geese alive in a winter were sighted. Serie, Trauger, and Sharp (1983) studied the migration and winter distribution of canvasbacks using a combination of band-recoveries of banded birds and sightings of color-marked birds. Unfortunately, replicate sightings of the same color-marked bird could not be distinguished, and different colors were found to be sighted at different rates. Because of these problems, the authors could not compute migration rates, but simply plotted the observed recoveries or resightings and tested (using the centroid method) if the sub-populations had different sighting or recovery distributions. Had the color-marked animals been individually distinguishable, the models of Chapter 3 could have been used.

Finally, some effort has been made to develop models combining recovery and sighting data. Mardekian and McDonald (1981) used only the last sighting and the recoveries to obtain estimates of the survival and recovery rates. Brownie and Robson (1983) examined the case of multiple sightings and allowed for a short term effect of initial marking on survival rates, but did not combine this information with band-recoveries.

1.3 THE ANALYSIS OF ORDINARY BAND-RECOVERY EXPERIMENTS

The modelling and analysis of ordinary band-recovery experiments is described in detail by Brownie *et al.* (1985). In particular, their model M_1, where only adult animals are banded, is the basis for the models in this Thesis.

1.3.1 MODEL STRUCTURE

In Model M_1 of Brownie *et al.* (1985, Section 2.2), adult animals are captured, banded, and released at regular intervals, usually one calendar year. The population is exploited, and bands (from killed animals) are returned to a central reporting site. Let N_i represent the number of animals released in year i, and R_{ij} represent the number of bands recovered between the time of banding in year j and year j+1 from those animals originally banded and released in year *i*. The data from the experiment can be displayed in an array as follows in the case of 3 years of releases and 4 years of recoveries:

Year Banded	Number Released	Recoveries by year 1	2	3	4
1	N_1	R_{11}	R_{12}	R_{13}	R_{14}
2	N_2		R_{22}	R_{23}	R_{24}
3	N_3			R_{33}	R_{34}

For example, R_{13} represents the number of bands recovered in year 3 from those animals banded and released in year 1.

Under certain assumptions (given in Section 1.3.3 of this Thesis), the numbers of recoveries in each year from a release can be modelled as multinomial random variables. For example, in the above array,

$\{R_{1j}, j=1...4\}$ follows a multinomial distribution with parameter N_1,
$\{R_{2j}, j=2...4\}$ follows a multinomial distribution with parameter N_2,
$\{R_{3j}, j=3...4\}$ follows a multinomial distribution with parameter N_3

and all distributions are independent of each other. The structural model underlying the individual cell probabilities for the cells of the multinomial distributions depend upon two types of parameters - S_i, the annual survival rates, and f_i, the annual band-recovery rates where:

- S_i = the conditional probability that an animal alive at banding time in year i will survive to banding time in year $i+1$;
- f_i = the conditional probability that an animal alive at banding time in year i will have its band recovered and reported during the next year.

Using these parameters, the respective cell probabilities of the $\{R_{ij}\}$ array given above can be modelled as:

Year Banded	Number Released	Probability that a band on an animal released in year i is recovered in year j: $j=1$	$j=2$	$j=3$	$j=4$
i=1	N_1	f_1	S_1f_2	$S_1S_2f_3$	$S_1S_2S_3f_4$
i=2	N_2		f_2	S_2f_3	$S_2S_3f_4$
i=3	N_3			f_3	S_3f_4

For example, the probability that a band on an animal released in year 1 is recovered in year 3 is computed as $S_1S_2f_3$ since:

- the animal must survive from the time of banding and release in year 1 to the time of banding in year 2 (S_1);
- the animal must survive from the time of banding in year 2 to the time of banding in year 3 (S_2);
- the band must be recovered some time between the time of banding in year 2 and the time of banding in year 3 (f_3).

The likelihood function can now be written in terms of these structural parameters:

$$L = \binom{N_1}{R_{11}, R_{12}, R_{13}, R_{14}} f_1^{R_{11}} (S_1f_2)^{R_{12}} (S_1S_2f_3)^{R_{13}} (S_1S_2S_3f_4)^{R_{14}}$$

$$\times (1-f_1-S_1f_2-S_1S_2f_3-S_1S_2S_3f_4)^{N_1-R_{11}-R_{12}-R_{13}-R_{14}}$$

$$\times \binom{N_2}{R_{22}, R_{23}, R_{24}} f_2^{R_{22}} (S_2f_3)^{R_{23}} (S_2S_3f_4)^{R_{24}} (1-f_2-S_2f_3-S_2S_3f_4)^{N_2-R_{22}-R_{23}-R_{24}}$$

$$\times \binom{N_3}{R_{33}, R_{34}} f_3^{R_{33}} (S_3f_4)^{R_{34}} (1-f_3-S_3f_4)^{N_3-R_{33}-R_{34}}$$

which can be reduced to:

$$L = \text{constant} \times f_1^{R_{11}} f_2^{R_{12}+R_{22}} f_3^{R_{13}+R_{23}+R_{33}} (S_3f_4)^{R_{14}+R_{24}+R_{34}}$$

$$\times\ S_1^{R_{12}+R_{13}+R_{14}}\ S_2^{R_{13}+R_{14}+R_{23}+R_{24}}$$

$$\times\ (1-f_1-S_1f_2-S_1S_2f_3-S_1S_2S_3f_4)^{N_1-R_{11}-R_{12}-R_{13}-R_{14}}$$

$$\times\ (1-f_2-S_2f_3-S_2S_3f_4)^{N_2-R_{22}-R_{23}-R_{24}}$$

$$\times\ (1-f_3-S_3f_4)^{N_3-R_{33}-R_{34}}$$

The individual parameters S_3 and f_4 always appear together in the likelihood in product form and cannot be estimated separately; only their product S_3f_4 can be estimated. This model has 6 unknown identifiable parameters $\{f_1, f_2, f_3, S_3f_4, S_1, S_2\}$.

The Minimal Sufficient Statistic (MSS, Cox and Hinkley, 1974, p. 23) can be identified, has dimension 6, and one representation is found to be:

$R_{\cdot 1} = R_{11}$ = column sum of recoveries in year 1

$R_{\cdot 2} = R_{12}+R_{22}$ = column sum of recoveries in year 2

$R_{\cdot 3} = R_{13}+R_{23}+R_{33}$ = column sum of recoveries in year 3

$R_{\cdot 4} = R_{14}+R_{24}+R_{34}$ = column sum of recoveries in year 4

$R_{1\cdot} = R_{11}+R_{12}+R_{13}+R_{14}$ = row sum of recoveries from releases in year 1

$R_{2\cdot} = R_{22}+R_{23}+R_{24}$ = row sum of recoveries from releases in year 2

Note that $R_{3\cdot}$ (the row sum of recoveries from releases in year 3) is a linear combination of these statistics:

$$R_{3\cdot} = R_{\cdot 1} + R_{\cdot 2} + R_{\cdot 3} + R_{\cdot 4} - R_{1\cdot} - R_{2\cdot}\ .$$

Maximum likelihood estimates (MLEs) for the identifiable parameters can be found (in this model) using the method of moments as explained in

Section 1.4, and they are found by equating the expected value of each component of the MSS to its observed value and solving for the unknown parameters. The MLEs are (Brownie *et al.*, 1985, Section 2.2):

$$\hat{f}_i = \frac{R_{i\cdot}}{N_i}\,\frac{R_{\cdot i}}{T_i} \qquad i=1\ldots3$$

$$\widehat{S_3 f_4} = \frac{R_{3\cdot}}{N_3}\,\frac{R_{\cdot 4}}{T_3}$$

$$\hat{S}_i = \frac{R_{i\cdot}}{N_i}\,\frac{(T_i - R_{\cdot i})}{T_i}\,\frac{N_{i+1}}{R_{i+1,\cdot}} \qquad i=1\ldots2$$

where

$$T_1 = R_{1\cdot}$$

$$T_2 = T_1 + R_{2\cdot} - R_{\cdot 1}$$

$$T_3 = T_2 + R_{3\cdot} - R_{\cdot 2} \quad .$$

The quantities $R_{\cdot i}/T_i$ estimate what fraction of the animals known to be alive in year *i* (T_i) are recovered in year *i*. This quantity is adjusted by the estimated probability of recovery in year *i* or later ($R_{i\cdot}/N_i$) to provide the estimated band-recovery rates. The quantity $(T_i - R_{\cdot i})/T_i$ estimates the fraction of animals known to be alive in year *i* that survive year *i* and are recovered in year *i*+1 or later. This is adjusted by the estimated probabilites of recovery in year *i* or later ($R_{i\cdot}/N_i$) or in year *i*+1 or later ($R_{i+1,\cdot}/N_{i+1}$) to provide the estimate of the survival rate. Variances and covariances of the estimates can be found using the delta-method (Seber, 1982, Section 1.3.3) and can be shown to be identical, to the same order of approximation, as those from the information matrix (Section 1.4). They are given in Brownie *et al.* (1985, pp. 17-18).

Brownie *et al.* (1985) then consider modifications to the model such as (among others):

- requiring all survival rates to be homogeneous over time;
- allowing both adult and young animals to be banded;
- allowing banding to occur twice a year.

They present methods for estimating the parameters and for differentiating among these and other models.

1.3.2 INTERPRETATION OF THE PARAMETERS

The band-recovery parameters (f_i) include several components: the probability that an animal will be killed; the probability that the killed animal is actually retrieved; and the probability that a band on a retrieved animal is actually reported to the central reporting site. The band-recovery rate is a product of these three components and only this product can be estimated in ordinary band-recovery experiments; the individual components are nonidentifiable. The product of the kill rate and the retrieval rate is called the HARVEST RATE; the conditional probability that a band is reported, given a banded animal is harvested, is called the BAND-REPORTING RATE. The band-recovery parameter may also be written as the product of these two rates. It should be noted that the number of animals harvested is typically less than the number of animals killed since not all dead animals are retrieved by the exploiters. Since any of these components may be heterogeneous over time or space, the band-recovery rates may also vary geographically and temporally. For example, different sub-populations could have different band-recovery rates because of attribute or behavioral aspects of the animal (e.g., the size or the coloration of the sexes makes one more vulnerable to exploitation in the same hunting area). Proper pre-release or post-release stratification can ensure that heterogeneity does not introduce large biases into the estimates. Techniques for estimating the harvest rate component of the band-recovery rate include bag inspections and mail surveys (Martin and Carney, 1977). These methods will give estimates of the harvest rate which are independent of the estimates of band-recovery rate from the banding study. Techniques for estimating the band-reporting rates are also well developed using, for example, reward bands (Henny and Burnham, 1976). Often the estimates of the band-reporting rates will be independent of the estimates of the band-recovery rates.

The survival parameters (S_i) represent the probability of survival from banding time to banding time. The complement (mortality) includes ALL forms of mortality, one component of which is the kill rate. It is not correct to assume, if an animal is not killed in a year, that it has survived, since it may have died of other causes. Similarly, if an animal's band is not returned in a year, it is not correct to assume that the animal has survived since it may have died from other causes other than exploitation, it may have been killed but not retrieved, or it may have been harvested and the band not reported.

1.3.3 THE USUAL ASSUMPTIONS OF ORDINARY BAND-RECOVERY MODELS

The usual assumptions of band-recovery experiments are given in Brownie *et al.* (1985, Section 1.3) and are further discussed by Nichols *et al.* (1982) and Pollock and Raveling (1982). These assumptions also apply to all models considered in this Thesis and may be summarized as follows:

· the sample is representative of the population, i.e., the survival and band-recovery components apply equally to banded and unbanded animals;

· the age, sex or other attributes of animals are correctly determined if these attributes are used as a stratification factor;

· there is no band loss;

· survival rates are not influenced by the banding process itself;

· the year and location of the band-recoveries are correctly tabulated;

· the fate of each banded animal is independent of the fate of other banded animals;

· all banded animals of an identifiable class have the same survival and band-recovery rates.

Careful study design, following the recommendations of Brownie *et al.* (1985, Chapter 9), will help ensure that the assumptions hold reasonably well in a banding experiment.

The conditions for using band-recovery data to study migratory populations have been considered before (Crissey, 1955). He recognized that:

· the animals banded must be a representative sample from the population or conclusions based upon the experiment may not be applicable to the population;

· the pre-stratum absolute or relative population sizes must be known in order to estimate the immigration and harvest-derivation rates;

· the band-reporting rate must be known in order to adjust the number of bands reported to reflect the number of animals harvested when estimating the harvest-derivation rates.

Furthermore, inferences are complicated by the possibility that the band-recovery rates may vary geographically, temporally, and among sub-populations.

Careful study design following the recommendations of Crissey (1955) and Brownie *et al.* (1985, Chapter 9) will help ensure that the banded animals are a representative sample of the population. It is usually impossible to obtain a simple random sample of the population at banding time, but steps must be taken to ensure that the animals banded are likely to be subject to the same survival and band-recovery rates as the population as a whole.

Since the ratio of marked animals to unmarked animals at banding time is not recorded, band-recovery models cannot be used to estimate the pre-stratum population sizes. Even if such information was recorded, there are concerns about using banding data. For example, suppose that a pre-stratum consists of the animals that nest in a large marshy area, only parts of which are accessible for banding. Then if the animals are faithful to their nesting sites, the ratio of banded to unbanded animals will be higher in the accessible sites than in the inaccessible sites. This violates a key assumption of capture-recapture models, namely that the marked animals completely mix with the rest of the population after release. The population estimate in this case will be biased downward. Modern cost-effective techniques for population estimation of migratory animals under such conditions include aerial surveys and production models (Pospahala, Anderson, and Henny, 1974). These techniques provide estimates of the pre-stratum population sizes that are independent of the estimates of survival and band-recovery from the band-recovery study.

As indicated earlier, the band-reporting rate can be estimated using other techniques.

Even after resolving the above concerns, heterogeneity in the band-recovery rates over time or space imply that there are serious problems in using ordinary band-recovery data to estimate migration parameters. In general, the parameters of interest are confounded with other parameters and cannot be estimated. Although this has been implicitly recognized by previous authors, no previous model explicitly introduced parameters to describe the migration process and nor provided proof as to which parametric functions are identifiable. Nor has any experimental methodology been developed that will overcome this nonidentifiability.

1.4 OVERVIEW OF METHODOLOGY

In all the models considered in the Thesis, the data can be modelled using independent, or conditionally independent, multinomial distributions. This will be illustrated, in detail, in Chapters 2 and 3; subsequent chapters proceed in a similar fashion. The likelihood is then simple to construct since it is a product of multinomial distributions. Once the likelihood has been constructed, the MSS can be extracted.

Because of the multinomial structure, estimation can be relatively straightforward and may follow the methods used in Brownie *et al.* (1985, Appendix B). Briefly, if the likelihood is in the exponential family and if the dimension of the MSS equals the number of parameters (the model is said to be of full rank), the MLEs can be found by the method of moments using the components of the MSS (Davidson and Solomon, 1974). Variances and covariances can be found using the delta method (Seber 1982, Section 1.3.3), and will be equivalent to the same order of approximation to those obtained from the information matrix (Brownie *et al.*, 1985, p. 215). If the dimension of the MSS is less than the number of parameters, not all parameters are identifiable; i.e., they cannot be estimated individually. However a full-rank set of identifiable functions of the parameters can often be found by equating the components of the MSS to their expected values and observing what functions of the parameters can be identified. The MLEs of these identifiable parametric functions can be found by the same method of moments and their variances and covariances can also be found using the delta-method. These techniques are used extensively in Chapters 2 and

3. If the dimension of the MSS exceeds the number of identifiable parameters, then closed form solutions for the estimators often do not exist, and numerical methods must be used. I have used the method of scoring (Rao, 1973, p. 366), but since the likelihood can often be written as a product of multinomial distributions, iteratively reweighted least squares (Green, 1985) could also be used.

In some cases, the method of scoring is complex because of the difficulty in deriving explicit formulae for the score statistic and the Hessian matrix. Standard methods using the Chain Rule for partial derivatives have been used to first find the score and Hessian in terms of 'natural parameters', and then to transform these into terms of the structural parameters; this is illustrated using the Partial-Fidelity Model of Chapter 3. As well, the method of scoring is modified using the results of Aitchison and Silvey (1958) and Don (1985) to find the MLEs and their estimated variances and covariances in the presence of restrictions on the parameters. This is illustrated, in detail, in the Partial-Fidelity Model in Chapter 3.

Discrimination among models can also be straightforward. In many cases two competing models are both of full rank and a similar test (Lehman, 1986, p. 135) can be developed by finding the distribution of the MSS of the more general model (the alternative hypothesis) conditional upon the MSS of the restricted model (the null hypothesis); symbolically:

$$P_H(\text{ MSS of A } \mid \text{ MSS of H }).$$

The potentially complex algebraic manipulations involved with finding this conditional distribution are demonstrated in Chapter 2; other Chapters proceed in a similar fashion. The tests resulting from the conditional distribution can be complex; however, in many cases a large-sample, asymptotically equivalent, chi-square test using a contingency table can be derived as demonstrated in Chapters 2 and 3. If either model is not of full rank, then the above test will be inefficient, and other procedures such as the method of Rao (1973, p. 395), or Likelihood Ratio Tests (Jolly, 1982; Brownie, Hines and Nichols, 1985) may be used. Typically, these methods do not permit analytic formulae for the distribution of the test statistic, but tests of significance can be derived numerically without much difficulty.

A general non-specific goodness-of-fit test for models of full rank can be constructed from the conditional distribution:

$$P_{Model}(\text{ Data } \mid \text{ MSS })$$

The test derived from this distribution often has a large sample contingency table approximation, and is to be preferred over the ordinary Pearson chi-square goodness-of-fit test based upon the difference between the observed and expected random variables especially when pooling of cells is necessary. Pollock, Hines, and Nichols (1985) give further details. Alternatively, a Likelihood Ratio test can be derived comparing the likelihood from a saturated model and the model in question; this method will be applicable in full and non-full rank models. Generally, the goodness-of-fit tests have poor power because of the generality of the alternative to the stated model.

Several methods can be used to approximate the power of the resulting tests. In some cases, an explicit expression for the power function can be obtained by using the power functions of the chi-square tests derived for contingency tables. These are illustrated in Chapter 2. An alternate method for computing power, applicable to all chi-square tests in multinomial models, is to use the expected cell values under the alternate hypothesis as "data" for the test statistic computation procedures. The resulting value of the chi-square goodness-of-fit test statistic for the hypothesized model has been shown to be asymptotically equivalent to the non-centrality parameter of the distribution of the test statistic of the test differentiating between the two models (Moore, 1974). However use of this method does not lead to ready insights into the nature of the dependence of the power function upon the parameters but is computationally convenient. This is illustrated in the numerical examples of Chapters 3 and 5.

1.5 A SIMPLE NUMERICAL ILLUSTRATION OF THE CONCEPTS, TERMINOLOGY, AND POTENTIAL PROBLEMS IN USING BAND-RECOVERY DATA IN MIGRATION MODELS.

A simple numerical example will be used to illustrate the concepts, terminology, and problems involved in using band-recovery data in migration studies. Table 1.5a gives the parameter values used in this example as defined in Section 1.3. It will be assumed, for the sake of demonstration, that the system is deterministic, i.e. that there is no variation about the expected values. Also, the movements in one year only will be considered. Tables of the expected number of animals migrating (Table 1.5b), expected number of animals harvested (Table 1.5c), expected number of bands reported (Table 1.5d), and

Table 1.5a

Parameters used for numerical example illustrating concepts and problems in migration studies

Case I (Section 1.5.1): Banding occurs in all pre-strata, and harvesting is allowed in all post-strata

Pre-Stratum	Population Size	Number Banded	Fraction of animals migrating to post-stratum			Harvest rate[1] in post-stratum			Band-reporting[2] rate in post-stratum			Survival rate in post-stratum		
			1	2	3	1	2	3	1	2	3	1	2	3
1	100,000	1,000	0.40	0.40	0.20	0.10	0.20	0.10	0.50	0.25	0.50	0.50	0.60	0.80
2	200,000	1,000	0.40	0.30	0.30	0.20	0.30	0.20	0.40	0.40	0.30	0.50	0.60	0.40
3	50,000	1,000	0.10	0.60	0.30	0.20	0.10	0.10	0.50	0.25	0.50	0.60	0.60	0.60

Case II (Section 1.5.2): Banding occurs only in the first two pre-strata, and harvesting is allowed only in the first two post-strata.

Pre-Stratum	Population Size	Number Banded	Fraction of animals migrating to post-stratum			Harvest rate[1] in post-stratum			Band-reporting[2] rate in post-stratum			Survival rate in post-stratum		
			1	2	3	1	2	3	1	2	3	1	2	3
1	100,000	1,000	0.40	0.40	0.20	0.10	0.20	0.00	0.50	0.25	n/a	0.50	0.60	0.80
2	200,000	1,000	0.40	0.30	0.30	0.20	0.30	0.00	0.40	0.40	n/a	0.50	0.60	0.40
3	50,000	0	0.10	0.60	0.30	0.20	0.10	0.00	n/a	n/a	n/a	0.60	0.60	0.60

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1 The harvest rate is the conditional probability that an animal will be killed and retrieved.

2 The band-reporting rate is the conditional probability that band from a harvested animal will be reported to the central reporting site.

expected number of animals surviving to the next year (Table 1.5e) can also be constructed assuming that the rates are representative of those in the populations. Of course, additional assumptions about how animals behave will be required for the more complex models of later chapters, and the actual computation of the derived rates will be more complicated, but the same concepts will still apply.

Suppose that our population of animals can be stratified at the time of banding into three pre-strata. The population size of each pre-stratum is assumed to be known, or has been estimated from other studies, and a known number of animals from each pre-stratum is banded as shown in Table 1.5a. Suppose that the animals must migrate to one of three post-strata in the proportions shown in Table 1.5a. Each pre-stratum may have a different migration pattern. Note that if the complete set of post-strata is unknown, a new post-stratum corresponding to "other" can always be constructed. (This "other" post-stratum should have no band-recoveries reported from it, Section 1.5.2). Since the banded animals are assumed to have the same migration rates as the rest of the pre-stratum populations, the distributions of the banded animals from each pre-stratum among the post-strata will mirror that of the total populations as shown in Table 1.5b. For example, the expected number of banded-animals from pre-stratum 2 that migrate to the three post-strata occur in the ratio 400:300:300 (40%:30%:30%) compared to the expected numbers from the total population in pre-stratum 2 that migrate to the three post-strata in the ratio 80,000:60,000:60,000 (40%:30%:30%). However, because of the different banding intensities, the numbers of banded animals that migrate into a post-stratum from the

Table 1.5b
Expected number of animals migrating

Pre-Stratum	Expected number of animals migrating to post-stratum			Expected number of banded animals migrating to post-stratum		
	1	2	3	1	2	3
1	40,000	40,000	20,000	400	400	200
2	80,000	60,000	60,000	400	300	300
3	5,000	30,000	15,000	100*	600*	300*
Totals	125,000	130,000	95,000	900	1300	800

Table 1.5c
Expected number of animals harvested

Pre-Stratum	Expected number of animals harvested in post-stratum			Expected number of banded animals harvested in post-stratum		
	1	2	3	1	2	3
1	4,000	8,000	2,000*	40	80	20*
2	16,000	18,000	12,000*	80	90	60*
3	1,000	3,000	1,500*	20*	60*	30*
Totals	21,000	29,000	15,500	140	230	110

* These figures will be zero in Case II when banding occurs only in the first two pre-strata, harvesting is allowed only in the first two post-strata.

pre-strata will not reflect the relative immigration of animals from the total populations. For example, in Table 1.5b, the expected number of animals migrating into post-stratum 1 from the three pre-strata occur in the ratio 40,000:80,000:5,000 (32%:64%:4%) while the expected number of banded animals that migrate into post-stratum 1 from the three pre-strata occur in the ratio 400:400:100 (44%;44%:12%).

When the animals migrate to the post-strata, they may be harvested (i.e., they may be killed and retrieved). The harvest rate may vary among post-strata, and it is possible that the harvest rate may also vary among the pre-strata within a specific post-stratum. For example, if the pre-strata are sex, then the sexes may exhibit distinct characteristics or behaviours (e.g. colorations or flight patterns) such that they are spotted and harvested at different rates in the harvest areas. The rates in Table 1.5a reflect this possibility. Then, (Table 1.5c), the expected number of animals from the total population in pre-stratum 2 that are harvested in the three post-strata occur in the ratio 16,000:18,000:12,000 (34.9%:39.1%:26.0%). Since the banded animals are assumed to migrate and get harvested at the same rate as unmarked animals, the expected number of banded animals from pre-stratum 2 that will be harvested in the post-strata occur in the same ratio 80:90:60 (34.9%:39.1%:26.0%). Note, however, that this is not equal to the migration rates into these post-strata (40%, 30%, 30%) because of the differing harvest rates (20%, 30%, 20%) among post-strata. Now, shifting our point of view to the post-stratum, let us examine the contribution to the harvest from the pre-strata. From Table 1.5c, the expected contribution within post-stratum 1 from the three pre-strata occurs in the ratio 4,000:16,000:1,000 (19.0%:76.2%:4.8%) while the expected number of banded animals in the harvest occurs in a different ratio 40:80:20 (28.6%:57.1%:14.3%) caused by the differing banding intensities.

Not all of the bands from the harvest of banded animals are reported. The band-reporting rate will likely differ among post-strata, and may differ among the pre-strata within a specific post-stratum. For example, public education programs may increase the band-reporting rate overall in a specific post-stratum, while bag regulations may cause hunters not to report bands from certain sizes or sexes of animals. The rates in Table 1.5a reflect both these possibilities. Table 1.5d illustrates the expected number of bands reported from the banded animals in the harvest. Clearly, no bands are returned from untagged animals. As well, the number of bands that are reported reflects neither the migration of the total populations to the post-strata nor the contribution to the harvest within each post-stratum. For example, the expected numbers of bands reported in the three post-strata from those banded in pre-stratum 2 occur in the ratio 32:36:18 (37.2%:41.9%:20.9%) compared to the 40%:30%:30% ratio of the expected number of animals that migrated from the total population in pre-stratum 2. Similarly, the expected numbers of bands reported in post-stratum 1 from the three pre-strata occur in the ratio 20:32:10 (32.2%:51.6%:16.1%) compared to the 19.0%:76.2%:4.8% ratio for the contribution to the harvest within post-stratum 1 from the three pre-strata.

Table 1.5d
Expected number of bands recovered

Pre-Stratum	Expected number of bands recovered in post-stratum 1	2	3
1	20	20	10*
2	32	36	18*
3	10*	15*	15*
Totals	62	71	43

Table 1.5e
Expected number of animals that survive in the post-strata

Pre-Stratum	Expected number of animals surviving in post-stratum 1	2	3	Total	Expected number of banded animals surviving from post-stratum 1	2	3	Total
1	20,000	24,000	16,000	60,000	200	240	160	600
2	40,000	36,000	24,000	100,000	200	180	120	500
3	3,000	18,000	9,000	30,000	60*	360*	180*	600

* These figures will be zero in Case II when banding occurs only in the first two pre-strata, and harvesting is allowed only in the first two post-strata.

Those animals not harvested or dying from natural causes leave the wintering areas at the end of the season. The post-stratum specific survival rates will likely differ among post-strata for animals from the same pre-stratum, and, conversely, may differ among the animals from different pre-strata within a specific post-stratum. The expected number of animals from the original populations and from the banded animals surviving within each post-stratum is shown in Table 1.5e, along with the expected overall total survivorship from each pre-stratum. For example, 100,000 of the animals from pre-stratum 2 survive the year for an overall survival rate of 50% (100,000/200,000) which is reflected in the proportion of banded animals that survive (500/1000=50%).

This cycle of migration, harvest, and band-reporting may then be repeated in subsequent years. However, additional complications are possible. Firstly, the surviving banded animals may migrate in subsequent years in a different way than in the year of release, and the harvest and band-reporting rates are also likely to differ in the following years. Secondly, additional banded animals may be released in subsequent years, and they may or may not behave similarly to the surviving banded animals of previous years. Nevertheless, the consequences of any well-defined behaviour can be worked out in much the same way as in the previous examples.

In a typical banding study, only the number of animals banded, the number of bands from each pre-stratum that are recovered in each post-stratum, and the year of recovery are known. The original pre-stratum population sizes and band-reporting rates may be available from other studies. The harvest rates are rarely known. Banding may take place in all pre-strata and recoveries may occur from all post-strata where animals may be found. This is the case in the extensive mallard banding project in North America where banding occurs in almost all breeding areas and recoveries are obtained from all migration flyways and wintering areas (Anderson and Henny, 1972 and subsequent publications in the same series). In other situations, banding may not take place in all pre-strata for reasons of expense or lack of interest in some pre-strata, and recoveries may not be received from all post-strata for any of several reasons, e.g., no harvest, or no knowledge of where the animals go. The set of parameters of biological interest and the types of problems that arise when using banding data to estimate these parameters differs between these two scenarios. Each scenario is discussed separately below.

1.5.1 BANDING OCCURS IN ALL PRE-STRATA AND RECOVERIES ARE RECEIVED FROM ALL POST-STRATA.

Suppose that banding takes place in all pre-strata, and that bands are recovered from all post-strata. The following quantities of interest can be defined: the absolute emigration rates from each pre-stratum to the post-strata, the absolute immigration rates into each post-stratum from the pre-strata, the absolute harvest-derivation rates within each post-stratum from the pre-strata, the post-stratum specific survival rates, and the pre-stratum specific net survival rates over all post-strata.

The absolute emigration rate is obtained from the ratio of the number of animals migrating to a post-stratum to the initial total population size. For example, the absolute emigration rates from pre-stratum 2 to post-strata 1, 2 and 3 are computed as 80,000/200,000 = 40%, 60,000/200,000 = 30%, and 60,000/200,000 = 30% respectively (Table 1.5b). The number of bands recovered will not reflect the absolute emigration rates since the band-recovery rate is a product of the emigration rate, the harvest rate, and the band-reporting rates. In this case, the band-recoveries occur in the ratios 32:36:18 or 37%:42%:21% (Table 1.5d).

The absolute immigration rate is computed as the ratio of the number of animals immigrating into the post-stratum from a pre-stratum to the total number of immigrants. For example, the absolute immigration rates into post-stratum 1 from the three pre-strata are computed as 40,000/125,000 = 32%, 80,000/125,000 = 64%, and 5,000/125,000 = 4% respectively (Table 1.5b). The number of bands recovered from each pre-stratum occur in the ratios 20/62 = 32%, 32/62 = 52%, and 10/62 = 16% respectively (Table 1.5d), and do not reflect the absolute immigration rates because of the confounding effects of the harvest rate and band-reporting rate.

The absolute harvest-derivation rate is computed as the ratio of the harvest from each pre-stratum to the total harvest in that post-stratum. For example, the absolute harvest-derivation rates of post-stratum 1 from the three pre-strata are computed as 4,000/21,000 = 19%, 16,000/21,000 = 76%, and 1,000/21,000 = 5% respectively (Table 1.5c). To obtain the harvest-derivation rates from the band-recoveries (Table 1.5d), the pre-stratum population sizes and the post-stratum band-reporting rates must be known (sometimes available from other studies). The band-recoveries are first weighted by the population size and the inverse of the band-reporting rate. Then the harvest-derivation is computed as the ratio of this weighted band-recovery to the total of the weighted band-recoveries. For example, the harvest-derivation of post-stratum 1 from the three pre-strata is computed as:

Pre-stratum	Band-recovery rate		Pre-stratum Population		Band-reporting rate		
1	20/1000	×	100,000	÷	0.50	=	4,000
2	32/1000	×	200,000	÷	0.40	=	16,000
3	10/1000	×	50,000	÷	0.50	=	1,000
Total							21,000

and the absolute harvest-derivations are computed as 4,000/21,000 = 19%, 16,000/21,000 = 76%, and 1,000/21,000 = 5% respectively.

The post-stratum specific survival rate is computed as the fraction of the animals migrating to a post-stratum that survive from the time of banding in one year to the time of banding in the next year. For example, the post-stratum specific survival rate of animals from pre-stratum 2 that migrate to post-stratum 3 is 0.40 (Table 1.5a). This implies that, of the animals that migrate from pre-stratum 2 to post-stratum 3, 40% will survive from the time of banding in one year until the next year's banding time. The post-stratum specific survival rates cannot be estimated from the band-recoveries unless banded animals are released in more than one year (Brownie *et al.*, 1985, p. 4). It should be noted that these survival rates contains survival components corresponding to the time spent in the pre- and post-strata since animals do not spend the entire year in the post-stratum. However, since the survival rate for the entire year is of interest, it is still convenient to refer to these survival rates by the post-stratum.

The pre-stratum specific net survival rate over all post-strata is computed as the fraction of the total animals alive at the time of banding in one year that survive to the banding time in the next year regardless of where the animal migrated (including to post-strata where recoveries were not received). It is found by summing the post-stratum specific survival rates weighted by the absolute emigration rates. For example, the net survival rate for pre-stratum 1 over all post-strata is computed as:

$$\sum_{\text{all post-strata}} \text{absolute emigration rates x post-stratum survival rates}$$

Or:

$$0.40(0.50) + 0.40(0.60) + 0.20(0.80) = 0.60.$$

This implies that 60% of the pre-stratum 1 animals alive at the time of banding in year 1, will survive to the banding time in year 2, as can be seen from the proportion of the total pre-stratum survivors (60,000/100,000 Table 1.5e). Again, unless banded animals are released in more than one year, it is impossible to estimate the net survival rates using band-recovery data.

Since only the number of banded animals released (Table 1.5a) and the number of bands recovered in the post-strata (Table 1.5d) are known, it should be clear that some confounding of the intermediate migration, harvest, and band-reporting rates takes place. For example, only 32 bands are expected to be returned from post-stratum 1 from the 1000 released in pre-stratum 2 for a gross band-recovery rate of 3.2%. This could occur in several ways (several of which are illustrated below):

Migration rate from pre-stratum 2 to post-stratum 1		Harvest rate in post-stratum 1		Band-reporting rate in post-stratum 1		Gross band-recovery rate
0.40	×	0.20	×	0.40	=	0.032
0.80	×	0.20	×	0.20	=	0.032
0.40	×	0.40	×	0.20	=	0.032
0.80	×	0.10	×	0.40	=	0.032

and it is impossible to distinguish among the possibilities based upon ordinary band-recovery data.

1.5.2 BANDING DOES NOT TAKE PLACE IN ALL PRE-STRATA, AND RECOVERIES ARE NOT RECEIVED FROM ALL POST-STRATA

Now suppose that animals are banded only in the first two pre-strata and that band-recoveries are available only from the first two post-strata. For example, if the pre-strata are breeding areas, then it may be difficult to band animals in all the different breeding areas. If the post-strata are wintering areas, then harvesting may be prohibited in some wintering areas. The modifications to the parameters that occur in this case are also shown in Table 1.5a.

The following quantities of interest can be defined: the total emigration rates for each pre-stratum to ALL the post-strata where recoveries occurred; the relative emigration rates for each pre-stratum to EACH of the post-strata where recoveries occurred; the total immigration rate into a post-stratum from ALL the pre-strata where banding occurred; the relative immigration rates into a post-stratum from EACH of the pre-strata where banding occurred; the total harvest-derivation rates within a post-stratum from ALL of the pre-strata where banding occurred; and the relative harvest-derivation rates within a post-stratum from EACH of the pre-strata where banding occurred. The post-stratum specific survival rates are defined as in Section 1.5.1. The pre-stratum specific net survival rates over all post-strata are also defined as in Section 1.5.1, noting that it is defined over all post-strata, including those from which no recoveries were received.

The total emigration rate from a pre-stratum to all of the post-strata where recoveries occurred is computed as the sum of the emigrations to the post-strata divided by the population size. For example, the total emigration rate from pre-stratum 2 to the first two post-strata is computed as (80,000+60,000)/200,000 = 70% (Table 1.5b). The relative emigration rates from a pre-stratum to each of the post-strata where recoveries occurred are computed as the ratio of the number of animals migrating to each post-stratum and the total migrating to all the post-strata where recoveries occurred. For example, the relative emigration rates from pre-stratum 2 to the first two post-strata are 80,000/140,000 = 57% and 60,000/140,000 = 43%, respectively (Table 1.5b). Once again the actual band-recoveries (32/68 = 47% and 36/68 = 53%, Table 1.5d) do not reflect these ratios because of the confounding effects of the harvest rate and the band-reporting rate. The absolute emigration rates to post-strata where recoveries occurred are obtainable as the product of the total emigration rate and the relative emigration rates. For example, the absolute emigration rate from pre-stratum 2 to post-stratum 1 is 70% x 57% = 40%. The relative emigration rates will equal the absolute emigration rates only if the total emigration is 100%; i.e., if there are no post-strata without recoveries.

The total immigration rate into a post-stratum from all of the pre-strata where banding occurred is computed as the ratio of the total immigrants from the pre-strata where banding occurred, to the total of immigrants from all pre-strata (including those where no banding occurred). For example, the total immigration rate into post-stratum 1 from the first two pre-strata is (40,000+80,000)/125,000 = 96% (Table 1.5b). Note that the number of animals that immigrated from pre-strata where no banding occurred is required to compute the denominator for the total immigration rates; this information is normally not available, and the total immigration rates cannot normally be computed. The relative immigration rate into a post-stratum from a pre-stratum where banding occurred is computed as the ratio of the number of immigrants from the pre-stratum to the total immigrants from all of the pre-strata where banding occurred. For example, the relative immigration rates into post-stratum 1 from pre-strata 1 and 2 are 40,000/120,000 = 33% and 80,000/120,000 = 67% respectively (Table 1.5b). The relative immigration rates only require information from pre-strata where banding occurred. Once again, the relative number of band-recoveries in each post-stratum (20/52 = 38.5% and 32/52 = 61.5%, Table 1.5d) do not reflect the relative immigration rates because of the confounding effect of the harvest rate and the band-reporting rate. If the set of pre-strata where banding occurred is the same as the set of all possible pre-strata for this population, then the relative immigration rates will equal the absolute immigration rates.

The total harvest derivation rate within a post-stratum from all of the pre-strata where banding occurred is computed as the ratio of the total harvest from the pre-strata where banding occurred to the total harvest from all pre-strata (including those where no banding occurred). For example, the total harvest derivation rate within post-stratum 1 from the first two pre-strata is (4,000+16,000)/21,000 = 95% (Table 1.5c). Computation of the total harvest-derivation requires information from pre-strata where no banding occurred, and cannot normally be computed. The relative harvest-derivation rates within a post-stratum are computed as the ratio of the harvest from a pre-stratum to the total harvest from all pre-strata where banding occurred. For example, the relative harvest-derivation rates within post-stratum 1 from the first two pre-strata are 4,000/20,000 = 20%, and 16,000/20,000 = 80%, respectively (Table 1.5c). These rates do not require information from pre-strata where no banding occurred. The relative harvest-derivation can be computed from the band-recoveries by weighting the recoveries by the pre-stratum population sizes and band-reporting rates as before. For example, the harvest-derivation within post-stratum 1 from the first two pre-strata are computed as:

Pre-stratum	Band-recovery rate		Pre-stratum Population		Band-reporting rate		
1	20/1000	×	100,000	÷	0.50	=	4,000
2	32/1000	×	200,000	÷	0.40	=	16,000
Total							20,000

and the relative harvest-derivation rates are then 4,000/20,000 = 20%, and 16,000/20,000 = 80% respectively. If the set of pre-strata where banding occurred contains all the pre-strata of the population, the relative harvest-derivation rates will equal the absolute harvest-derivation rates.

Since no animals are banded in some pre-strata, survival rates for these pre-strata cannot be estimated. Similarly, since no recoveries were reported from some post-strata, the post-stratum specific survival rates for these post-strata cannot be estimated. The net survival rate over all post-strata (including those without recoveries) is computed as shown in Section 1.5.1.

If banding does not take place in all pre-strata, and if recoveries are not received from all post-strata, then the same confounding among emigration, harvest, and band-reporting rates still takes place. In addition, some of the biological parameters of interest such as total immigration and total harvest-derivation cannot normally be computed, and consequently, only relative immigration and relative harvest-derivation rates are available.

Chapter 2
General Post-release Stratification Models*

Summary

Brownie *et al.* (1985) present methodology for the analysis of band-recovery data when animals can be stratified at banding time into independent groups and animals within a group are assumed to be homogeneous with respect to annual survival and band-recovery rates. These results are extended to investigate band-recovery models in cases where stratum assignment takes place after releasing the banded animals, usually at recovery time, and each stratum may have different annual survival rates or band-recovery rates or both. Estimation under four possible models is examined. Tests to distinguish among models, the asymptotic power of the tests, and goodness-of-fit tests for each model are also developed. The methods are applied to band-recoveries of North American mallards by flyways. The models in this Chapter serve as a basis for the models developed in subsequent Chapters.

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* A paper, based upon the contents of this chapter has been submitted to *Biometrics* as:

Schwarz, C.J., Burnham, K.P., Arnason, A.N. (1988). Post-release stratification in band-recovery models.

This chapter contains additional appendices containing the detailed derivation of the conditional distributions of the test statistics. Some introductory material in the submitted paper is not included here, but can be found in greater detail in Chapter 1.

Chapter 2
General Post-release Stratification Models

2.1 **INTRODUCTION**

Brownie *et al.* (1985) presented methodology for the analysis of band-recovery data when animals can be stratified at banding time into independent groups, and all animals within a group are homogeneous with respect to annual survival and band-recovery rates. These results are extended to investigate band-recovery models in cases where the stratum assignments takes place only after releasing the banded animals, usually at recovery time, and each post-stratum may have different annual survival rates, band-recovery rates, or both. The reason such models are considered is that heterogeneity in these rates among animals can cause substantial positive or negative bias in the estimates of the parameters (Pollock and Raveling (1982); Nichols *et al.* (1982)). By dividing the animals into homogeneous post-strata, the biases can be reduced and post-stratum-specific estimates can be obtained and compared. Examples of such post-release stratification events are: animals recovered in different areas (pin-tails as described by Anderson and Sterling, 1974); animals recovered by hunting and by live-trapping (Mardekian and McDonald, 1981); animals shot using steel or lead shot; or sex or age determination when this is difficult at banding time, but may be done at recovery time (Pollock and Raveling, 1982).

If the post-release stratification is on the basis of area of recovery, then the number of animals recovered in the different areas should contain some information about the migration rates from the pre- to post-strata. However, in this Chapter the migration process itself will not be modelled explicitly; the remaining Chapters of the Thesis generalize the results in this Chapter by explicitly modelling the migration process. Since the migration processes are hidden in the models considered here, I do not consider estimation of the emigration or immigration rates; the harvest-derivation rates may be estimated as shown in Section 1.5.

Four models are developed that may represent the possible heterogeneity in annual survival and band-recovery rates among post-strata: Model 1 with homogeneous annual survival and band-recovery rates; Model 2a with homogeneous annual survival rates and heterogeneous band-recovery rates; Model 2b with heterogeneous annual survival rates and homogeneous band-recovery rates; and Model 3 with heterogeneous annual survival and band-recovery rates. There is a hierarchial relationship among the models from Model 1 (the most restrictive) to Model 3 (the most general) with Models 2a and 2b being two alternate paths between Models 3 and 1.

In each of the models, I consider the case of a single pre-stratum that is stratified into several post-strata. These results are easily extended to cases with several pre-strata since each pre-stratum is analyzed separately. Procedures and results are developed for estimating the annual survival rates and the band-recovery rates in all four models; for goodness-of-fit tests for each model; for hierarchical tests to distinguish between models; and for finding the asymptotic power function for the tests.

2.2 NOTATION

Following the notation of Brownie *et al.* (1985), let there be k years of banding, l years of recovery, and m post-strata.

Parameters:

f_i^s = annual band-recovery rate for animals recovered in post-stratum s in year i; i=1...l but only band-recovery rates in years 1...k are identifiable.

S_i^s = annual survival rate for animals subsequently recovered in post-stratum s from the banding time in year i to the banding in year i+1; i=1...l-1 but only survival rates in years 1...k-1 are indentifiable.

θ_i^s = product of survival and band-recovery rates in years i=k+1...l

Model 3 : $\theta_i^s = S_k^s S_{k+1}^s \ldots S_{i-1}^s f_i^s$

Model 2a: $\theta_i^s = S_k S_{k+1} \ldots S_{i-1} f_i^s$

Model 2b: $\theta_i^s = S_k^s S_{k+1}^s \ldots S_{i-1}^s f_i$

Model 1: $\theta_i = S_k S_{k+1} \ldots S_{i-1} f_i$

If a superscript is not present, then the associated parameter is invariant across post-strata.

Statistics:

N_i = number of animals banded and released in year i; i=1...k.

R_{ij}^s = number of animals recovered in year j in post-stratum s that were released in year i; i=1...k, j=i...l, s=1...m.

A dot in a superscript or a subscript means summation over the index; a plus-sign after the subscripts indicates a partial sum.

R_{ij+}^s= number of animals recovered in year j in post-stratum s that were released in year i or earlier:

$$R_{ij+}^s = R_{1j}^s + R_{2j}^s + \ldots + R_{ij}^s, \quad i=1\ldots k; \quad j=1\ldots l; \quad s=1\ldots m.$$

R_i^s = total number of animals recovered in post-stratum s from those released in year i:

$$R_i^s = R_{i\cdot}^s = R_{ii}^s + R_{i,i+1}^s + \ldots + R_{il}^s, \quad i=1\ldots k.$$

C^s_i = total number of animals recovered in post-stratum *s* in year *i* from all releases:

$$C^s_i = R^s_{\cdot i} = R^s_{ii+} = R^s_{1i} + R^s_{2i} + \ldots + R^s_{ii}, \qquad i=1\ldots l.$$

T^s_i = total number of animals recovered in post-stratum *s* in year *i* or later that were known to be alive in year *i*:

$$T^s_1 = R^s_1;$$

$$T^s_i = T^s_{i-1} + R^s_i - C^s_{i-1}, \qquad i=2\ldots k;$$

$$T^s_i = T^s_{i-1} - C^s_{i-1}, \qquad i=k+1\ldots l.$$

Z^s_i = total number of animals recovered in post-stratum *s* after year *i* that were known to be alive in year *i*:

$$Z^s_i = T^s_i - C^s_i = T^s_{i+1} - R^s_{i+1}, \qquad i=1\ldots k;$$

These statistics can be represented in tabular form (Figure 2.2) following the conventions of Brownie *et al*. (1985, p. 13).

2.3 MODELS, ASSUMPTIONS, AND INTERPRETATION OF THE PARAMETERS

In all models, the numbers of recoveries from the N_i releases in year *i*, the $\{R^s_{ij}, j=i\ldots l, s=1\ldots m\}$, are assumed to be multinomially distributed. The expected numbers of band recoveries in the case of k=3 years of banding, l=4 years of recovery, and m=2 post-strata for the four models are shown in Figure 2.3a. The individual annual survival and band-recovery rates are not separately identifiable for recoveries occurring after year *k*; only the product terms (θ^s_i) are identifiable (the underlying form of the θ^s_i differs slightly among the four models). An illustration of the potential fates of an animal banded and released, assuming that Model 3 is appropriate, is given in Figure 2.3b. This Figure will aid in identifying the hidden components of the formal parameters as discussed below.

Figure 2.2
Illustration of computation of statistics from a recovery matrix with
k=3 years of banding, l=4 years of recoveries and m=2 post-strata

Recovery Matrix by Year

Year Banded	Number Banded	Post-stratum 1: 1	2	3	4	Row Total	Post-stratum 2: 1	2	3	4	Row Total
1	N_1	R^1_{11}	R^1_{12}	R^1_{13}	R^1_{14}	R^1_1	R^2_{11}	R^2_{12}	R^2_{13}	R^2_{14}	R^2_1
	T^1_1						Z^2_1				
2	N_2		R^1_{22}	R^1_{23}	R^1_{24}	R^1_2		R^2_{22}	R^2_{23}	R^2_{24}	R^2_2
		T^1_2						Z^2_2			
3	N_3			R^1_{33}	R^1_{34}	R^1_3			R^2_{33}	R^2_{34}	R^2_3
			T^1_3						Z^2_3		
		====	====	====	====		====	====	====	====	
		C^1_1	C^1_2	C^1_3	C^1_4		C^2_1	C^2_2	C^2_3	C^2_4	

Here, T^s_i, and Z^s_i refer to the nearest block total, R^s_i are the row sums, and C^s_i are column sums following the conventions of Brownie *et al.* (1985).

Figure 2.3a
Expected number of recoveries under the four models in the case of k=3 years of banding, l=4 years of recoveries, and m=2 post-strata.

Model 3

Year Banded	Number Banded	Expected Recoveries by Year Post-stratum 1: 1	2	3	4	Post-stratum 2: 1	2	3	4
1	N_1	$N_1f_1^1$	$N_1S_1^1f_2^1$	$N_1S_1^1S_2^1f_3^1$	$N_1S_1^1S_2^1\theta_3^1$	$N_1f_1^2$	$N_1S_1^2f_2^2$	$N_1S_1^2S_2^2f_3^2$	$N_1S_1^2S_2^2\theta_3^2$
2	N_2		$N_2f_2^1$	$N_2S_2^1f_3^1$	$N_2S_2^1\theta_3^1$		$N_2f_2^2$	$N_2S_2^2f_3^2$	$N_2S_2^2\theta_3^2$
3	N_3			$N_3f_3^1$	$N_3\theta_3^1$			$N_3f_3^2$	$N_3\theta_3^2$

Model 2a

Year Banded	Number Banded	Expected Recoveries by Year Post-stratum 1: 1	2	3	4	Post-stratum 2: 1	2	3	4
1	N_1	$N_1f_1^1$	$N_1S_1f_2^1$	$N_1S_1S_2f_3^1$	$N_1S_1S_2\theta_3^1$	$N_1f_1^2$	$N_1S_1f_2^2$	$N_1S_1S_2f_3^2$	$N_1S_1S_2\theta_3^2$
2	N_2		$N_2f_2^1$	$N_2S_2f_3^1$	$N_2S_2\theta_3^1$		$N_2f_2^2$	$N_2S_2f_3^2$	$N_2S_2\theta_3^2$
3	N_3			$N_3f_3^1$	$N_3\theta_3^1$			$N_3f_3^2$	$N_3\theta_3^2$

Figure 2.3a (cont.)

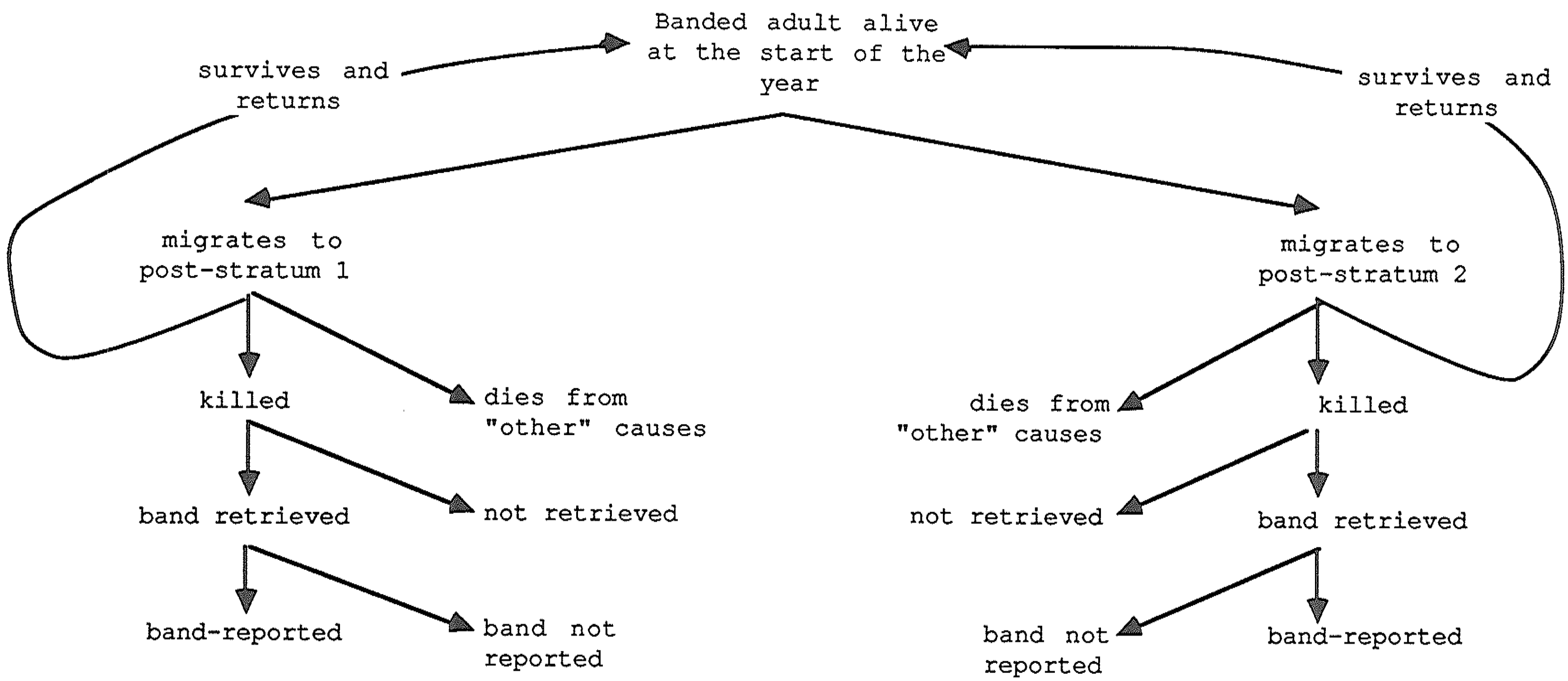
------------------------- Model 2b -------------------------

Year Banded	Number Banded	Expected Recoveries by Year Post-stratum 1 1	2	3	4	Post-stratum 2 1	2	3	4
1	N_1	N_1f_1	$N_1S_1^1f_2$	$N_1S_1^1S_2^1f_3$	$N_1S_1^1S_2^1\theta_3^1$	N_1f_1	$N_1S_1^2f_2$	$N_1S_1^2S_2^2f_3$	$N_1S_1^2S_2^2\theta_3^2$
2	N_2		N_2f_2	$N_2S_2^1f_3$	$N_2S_2^1\theta_3^1$		N_2f_2	$N_2S_2^2f_3$	$N_2S_2^2\theta_3^2$
3	N_3			N_3f_3	$N_3\theta_3^1$			N_3f_3	$N_3\theta_3^2$

------------------------- Model 1 -------------------------

Year Banded	Number Banded	Expected Recoveries by Year Post-stratum 1 1	2	3	4	Post-stratum 2 1	2	3	4
1	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2\theta_3$	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2\theta_3$
2	N_2		N_2f_2	$N_2S_2f_3$	$N_2S_2\theta_3$		N_2f_2	$N_2S_2f_3$	$N_2S_2\theta_3$
3	N_3			N_3f_3	$N_3\theta_3$			N_3f_3	$N_3\theta_3$

Figure 2.3b
Potential outcomes for a banded animal assuming Model 3 is appropriate
based upon geographical post-stratifaction illustrated in the case of two post-strata



The usual assumptions made for band-recovery studies (Section 1.3.3) are made here. As well, in all four models, it is assumed that each animal, following release, is completely faithful to one, and only one, post-stratum. For example, consider the expected number of animals released in year 1 and recovered in year 3 in post-stratum 2 under Model 3 ($N_1 S_1^2 S_2^2 f_3^2$; Figure 2.3). These animals are assumed to be subject to the annual survival rate for post-stratum 2 in the years between release and recovery. This fidelity assumption clearly holds when the post-release stratification factor is an unchanging attribute of the animal, such as sex, but is unlikely to hold if the stratification factor is geographic area of recovery. However, in some circumstances, Models 1 and 2a are still applicable in the absence of fidelity. If each animal chooses its post-stratum in the next year completely independently of its post-stratum of previous years, then the annual survival rate will be the "average" gross survival rate over all post-strata, provided animals are sampled at random at banding time. This is the basis for the Partial-Fidelity Model of Chapter 3.

The band-recovery parameters must be interpreted carefully. In these models, these parameters include not only the usual components of, survival from banding season to hunting season, the harvest probability, and the band-reporting rate (Brownie *et al.*, 1985, p. 14) but also a component for the probability of post-stratum membership for each year of release (Figure 2.3b). Differences in any component among the post-strata will cause the recovery rates to differ and tests of homogeneity among recovery rates may reject for reasons unrelated to the usual components of the recovery rate. For example, if the animals are stratified at recovery time on the basis of sex, the band-recovery rates will include a component for the sex ratio at banding time. Unless the sex ratio is 1:1, the post-stratum-specific recovery rates will differ, even if all other components are equal among post-strata. Moreover, if the sex ratio changes among releases, then the band-recovery rates are both year-of-release and year-of-recovery dependent, and the model no longer satisfies the usual assumptions of band-recovery studies. Modifications to the models and tests to allow for a known time-invariant sex ratio are straightforward. Similarly, if the animals are stratified at recovery time by geographical area, the band-recovery rates will incorporate a migration component. Recovery rates will be equal only if animals select post-strata uniformly. Thus a test of homogeneous recovery rates might be useful as a test for no post-stratum preference provided post-strata were homogeneous with respect to hunting behaviour and to natural survival between banding and recovery seasons (e.g., if this interval is very short or survival rates are very high). More commonly, migration rates are higher to some post-strata than to others for reasons of preference, accessibility, stratum size, etc. The models can be reparameterized to include non-uniform migration-rate patterns provided these are consistent among releases. The migration rates are not separately identifiable from the usual recovery-rate components without additional data, such as live resightings, or further restrictive assumptions. The models presented in this Chapter constitute a basis for developing and understanding these more complex migration models presented in later chapters.

2.4 ESTIMATION

Since each year's releases are independent, the likelihood is a product of multinomial distributions. For example, the likelihood function for Model 3 in the case of k=3 years of releases, l=4 years of recovery, and m=2 post-strata is:

$$L = \binom{N_1}{R^1_{11}, R^1_{12}, R^1_{13}, R^1_{14}, R^2_{11}, R^2_{12}, R^2_{13}, R^2_{14}} (f^1_1)^{R^1_{11}} (s^1_1 f^1_2)^{R^1_{12}} (s^1_1 s^1_2 f^1_3)^{R^1_{13}} (s^1_1 s^1_2 \theta^1_4)^{R^1_{14}}$$

$$\times\ (f^2_1)^{R^2_{11}} (s^2_1 f^2_2)^{R^2_{12}} (s^2_1 s^2_2 f^2_3)^{R^2_{13}} (s^2_1 s^2_2 \theta^2_4)^{R^2_{14}}$$

$$\times\ (1-f^1_1-s^1_1 f^1_2-s^1_1 s^1_2 f^1_3-s^1_1 s^1_2 \theta^1_4-f^2_1-s^2_1 f^2_2-s^2_1 s^2_2 f^2_3-s^2_1 s^2_2 \theta^2_4)^{N_1-R^{\cdot}_1}$$

$$\times \binom{N_2}{R^1_{22}, R^1_{23}, R^1_{24}, R^2_{22}, R^2_{23}, R^2_{24}} (f^1_2)^{R^1_{22}} (s^1_2 f^1_3)^{R^1_{23}} (s^1_2 \theta^1_4)^{R^1_{24}}$$

$$\times\ (f^2_2)^{R^2_{22}} (s^2_2 f^2_3)^{R^2_{23}} (s^2_2 \theta^2_4)^{R^2_{24}}$$

$$\times\ (1-f^1_2-s^1_2 f^1_3-s^1_2 \theta^1_4-f^2_2-s^2_2 f^2_3-s^2_2 \theta^2_4)^{N_2-R^{\cdot}_2}$$

$$\times \binom{N_3}{R^1_{33}, R^1_{34}, R^2_{33}, R^2_{34}} (f^1_3)^{R^1_{33}} (\theta^1_4)^{R^1_{34}} (f^2_3)^{R^2_{33}} (\theta^2_4)^{R^2_{34}} (1-f^1_3-\theta^1_4-f^2_3-\theta^2_4)^{N_3-R^{\cdot}_3}$$

which can be reduced to:

$$L = \text{constant} \times (f^1_1)^{C^1_1} (f^1_2)^{C^1_2} (f^1_3)^{C^1_3} (\theta^1_4)^{C^1_4}$$

$$\times\ (f^2_1)^{C^2_1} (f^2_2)^{C^2_2} (f^2_3)^{C^2_3} (\theta^2_4)^{C^2_4}$$

$$\times\ (s^1_1)^{Z^1_1} (s^1_2)^{Z^1_2} (s^2_1)^{Z^2_1} (s^2_2)^{Z^2_2}$$

$$\times\ (1-f^1_1-s^1_1 f^1_2-s^1_1 s^1_2 f^1_3-s^1_1 s^1_2 \theta^1_4-f^2_1-s^2_1 f^2_2-s^2_1 s^2_2 f^2_3-s^2_1 s^2_2 \theta^2_4)^{N_1-R^{\cdot}_1}$$

$$\times\ (1-f_2^1-s_2^1f_3^1-s_2^1\theta_4^1-f_2^2-s_2^2f_3^2-s_2^2\theta_4^2)^{N_2-R_2^{\cdot}}$$

$$\times\ (1-f_3^1-\theta_4^1-f_3^2-\theta_4^2)^{N_3-R_3^{\cdot}}\ .$$

The likelihoods for Models 2a, 2b, and 1 are found by applying various restrictions on the individual band-recovery and survival rates among the post-strata. The likelihood for Model 3 has twelve identifiable parameters:

$$\{\ f_1^1,\ f_1^2,\ f_2^1,\ f_2^2,\ f_3^1,\ f_3^2,\ \theta_4^1,\ \theta_4^2,\ S_1^1,\ S_1^2,\ S_2^1,\ S_2^2\ \}.$$

The MSS also has dimension twelve and one representation is:

$$\{\ C_1^1,\ C_1^2,\ C_2^1,\ C_2^2,\ C_3^1,\ C_3^2,\ C_4^1,\ C_4^2,\ R_1^1,\ R_1^2,\ R_2^1,\ R_2^2\ \}.$$

[Note that R_3^s can be expressed as a linear combination of these statistics.]

Since the number of identifiable parameters equals the dimension of the MSS in all four models, the MLEs can be found through the method of moments by equating the components of the MSS to their expectations and solving for the unknown parameters as outlined in Chapter 1. The variances and covariances can be found using the delta-method. Of the four models, all but Model 2b allow closed-form estimation of the parameters and their variances and covariances. For Model 2b, one must use numerical methods such as the method of scoring.

One representation for the MSS, the dimension of the MSS, and the MLEs for all four models are summarized in Table 2.4. The variances and non-zero covariances for Models 3 and 2a are given in Appendix 2.A;

Table 2.4
One representation of the MSS and the MLEs of the parameters under Models 1, 2a, 2b, and 3.

Variances and covariances for the MLEs are given in Appendix 2.A

	Model 1	Model 2a	Model 2b	Model 3
One representation of MSS	$R_i^{\cdot}$ $i=1\ldots k$	$R_i^{\cdot}$ $i=1\ldots k-1$	Z_i^s $s=1\ldots m$, $i=1\ldots k-1$	R_i^s $s=1\ldots m$, $i=1\ldots k$
	$C_i^{\cdot}$ $i=1\ldots l-1$	C_i^s $s=1\ldots m$, $i=1\ldots l$	$C_i^{\cdot}$ $i=1\ldots k$	C_i^s $s=1\ldots m$, $i=1\ldots l-1$
			C_i^s $s=1\ldots m$, $i=k+1\ldots l$	
Dimension of MSS	$l+k-1$	$ml+k-1$	$ml+k-m$	$m(l+k-1)$
MLE	$\hat{f}_i = \frac{1}{m}\frac{R_i^{\cdot}\ C_i^{\cdot}}{N_i\ T_i^{\cdot}}$	$\hat{f}_i^s = \frac{R_i^{\cdot}\ C_i^s}{N_i\ T_i^{\cdot}}$	numerical methods must be used	$\hat{f}_i^s = \frac{R_i^s\ C_i^s}{N_i\ T_i^s}$
	$\hat{\theta}_i = \frac{1}{m}\frac{R_k^{\cdot}\ C_i^{\cdot}}{N_k\ T_k^{\cdot}}$	$\hat{\theta}_i^s = \frac{R_k^{\cdot}\ C_i^s}{N_k\ T_k^{\cdot}}$		$\hat{\theta}_i^s = \frac{R_k^s\ C_i^s}{N_k\ T_k^s}$
	$\hat{S}_i = \frac{R_i^{\cdot}\ Z_i^{\cdot}\ N_{i+1}}{N_i\ T_i^{\cdot}\ R_{i+1}^{\cdot}}$	$\hat{S}_i = \frac{R_i^{\cdot}\ Z_i^{\cdot}\ N_{i+1}}{N_i\ T_i^{\cdot}\ R_{i+1}^{\cdot}}$		$\hat{S}_i^s = \frac{R_i^s\ Z_i^s\ N_{i+1}}{N_i\ T_i^s\ R_{i+1}^s}$

those for Model 2b must be found numerically; those for Model 1 may be found in Brownie *et al.* (1985, Section 2.2) as explained in Appendix 2.A.

Inference in Model 3 is performed by simply estimating each post-stratum's parameters separately, while treating animals recovered in other post-strata as never seen. Inference about the annual survival rates in Model 2a is performed by combining recoveries over the post-strata and treating the sum of the band-recovery rates as a "new" gross recovery rate. Inference in Model 1 is performed by simply combining over all post-strata and treating the data as arising from an ordinary band-recovery experiment (Section 1.3). In all cases, the methods of Brownie *et al.* (1985) are directly applicable.

2.5 MODEL TESTS

Since all the models are of full rank, similar tests may be constructed by finding:

$$P_H(\text{ MSS under A} \mid \text{MSS under H })$$

where H and A refer to the null and alternate hypotheses, respectively. This methodology has wide applicability to band-recovery and capture-recapture models and has been used frequently (Brownie *et al.*, 1985; Brownie and Robson, 1976; and Pollock, 1975). The joint distribution of the MSS under H or A is difficult to write down directly, but it can sometimes be factored into the product of conditionally independent binomial or multinomial distributions. The ease of this factorization may depend upon the order in which the conditioning is performed and the choice of MSS. The factorizations and the detailed algebraic derivations used to derive the tests presented here may be found in Appendices 2.B through 2.E.

Each test in this Chapter can be broken into finer subtests each of which is either a test for uniform multinomial proportions, or a test for homogeneity of two sets of multinomial proportions. As a result, large-sample chi-square approximations can be developed for each subtest simplifying the computation of the significance level (p-value) and illuminating the test properties. All subtests are asymptotically independent and an approximate test statistic for the overall test is obtained by summing the subtest chi-square test statistics and their degrees of freedom.

The power function of the subtests can be approximated using the following two results:

- Lehmann (1986, p. 480) shows that the power function for chi-square goodness-of-fit tests for uniformity of multinomial proportions against local alternatives can be approximated using a non-central chi-square distribution with (m-1) degrees of freedom and non-centrality parameter

$$\lambda^2 = N \cdot m \cdot \sum_{s=1}^{m} (\pi_{As} - 1/m)^2$$

where N is the total number of observations, m is the number of classes, and π_{As} is the probability of falling into class s under the alternative.

· Meng and Chapman (1966) found that the power function of tests of homogeneity of 2 sets of multinomial proportions in 2xm contingency tables with fixed row totals under local alternatives can be approximated using a non-central chi-square distribution with (m-1) degrees of freedom and non-centrality parameter

$$\lambda^2 = \frac{N_1 N_2}{N_1 + N_2} \sum_{s=1}^{m} \frac{(\pi_{A1s} - \pi_{A2s})^2}{\pi_{Hs}}$$

where N_1 and N_2 are the fixed row totals, π_{Hs} are the common cell proportions under the null hypothesis, π_{A1s} and π_{A2s} are the cell proportions of the two rows under the alternate hypothesis, and m is the number of cells in each row.

In either case, the non-centrality parameter can be determined for each subtest; the overall test-statistic under the alternate hypothesis then has, asymptotically, a non-central chi-square distribution whose non-centrality parameter and degrees of freedom are the respective sums over the subtests. The power function will, except where noted below, depend upon all of the unknown parameters.

The results for all the tests considered in this Chapter are summarized in Table 2.5 by giving the null and alternate hypotheses, the distribution used in the exact test, a large sample contingency table that can be used to obtain a chi-square approximation for each subtest, and the asymptotic non-centrality parameter of each subtest. In the rest of this section, the logical basis of each test, the use of the subtests for testing hypotheses about individual parameters, and special features of the power function are examined.

Table 2.5
A summary of the testing procedures for differentiating between models

	Model 2a vs Model 3	**Model 1 vs Model 2a**
Hypotheses	H: $S_i^t=S_i \; {}^{i=1\ldots k-1}_{t=1\ldots m}$; θ_i^t, f_i^t unrestricted A: S_i^t, f_i^t unrestricted	H: $S_i^t=S_i \; {}^{i=1\ldots k-1}_{t=1\ldots m}$; $f_i^t=f_i \; {}^{i=1\ldots k}_{t=1\ldots m}$; $\theta_i^t=\theta_i \; {}^{i=k+1\ldots l}_{t=1\ldots m}$ A: $S_i^t=S_i \; {}^{i=1\ldots k-1}_{t=1\ldots m}$; θ_i^t, f_i^t unrestricted
Distribution upon which test is based	$\prod_{i=2}^{k} \binom{R_i^{\cdot}}{R_i^1,\ldots,R_i^m}\binom{T_i^{\cdot}-R_i^{\cdot}}{T_i^1-R_i^1,\ldots,T_i^m-R_i^m} \div \binom{T_i^{\cdot}}{T_i^1,\ldots,T_i^m}$	$\prod_{i=1}^{l} \binom{C_i^{\cdot}}{C_i^1,\ldots,C_i^m} \div m^{C_i^{\cdot}}$
Large sample contingency table	The i^{th} subtest is a test for homogeneous cell proportions, i=2...k $\begin{array}{c\|cccc} R_i^{\cdot} & R_i^1, & R_i^2, & \ldots, & R_i^m \\ T_i^{\cdot}-R_i^{\cdot} & T_i^1-R_i^1, & T_i^2-R_i^2, & \ldots, & T_i^m-R_i^m \end{array}$	The i^{th} subtest is a test for uniform multinomial proportions, $i=1\ldots l$ $\begin{array}{c\|c} C_i^{\cdot} & C_i^1, C_i^2, \ldots, C_i^m \end{array}$
Asymptotic non-centrality parameter	$\lambda_i^2 = \frac{R_i^{\cdot}(T_i^{\cdot}-R_i^{\cdot})}{T_i^{\cdot}} \sum_{s=1}^{m} \frac{(\pi_{A1s}-\pi_{A2s})^2}{\pi_{Hs}}$ where $\pi_{Hs} = \rho_i^s/\rho_i^{\cdot}$ $\pi_{A1s} = \rho_i^{s*}/\rho_i^{\cdot *}$ $\pi_{A2s} \approx (\xi_i^s-N_i)\rho_i^{s*} \;/\; \sum_s(\xi_i^s-N_i)\rho_i^{s*}$ $\rho_i^s = f_i^s + S_i f_{i+1}^s + \ldots + S_i S_{i+1} \ldots S_k \theta_l^s$ $\rho_i^{s*} = f_i^s + S_i^s f_{i+1}^s + \ldots + S_i^s S_{i+1}^s \ldots S_k^s \theta_l^s$ $\xi_i^s = N_1 S_1^s S_2^s \ldots S_{i-1}^s + N_2 S_2^s \ldots S_{i-1}^s + \ldots + N_i$	$\lambda_i^2 = m(C_i^{\cdot}) \sum_{s=1}^{m}[(f_i^s/f_i^{\cdot}) - 1/m]^2$

Table 2.5 (cont.)

	Model 1 vs Model 2b	**Model 2b vs Model 3**
Hypotheses	H: $S_i^t=S_i \ \begin{smallmatrix} i=1\ldots k-1 \\ t=1\ldots m \end{smallmatrix}$; $f_i^t=f_i \ \begin{smallmatrix} i=1\ldots k \\ t=1\ldots m \end{smallmatrix}$; $\theta_i^t=\theta_i \ \begin{smallmatrix} i=k+1\ldots l \\ t=1\ldots m \end{smallmatrix}$ A: $f_i^t=f_i \ \begin{smallmatrix} i=1\ldots k \\ t=1\ldots m \end{smallmatrix}$; θ_i^t, S_i^t unrestricted	H: $f_i^t=f_i \ \begin{smallmatrix} i=1\ldots k \\ t=1\ldots m \end{smallmatrix}$; θ_i^t, S_i^t unrestricted A: f_i^t, S_i^t unrestricted
Distribution upon which test is based	$\prod_{i=1}^{k-1} \begin{pmatrix} z_i^{\cdot} \\ z_i^1, \ldots, z_i^m \end{pmatrix} \div {}_m z_i^{\cdot} \times \prod_{i=k+1}^{l} \begin{pmatrix} C_i^{\cdot} \\ C_i^1, \ldots, C_i^m \end{pmatrix} \div {}_m C_i^{\cdot}$	$\prod_{i=1}^{k-1} \begin{pmatrix} C_i^{\cdot} \\ C_i^1, \ldots, C_i^m \end{pmatrix} \begin{pmatrix} R_i^{\cdot} \\ R_i^1, \ldots, R_i^m \end{pmatrix} \div \begin{pmatrix} T_i^{\cdot} \\ T_i^1, \ldots, T_i^m \end{pmatrix} \times {}_m T_i^{\cdot}-R_i^{\cdot}-C_i^{\cdot}$
Large sample contingency table	The i^{th} subtest is one of two forms each of which is a test for uniform multinomial proportions. $i=1\ldots k-1$: $z_i^{\cdot}$ | $z_i^1, z_i^2, \ldots, z_i^m$ | $i=k+1\ldots l$: $C_i^{\cdot}$ | $C_i^1, C_i^2, \ldots, C_i^m$ |	The i^{th} simple subtest is a test for uniform multinomial proportions. $R_{ii}^{\cdot}$ | $R_{ii}^1, R_{ii}^2, \ldots, R_{ii}^m$ |
Asymptotic non-centrality parameter	$\lambda_i^2=m(z_i^{\cdot})\sum_{s=1}^{m}[S_i^s\rho_{i+1}^s/\sum_{v=1}^{m}S_i^v\rho_{i+1}^v-1/m]^2$ where $\rho_i^s=f_i+S_if_{i+1}^s+\ldots+S_i^sS_{i+1}^s\ldots\theta_l^s$ $\lambda_i^2=m(C_i^{\cdot})\sum_{s=1}^{m}[(\theta_i^s/\theta_i^{\cdot})-1/m]^2$	$\lambda_i^2= m(R_{ii}^{\cdot})\sum_{s=1}^{m}[(f_i^s/f_i^{\cdot}) - 1/m]^2$ (simple test)

Table 2.5 (cont.)

	Goodness-of-fit test to Model 3
Hypotheses	H: Model 3 is appropriate A: Model 3 is not appropriate
Distribution upon which test is based	$\prod_{s=1}^{m}\prod_{i=2}^{k}\binom{R_i^s}{R_{ii}^s,\ R_{i,i+1}^s,\ldots,\ R_{il}^s}\binom{T_i^s - R_i^s}{R_{ii+}^s - R_{ii}^s,\ldots,\ R_{il+}^s - R_{il}^s} \div \binom{T_i^s}{R_{ii+}^s,\ \ldots,\ R_{il+}^s}$
Large sample contingency table	The $(i,s)^{th}$ subtest is a test for homogeneous cell proportions $i=2\ldots k$, $s=1\ldots m$. R_i^s: R_{ii}^s, $R_{i,i+1}^s$,..., R_{il}^s $T_i^s - R_i^s$: $R_{ii+}^s - R_{ii}^s$, $R_{i,i+1,+}^s - R_{i,i+1}^s$,..., $R_{il+}^s - R_{il}^s$
Asymptotic non-centrality parameter	not applicable due to lack of specific alternative

2.5.1 TESTS BETWEEN MODELS

The test of Model 2a vs. Model 3 is a test for homogeneous survival allowing post-stratum-dependent recovery rates. Under the null hypothesis, recoveries from the i^{th} release should have the same relative distribution among post-strata as animals which are known to have survived to year i from all previous releases. This is the intuitive interpretation of the $2 \times m$ contingency table presented in Table 2.5 based upon the conditional distribution derived in Appendix 2.B.

The i^{th} subtest actually tests if the survival rates prior to year i are homogeneous among post-strata. It is a test that a specific year's annual survival rates are homogeneous among post-strata only if it is assumed that the survival rates in each previous year are homogeneous among post-strata. A sequential procedure could be used starting with year 1 (corresponding to i=2) and continuing until the test rejects. At this point, it may no longer be useful to test subsequent individual annual survival rates for homogeneity among post-strata since the test may reject due to earlier heterogeneity.

In deriving the asymptotic power function for the i^{th} subtest, it should be noted that the distribution of the $\{T_i^s - R_i^s,\ s=1,\ldots,m\}$, conditional upon their total, is no longer multinomial since the total is formed as the sum of several multinomials each with different cell probabilities. However, in large samples, the cell probabilities can be approximated by the ratio of each cell's expected value to the total expected value.

The test of Model 1 vs. Model 2a is a test for homogeneous recovery rates conditional upon the survival rates being homogeneous among post-strata. Under the null hypothesis, the recoveries in year i in post-stratum s for each year of release should occur with proportion $1/m$ relative to the overall recoveries in year i. This leads to the l chi-square subtests shown in Table 2.5 that C_i^1, ..., C_i^m are uniformly distributed among the m post-strata (derived in Appendix 2.C). However, the band-recovery rates include a hidden component for the relative post-stratum abundances at banding time (e.g., the sex ratio) or at recovery time (e.g., the migration rates), and unless the relative abundances are known to be equal for all post-strata, this test may reject the null hypothesis for reasons that are biologically obvious. The i^{th} subtest can be interpreted as a test for homogeneous band-recovery rates among post-strata in year i (assuming Model 2a holds) whether or not there is homogeneity of the band-recovery rates in other years. The individual subtests can be carried out in any order. The power function is independent of the annual survival rates for alternatives that satisfy Model 2a since the MSS(Model 1) are sufficient for the survival rates under Model 2a.

The test of Model 1 vs. Model 2b is a test for homogeneous survival conditional upon the band-recovery rates being homogeneous among post-strata. The distribution used in the exact test (derived in Appendix 2.D) has two components given by the two product terms shown in Table 2.5. For reasons similar to those outlined above, the first component leads to (k-1) chi-square subtests that the Z_i^1, ..., Z_i^m are uniformly distributed among the m post-strata. Intuitively, if the homogeneity of survival rates between year i and year i+1 are tested, those animals known to be alive and subject to survival from year i to year i+1 and recovered in post-stratum s (Z_i^s) are a sample of all animals known to be alive and subject to survival from i to i+1 ($Z_i^{\cdot}$). When H is true, there will be no difference in the annual survival rates or the band-recovery rates, and the recoveries from each post-stratum should occur in the ratio $1/m$ relative to the total recovered over all post-strata. The i^{th} subtest is then a test of homogeneous annual survival in year i or later, conditional upon survival rates before year i being homogeneous among post-strata. Hence, the i^{th} subtest can be interpreted as a test for homogeneous annual survival rates between banding in year i and banding in year i+1 only if all other rates are assumed homogeneous.

The second component of the distribution is identical to the last (l-k) subtests of the test of Model 1 vs. Model 2a. This is because the band-recovery rates and survival rates are not separately identifiable in the last (l-k) recovery years and changes in survival are indistinguishable from changes in band-recovery. Hence, the i^{th} subtest can be interpreted as a test for homogeneity of the product parameters (θ_i^s) among post-strata.

The test of Model 2b vs. Model 3 is a test for homogeneous recovery rates allowing for heterogeneous survival rates. A test may be developed by the methods used earlier. However, since the overall test of Model 1 vs. Model 3 must be the same regardless whether the path through Model 2a or Model 2b is chosen, the conditional distribution may be derived by straightforward algebraic division:

$$\begin{array}{l}\text{Distribution for}\\ \text{the test of}\\ \text{Model 2b vs. Model 3}\end{array} = \frac{\begin{array}{l}\text{Distribution for the}\\ \text{test of Model 1 vs. Model 3}\end{array}}{\begin{array}{l}\text{Distribution for the}\\ \text{test of Model 1 vs. Model 2b}\end{array}} .$$

The p-value is tedious to compute using the distribution shown in Table 2.5, and it is difficult to find a large-sample approximation. Tests using the likelihood ratio or Rao's (1973, p. 393) method are not in closed form and lead to equally difficult computations. An easier approach is to develop a less powerful test using only the direct recoveries, the $\{R^s_{ii}, i=1\ldots k, s=1\ldots m\}$. If there are no differences in the band-recovery rates among post-strata in year i, then the $\{R^s_{ii}, s=1\ldots m\}$ would be expected to be split equally among all post-strata. A large-sample contingency table can be developed for this simple test as shown in Table 2.5. The simple test is identical to the full test when i=1. When i is greater than 1, the simple test ignores recoveries from previous years' releases that the full test does not. However, since the first year's recoveries are often the largest, the loss of power is expected to be small. In any case, if the simple test rejects the null hypothesis, it is not necessary to carry out one of the more efficient tests.

Whether the full or simple test is used, only the first k years may be examined for homogeneous band-recovery rates since recovery rates in years k+1 to l are not separately identifiable. If the simple test is used, tests of homogeneity of each year's band-recovery rates do not require assumptions about the other parameters.

2.5.2 GOODNESS-OF-FIT TESTS

A general, non-specific goodness-of-fit test to Model 3 is constructed using the residual distribution of the data given the MSS as in Pollock, Hines and Nichols (1985), or

$$P_{\text{Model 3}}(\{R_{ij}^{s}\}\ i=1\ldots k,\ j=i\ldots l,\ s=1\ldots m \mid \text{MSS(Model 3)})\ .$$

The derivation of this distribution is straightforward using the same techniques as used in finding the distribution of the between model test statistics (Appendix 2.E). As before, large sample chi-square tests based upon contingency tables can be found (Table 2.5). It is only necessary to derive the goodness-of-fit test for Model 3, since goodness-of-fit tests for any other, more restrictive, model can be found using the goodness-of-fit test for Model 3 and the test of the restricted model vs. Model 3.

If Model 3 is correct, then both rows of the large sample contingency table have common cell probabilities. Pooling of cells, and a corresponding reduction in the degrees of freedom, may be required within each of the individual tables to avoid small expected counts. Each subtest is the same as the Robson and Youngs (1971) goodness-of-fit test, treating all other post-strata as never seen. The power of the goodness-of-fit test could, in principle, be determined using the results of Meng and Chapman (1966), but further investigations are foregone for the lack of an obvious alternative.

2.6 EXAMPLE

Adult male and female mallards were banded in south-west Alberta in 1975-1982. Birds were recovered either: in Canada before it was clear which flyway they would take later in the year; in the Pacific flyway; or in the Eastern (Central, Mississippi, and Atlantic) flyways. The Canadian recoveries cannot be used, and for demonstration purposes, only the male birds recovered in the Pacific flyway (P) or the Eastern flyways (E) banded in 1975-1982 and recovered in 1975-1982 are used. Banding experiments with North American mallards are discussed in more detail in Anderson and Henny (1972). In particular, they mention (p. 86) that only a small percentage of male mallards shift from one flyway to another, implying that the fidelity assumption is not seriously violated.

The arrays of actual recoveries along with derived summary statistics are shown in Table 2.6a. The band-recovery and annual survival rate estimates and their estimated standard errors are shown for each of the four models in Table 2.6b. A goodness-of-fit test of Model 3 (Table 2.6c) was not rejected (p=.68) indicating an adequate fit when each post-stratum is allowed to have a distinct survival and band-recovery rate. Cells were pooled within tables from right to left until all expected cell counts exceeded 3; this accounts for the reduction in the degrees of freedom.

The estimated annual survival rates under Model 3 (Table 2.6b) are similar in the two post-strata. An overall test of homogeneity of the survival rates allowing for heterogeneous band-recovery rates (Model 2a

Table 2.6a

Raw band-recovery matrix for adult male mallards released in Southern Alberta and stratified by area of recovery

Number Banded	Year Banded	Number recovered in the Pacific flyway 1975	1976	1977	1978	1979	1980	1981	1982	Statistics R_i^1	T_i^1	Z_i^1
453	1975	6	3	3	1	1	0	0	2	16	16	10
1337	1976		25	12	9	6	3	4	1	60	70	42
1380	1977			22	18	12	7	5	2	66	108	71
1079	1978				17	13	9	8	4	51	122	77
2253	1979					29	25	18	13	85	162	101
888	1980						12	10	5	27	128	72
1924	1981							28	23	51	123	50
1107	1982								19	19	69	0
	C_i^1	6	28	37	45	61	56	73	69			

Year Banded	Number recovered in the Eastern flyways 1975	1976	1977	1978	1979	1980	1981	1982	Statistics R_i^2	T_i^2	Z_i^2
1975	9	18	4	3	4	1	1	1	41	41	32
1976		26	31	16	8	7	5	4	97	129	85
1977			35	24	18	13	10	2	102	187	117
1978				17	12	16	9	8	62	179	119
1979					37	33	18	19	107	226	147
1980						19	14	9	42	189	100
1981							50	21	71	171	64
1982								23	23	87	0
C_i^2	9	44	70	60	79	89	107	87			

Table 2.6b
Estimates and estimated standard errors under the four models

Band-Recovery Rates

		Model 3				Model 2a				Model 2b		Model 1	
		Pacific		Eastern		Pacific		Eastern		Pacific and Eastern[2]		Pacific and Eastern	
Year	i	f(i)	s.e.	f(i)	s.e.	f(i)	s.e.	f(i)	s.e.	f(i)	s.e.	f(i)	s.e.
1975	1	0.013	0.0054	0.020	0.0066	0.013	0.0054	0.020	0.0066	0.017	0.0042	0.017	0.0042
1976	2	0.018	0.0035	0.025	0.0039	0.017	0.0031	0.026	0.0040	0.022	0.0025	0.021	0.0026
1977	3	0.016	0.0029	0.028	0.0037	0.015	0.0026	0.029	0.0037	0.022	0.0021	0.022	0.0023
1978	4	0.017	0.0032	0.019	0.0031	0.016	0.0026	0.021	0.0030	0.018	0.0018	0.018	0.0022
1979	5	0.014	0.0021	0.017	0.0022	0.013	0.0018	0.017	0.0021	0.015	0.0013	0.015	0.0015
1980	6	0.013	0.0029	0.022	0.0038	0.014	0.0023	0.022	0.0032	0.018	0.0015	0.018	0.0023
1981	7	0.016	0.0025	0.023	0.0030	0.016	0.0021	0.023	0.0027	0.019	0.0014	0.019	0.0019
1982	8	0.017	0.0039	0.021	0.0043	0.017	0.0030	0.021	0.0035	0.019	0.0015	0.019	0.0029

Annual Survival Rates

		Model 3				Model 2a		Model 2b				Model 1	
		Pacific		Eastern		Pacific and Eastern[1]		Pacific		Eastern		Pacific and Eastern	
Year	i	S(i)	s.e.	S(i)	s.e.	S(i)	s.e.	S(i)	s.e.	S(i)	s.e.	S(i)	s.e.
1975	1	0.49	0.166	0.97	0.191	0.79	0.130	0.45	0.142	1.03	0.175	0.79	0.130
1976	2	0.56	0.112	0.65	0.097	0.62	0.072	0.49	0.075	0.71	0.075	0.62	0.072
1977	3	0.67	0.130	0.80	0.133	0.74	0.091	0.68	0.080	0.79	0.071	0.74	0.091
1978	4	0.79	0.147	0.80	0.132	0.80	0.096	0.77	0.087	0.82	0.074	0.80	0.096
1979	5	0.77	0.175	0.65	0.120	0.70	0.098	0.63	0.062	0.77	0.062	0.70	0.098
1980	6	0.65	0.159	0.68	0.137	0.66	0.102	0.65	0.076	0.67	0.067	0.66	0.102
1981	7	0.63	0.181	0.66	0.171	0.65	0.123	0.62	0.088	0.67	0.083	0.65	0.123

[1]Under Model 2a, annual survival rates are homogeneous among strata.
[2]Under Model 2b, band-recovery rates are homogeneous among strata.

Table 2.6c
Goodness-of-fit test for Model 3

Overall test

	Pacific Flyway		Eastern Flyway	
i	χ^2	d.f.	χ^2	d.f.
2	0.01	1	10.39	3
3	1.25	4	3.74	5
4	0.78	4	5.28	4
5	1.33	3	1.52	3
6	0.15	2	0.26	2
7	0.71	1	3.19	1
8	0.00	0	0.00	0
Total	28.62, 33 d.f., p=.685			

Example of one subtest (i=2, s=2)

Eastern Flyway

R_2^2	97	26	31	16	8	7	5	4
$T_2^2-R_2^2$	32	18	4	3	4	1	1	1
T_2^2	129	44	35	19	12	8	6	5

Pooled cells

Table 2.6d
Test Model 2a vs. Model 3

Overall test

i	χ^2	d.f.	
2	3.02	1	
3	1.20	1	
4	1.59	1	
5	0.99	1	
6	0.06	1	
7	0.00	1	
8	0.02	1	
Total	6.88	7	p=.441

Example of one subtest (i=2)

		Flyway P	Flyway E
$R_2^1+R_2^2$	157	60	97
$T_2^1+T_2^2-R_2^1-R_2^2$	42	10	32
$T_2^1+T_2^2$	199	70	129

vs. Model 3) is shown in Table 2.6d and is not rejected (p=.44). Moreover, no individual subtest gives a significant value. A goodness-of-fit test to Model 2a is constructed by adding the chi-square statistics and degrees of freedom for the goodness-of-fit test for Model 3 and the test of Model 2a vs. Model 3. The chi-square value of 35.5 (40 d.f.) is non-significant. If a reduced model is considered, by testing if the band-recovery rates as well as the annual survival rates are homogeneous among post-strata (Model 1 vs Model 2a, Table 2.6e), the test statistic rejects this simplification (p<.0001).

Under Model 3, the differences in the estimated band-recovery rates between the two flyways are of the same order of magnitude as the standard errors. An overall test of the homogeneity of the band-recovery rates allowing for heterogeneous survival rates (Model 2b vs. Model 3, Table 2.6f) was conducted using the simple test. The test is marginally not rejected (p=.12), but the simple test is not fully efficient. One of the individual terms (1981, i=7) shows some heterogeneity (chi-square 6.21, 1 d.f., p<.01). A goodness-of-fit test to Model 2b gives a non-significant chi-square of 41.3 (41 d.f.) where the chi-square value and degrees of freedom are obtained by adding those from the goodness-of-fit test to Model 3 and the test of Model 2b vs. Model 3. Model 1 is rejected relative to Model 2b (p<.0001, Table 2.6g), just as it was relative to Model 2a.

In view of the consistent sign and magnitude of the differences between flyways in band-recovery rates (Model 3, Table 2.6b), it is worth investigating the ability of the tests to detect such a pattern

Table 2.6e
Test Model 1 vs. Model 2a

Overall test

i	χ^2	d.f.	
1	0.60	1	
2	3.56	1	
3	10.18	1	
4	2.14	1	
5	2.31	1	
6	7.51	1	
7	6.42	1	
8	2.08	1	
Total	34.80	8	p<.0001

Example of one subtest (i=1)

		Flyway P	Flyway E
$C_1^1+C_1^2$	15	6	9

Table 2.6f
Test Model 2b vs. Model 3

Overall test

i	χ^2	d.f.	
1	0.60	1	
2	0.02	1	
3	2.96	1	
4	0.00	1	
5	0.97	1	
6	1.58	1	
7	6.21	1	
8	0.38	1	
Total	12.72	8	p=.122

Example of one subtest (i=1)

		Flyway P	Flyway E
$R_{11}^1+R_{11}^2$	15	6	9

Table 2.6g
Test Model 1 vs. Model 2b

Overall test

i	χ^2	d.f.	
1	11.52	1	
2	14.56	1	
3	11.26	1	
4	9.00	1	
5	8.53	1	
6	4.56	1	
7	1.72	1	
Total	61.15	7	p<.0001

Example of one subtest (i=1)

		Flyway P	Flyway E
$Z_1^1+Z_1^2$	42	10	32

of differences, assuming it to be real. Suppose the Pacific and Eastern flyways had band-recovery rates of 0.016 and 0.022, respectively, in all years (near their average estimated values). The power function of the simple test of Model 2b vs Model 3 is approximated using a non-central chi-square distribution with 8 degrees of freedom and non-centrality parameter 9.57. This leads to a power of 58% when testing at the 5% level, and 69% when testing at the 10% level. Similarly, when the same assumptions are made, the asymptotic power function of the test of Model 1 vs. Model 2a has 8 degrees of freedom, a non-centrality parameter of 23.73, and gives a power of 96% when testing at the 5% level, and 98% when testing at the 10% level. Thus, although Model 2b was not rejected by the tests, this experiment provides only marginal power to detect the degree of difference in the band-recovery rates likely to have occurred, unless it is assumed that survival rates are the same in both flyways. If the actual band-recovery rates were 0.014 and 0.024, then the power of the test of Model 2b vs Model 3 is increased to 97% and 99% at the 5 and 10% levels, respectively. Now, even the simple test permits detection of this larger difference in recovery rates almost with certainty.

Model 2a was not rejected in favour of Model 3, indicating that there is no evidence of different survival rates between the two flyways. But suppose that the Pacific and Eastern flyways had annual survival rates of 0.65 and 0.75, respectively, in all years (near the averages of the estimates for Model 3). Then using the band-recovery rates from above and the observed number of releases, the asymptotic power function has 7 degrees of freedom, non-centrality parameter of

6.99, and yields a power of 43% when testing at the 5% level, and 57% when testing at the 10% level. If the survival rates were 0.65 and 0.80, then the power is 83% and 90% at the 5 and 10% levels, respectively. The current banding study permits detection of these larger differences in survival rates reasonably well, but has less than a 50% chance of detecting a difference of 0.10 or less.

Based upon these results, either Model 2a (homogeneous annual survival rates, heterogeneous band-recovery rates) or Model 2b (heterogeneous annual survival rates, homogeneous band-recovery rates) provide an adequate fit to the data. One possible reason for this may be the reduced power of the test of Model 2b vs. Model 3. As well, it may be that both the band-recovery and survival rates are different among post-strata, but the differences are not sufficiently large to be detected. It is unlikely that the differences between flyways in the survival rates exceeds 0.15 and in recovery rates exceeds 0.01.

2.7 DISCUSSION

Pollock and Raveling (1982) and Nichols *et al.* (1982) showed that heterogeneity can cause substantial bias in the parameter estimates when strata are ignored and the data analyzed using Model 1 of Brownie *et al.* (1985, Section 2.2), especially when the true survival and band-recovery rates are highly related as is usual in practice. However, in the special case where Model 2a holds (homogeneous annual survival rates, heterogeneous band-recovery rates) and the data are analyzed ignoring post-strata, the survival estimates are nearly unbiased and the band-recovery rates estimate the average recovery rates. In other cases, the bias can be eliminated and insight into post-stratum differences can be gained by using an appropriate post-release stratified analysis. The tradeoff is that post-stratum estimates are now based on fewer recoveries and have lower precision. If a fixed number of animals is split equally among *m* post-strata, then the variances of the estimators of the post-stratum-specific parameters under Model 3 will be about *m* times that of the estimators under a model ignoring post-strata. (The change in the other, more restrictive, models will be less.) In large banding studies, this loss of precision may be acceptable in return for a reduction in bias; in smaller studies, the variation of the estimators is probably so large that any additional error caused by bias could be ignored.

The results of this Chapter complement the methodology described by Pollock and Raveling (1982) and Nichols *et al.* (1982) for computing the bias and mean square error in estimates formed ignoring differences among post-stratum-specific parameters. For a given set of data, Model 3 of this Chapter can provide estimates of the required post-stratum-specific parameters, and, as shown in the example, the power results can be used to determine the degree of heterogeneity that is largely undetectable (e.g., that gives a power less than 75% at the 10% level). Then, the potential bias in the parameter estimates from a restricted model can be compared to their standard errors. If this ratio is large (e.g., greater than 1; Cochran, 1977, pp.12-15), a less stringent (larger) alpha level might be adopted so that the power to differentiate between models is increased. Caution is advised before accepting and using estimates from one of the reduced models, since undetected heterogeneity does not imply that it is absent or even small enough to avoid unacceptable bias in the estimates. A similar exercise can be carried out before experiments in which post-stratum heterogeneity is expected to exist and interest centres on these differences. In this case, the experimenter must make a guess at likely post-stratum-specific parameter values and the numbers of animals banded given the planned effort. The bias and power computation can then be carried out using the expected values computed using the formulae given in Figure 2.3 in place of the observable statistics. The experimenter can vary the proposed banding effort to ensure both a reasonable ability to detect differences and an acceptable precision of the estimates.

The models presented in this Chapter also provide a basis for the models in subsequent Chapters. In particular, the band-recovery rate is partitioned into its migration and band-recovery components for cases where stratification is based upon area of recovery.

Appendix 2.A

Estimated non-zero covariances

Non-zero covariances for Model 3

$$\hat{\mathrm{cov}}(\hat{f}_i^s, \hat{f}_j^t) \quad \text{when} \quad \begin{matrix} i=j \\ s=t \end{matrix} \quad = \left(\hat{f}_i^s\right)^2 \left[\frac{1}{R_i^s} - \frac{1}{N_i} + \frac{1}{C_i^s} - \frac{1}{T_i^s} \right]$$

$$\text{when} \quad \begin{matrix} i=j \\ s\neq t \end{matrix} \quad = - \hat{f}_i^s \hat{f}_i^t \left[\frac{1}{N_i} \right]$$

$$\hat{\mathrm{cov}}(\hat{S}_i^s, \hat{S}_j^t) \quad \text{when} \quad \begin{matrix} i=j \\ s=t \end{matrix} \quad = \left(\hat{S}_i^s\right)^2 \left[\frac{1}{R_i^s} - \frac{1}{N_i} + \frac{1}{R_{i+1}^s} - \frac{1}{N_{i+1}} + \frac{1}{Z_i^s} - \frac{1}{T_i^s} \right]$$

$$\text{when} \quad \begin{matrix} j=i+1 \\ s=t \end{matrix} \quad = - \hat{S}_i^s \hat{S}_{i+1}^s \left[\frac{1}{R_{i+1}^s} - \frac{1}{N_{i+1}} \right]$$

$$\text{when} \quad \begin{matrix} i=j \\ s\neq t \end{matrix} \quad = - \hat{S}_i^s \hat{S}_i^t \left[\frac{1}{N_i} + \frac{1}{N_{i+1}} \right]$$

$$\text{when} \quad \begin{matrix} j=i+1 \\ s\neq t \end{matrix} \quad = \hat{S}_i^s \hat{S}_{i+1}^t \left[\frac{1}{N_{i+1}} \right]$$

$$\hat{\mathrm{cov}}(\hat{f}_i^s, \hat{S}_j^t) \quad \text{when} \quad \begin{matrix} i=j \\ s=t \end{matrix} \quad = \hat{f}_i^s \hat{S}_i^s \left[\frac{1}{R_i^s} - \frac{1}{N_i} - \frac{1}{T_i^s} \right]$$

$$\text{when} \quad \begin{matrix} j=i-1 \\ s=t \end{matrix} \quad = - \hat{f}_i^s \hat{S}_{i-1}^s \left[\frac{1}{R_i^s} - \frac{1}{N_i} \right]$$

$$\text{when} \quad \begin{matrix} i=j \\ s\neq t \end{matrix} \quad = - \hat{f}_i^s \hat{S}_i^t \left[\frac{1}{N_i} \right]$$

$$\text{when} \quad \begin{matrix} j=i-1 \\ s\neq t \end{matrix} \quad = \hat{f}_i^s \hat{S}_{i-1}^t \left[\frac{1}{N_i} \right]$$

Appendix 2.A (cont.)

Non-zero covariances for Model 2a

$$\widehat{\mathrm{cov}}(\hat{f}_i^s, \hat{f}_j^t) \quad \text{when} \quad \begin{matrix} i=j \\ s=t \end{matrix} \quad = \left(\hat{f}_i^s\right)^2 \left[\frac{1}{\dot{R}_i} - \frac{1}{N_i} + \frac{1}{C_i^s} - \frac{1}{\dot{T}_i} \right]$$

$$\text{when} \quad \begin{matrix} i=j \\ s\neq t \end{matrix} \quad = \hat{f}_i^s \hat{f}_i^t \left[\frac{1}{\dot{R}_i} - \frac{1}{N_i} - \frac{1}{\dot{T}_i} \right]$$

$$\widehat{\mathrm{cov}}(\hat{S}_i, \hat{S}_j) \quad \text{when} \quad i=j \quad = \left(\hat{S}_i\right)^2 \left[\frac{1}{\dot{R}_i} - \frac{1}{N_i} + \frac{1}{\dot{R}_{i+1}} - \frac{1}{N_{i+1}} + \frac{1}{\dot{Z}_i} - \frac{1}{\dot{T}_i} \right]$$

$$\text{when} \quad j=i+1 \quad = - \hat{S}_i \hat{S}_{i+1} \left[\frac{1}{\dot{R}_{i+1}} - \frac{1}{N_{i+1}} \right]$$

$$\widehat{\mathrm{cov}}(\hat{f}_i^s, \hat{S}_j) \quad \text{when} \quad i=j \quad = \hat{f}_i^s \hat{S}_i \left[\frac{1}{\dot{R}_i} - \frac{1}{N_i} - \frac{1}{\dot{T}_i} \right]$$

$$\text{when} \quad j=i-1 \quad = - \hat{f}_i^s \hat{S}_{i-1} \left[\frac{1}{\dot{R}_i} - \frac{1}{N_i} \right]$$

Non-zero covariance for Model 2b

These must be found numerically.

Non-zero covariances for Model 1

These may be found using Brownie *et al.* (1985, pp. 18-19) by simply replacing R_i, C_i, and T_i by $\dot{R}_i$, $\dot{C}_i$, and $\dot{T}_i$ respectively, and multiplying by the factor 1/m whenever f_i appears since f_i is the band-recovery rate in each of the m post-strata.

Appendix 2.B
Derivation of the conditional distribution for the test of Model 2a vs. Model 3.

The derivation will be illustrated using the case when k=3, l=4, and m=2. The extension to more than two post-strata will be obvious.

The conditional distribution is found as:

$$P_{\text{Model 2a}}(\text{ MSS of Model 3 } \mid \text{ MSS of Model 2a})$$

$$= \frac{P_{\text{Model 2a}}(\{R_i^1, R_i^2\}\ i=1\ldots k,\ \{C_j^1, C_j^2\}\ j=1\ldots l-1\ )}{P_{\text{Model 2a}}(\{(R_i^1+R_i^2)\}\ i=1\ldots k-1,\ \{C_j^1, C_j^2\}\ j=1\ldots l\ )}\ .$$

The numerator may be factored, using the MSS from Table 2.4, into conditionally independent distributions by starting at the last release time and working backwards, or:

$$P(\{C_j^1, C_j^2\}\ j=k+1\ldots l-1 \mid \{R_i^1, R_i^2\}\ i=1\ldots k,\ \{C_j^1, C_j^2\}\ j=1..k)$$

$$\times\ P(\{C_k^1, C_k^2\} \mid \{R_i^1, R_i^2\}\ i=1\ldots k,\ \ \{C_j^1, C_j^2\}\ j=1\ldots k-1)$$

$$\times\ P(\{R_k^1, R_k^2\} \mid \{R_i^1, R_i^2\}\ i=1\ldots k-1,\ \{C_j^1, C_j^2\}\ j=1\ldots k-1)$$

$$\vdots$$

$$\times\ P(\{C_1^1, C_1^2\} \mid \{R_1^1, R_1^2\}\ )$$

$$\times\ P(\{R_1^1, R_1^2\}\ ).$$

Each of these distributions is either a binomial or a multinomial distribution:

$$P(\{C_j^1, C_j^2\}\ j=k+1\ldots l-1 \mid \{R_i^1, R_i^2\}\ i=1\ldots k,\ \{C_j^1, C_j^2\}\ j=1..k)$$

$$= \text{Multinomial}(\ T_{k+1}^1,\ \{\theta_v^1 \ /\ \sum_{j=k+1}^{l} \theta_j^1\}\ v=k+1\ldots l-1) \quad \times$$

$$\text{Multinomial}\left(T_{k+1}^{2},\ \{\theta_v^{2} \Big/ \sum_{j=k+1}^{l} \theta_j^{2}\}\ v=k+1\ldots l-1\right).$$

And:

$$P(\{C_v^1,C_v^2\} \mid \{R_i^1,R_i^2\}\ i=1\ldots v,\quad \{C_j^1,C_j^2\}\ j=1\ldots v-1)$$

$$= \text{Binomial}(\ T_v^1,\ \{f_v^1/\rho_v^1\}) \times \text{Binomial}(\ T_v^2,\ \{f_2^v/\rho_2^v\})$$

where $\rho_v^s = f_v^s + S_v f_{v+1}^s + \ldots + S_v S_{v+1} S_{v+2} \ldots \theta_l^s$ is the total probability of observing animals released in year v in post-stratum s under Model 2a.

And:

$$P(\{R_v^1,R_v^2\} \mid \{R_i^1,R_i^2\}\ i=1\ldots v-1,\ \{C_j^1,C_j^2\}\ j=1\ldots v-1)$$

$$= \text{Trinomial}(\ N_v,\ \{\rho_v^1,\ \rho_v^2\}).$$

The denominator can be factored into slightly different but similar independent multinomial or binomial conditional distributions, or:

$$P(\{C_j^1,C_j^2\}\ j=k+1\ldots l \mid \{R_i^1+R_i^2\}\ i=1\ldots k,\ \{C_j^1,C_j^2\}\ j=1..k)$$

$$\times\ P(\{C_k^1,C_k^2\} \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\quad \{C_j^1,C_j^2\}\ j=1\ldots k-1)$$

$$\times\ P((R_k^1+R_k^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k-1,\ \{C_j^1,C_j^2\}\ j=1\ldots k-1)$$

$$\vdots$$

$$\times\ P(\{C_1^1,C_1^2\} \mid (R_1^1+R_1^2))$$

$$\times\ P((R_1^1+R_1^2)).$$

The individual distributions can now be identified:

$$P(\{C_j^1,C_j^2\}\ j=k+1\ldots l \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{C_j^1,C_j^2\}\ j=1\ldots k)$$

$$= \text{Multinomial}\left(T^1_{k+1}+T^2_{k+1},\ \{\theta^s_v \Big/ \sum_{j=k+1}^{l} (\theta^1_j + \theta^2_j)\}\ s=1\ldots2,\ v=k+1\ldots l\right).$$

And:

$$P(\{C^1_v, C^2_v\} \mid \{(R^1_i+R^2_i)\}\ i=1\ldots v,\quad \{C^1_j, C^2_j\}\ j=1\ldots v-1)$$

$$= \text{Trinomial}\left(T^1_v + T^2_v,\ \{f^1_v/(\rho^1_v+\rho^2_v),\ f^2_v/(\rho^1_v+\rho^2_v)\}\right).$$

And:

$$P((R^1_v+R^2_v) \mid \{(R^1_i+R^2_i)\}\ i=1\ldots v-1,\ \{C^1_j, C^2_j\}\ j=1\ldots v-1)$$

$$= \text{Binomial}\left(N_v\ ,\{\rho^1_v+\rho^2_v\}\right).$$

The ratio of the joint distributions of the two MSS can now be evaluated, and, as expected, all the nuisance parameters (the annual survival and band-recovery rates) cancel. The test is then based upon the conditional distribution:

$$= \frac{\binom{T^1_{k+1}}{C^1_{k+1},\ C^1_{k+2}\ ,\ldots,\ C^1_l}\binom{T^2_{k+1}}{C^2_{k+1},\ C^2_{k+2}\ ,\ldots,\ C^2_l}}{\binom{T^1_{k+1}+T^2_{k+1}}{C^1_{k+1},\ C^1_{k+2}\ ,\ldots,\ C^1_l,\ C^2_{k+1},\ C^2_{k+2}\ ,\ldots,\ C^2_l}} \prod_{i=1}^{k} \binom{R^1_i + R^2_i}{R^1_i\ ,\ R^2_i} \prod_{i=1}^{k} \frac{\binom{T^1_i}{C^1_i}\binom{T^2_i}{C^2_i}}{\binom{T^1_i + T^2_i}{C^1_i\ ,\ C^2_i}}$$

Further algebraic manipulation, and noting that

$$T^s_i - C^s_i = T^s_{i+1} - R^s_{i+1}$$

leads to the distribution (with s=2) given in Table 2.5. The *i*th term of the product in Table 2.5 is the distribution that results when Fisher's exact test for homogeneous binomial proportions is extended to the multinomial case (Rao, 1973, p. 412), and hence the contingency table test in Table 2.5 is clearly equivalent to this exact test in large samples.

Appendix 2.C
Derivation of the conditional distribution used in the test of Model 1 vs. Model 2a

The derivation will be illustrated using the case when k=3, l=4, and m=2. The extension to more than two post-strata will be obvious.

The conditional distribution is found as:

$$P_{\text{Model 1}}(\text{ MSS of Model 2a } | \text{ MSS of Model 1})$$

$$= \frac{P_{\text{Model 1}}(\ \{(R_i^1+R_i^2)\}\ i=1...k-1,\quad \{C_j^1,C_j^2\},\ j=1...l\ )}{P_{\text{Model 1}}(\ \{(R_i^1+R_i^2)\}\ i=1...k,\quad \{(C_j^1+C_j^2)\},\ j=1...l-1\ )}.$$

The numerator may be factored, using the MSS from Table 2.4, into the conditionally independent distributions by starting at the last release and working backwards:

$$P(\{C_j^1,C_j^2\}\ j=k+1...l\ |\{(R_i^1+R_i^2)\}\ i=1...k,\ \{C_j^1,C_j^2\}\ j=1..k)$$

$$\times\ P(\{C_k^1,C_k^2\}\ \ |\ \ \{(R_i^1+R_i^2)\}\ i=1...k,\quad \{C_j^1,C_j^2\}\ j=1...k-1)$$

$$\times\ P((R_k^1+R_k^2)\ \ |\ \ \{(R_i^1+R_i^2)\}\ i=1...k-1,\ \{C_j^1,C_j^2\}\ j=1...k-1)$$

$$\vdots$$

$$\times\ P(\{C_1^1,C_1^2\}\ \ |\ \ (R_1^1+R_1^2)\ )$$

$$\times\ P((R_1^1+R_1^2)\ ).$$

Each of these distriubutions is either a binomial, trinomial or multinomial distribution:

$$P(\{C_j^1,C_j^2\}\ j=k+1...l\ |\ \{(R_i^1+R_i^2)\}\ i=1...k,\ \{C_j^1,C_j^2\}\ j=1..k)$$

$$= \text{Multinomial}(\ T_{k+1}^1+T_{k+1}^2,\ \{\frac{s_k s_{k+1}..s_{v-1} f_v}{\sum_{j=k+1}^{l} 2\, s_k s_{k+1}..s_{j-1} f_j}\}\ \begin{matrix} s=1...2 \\ v=k+1...l \end{matrix}\ ).$$

And:

$$P(\{C_v^1, C_v^2\} \mid \{(R_i^1+R_i^2)\}\ i=1\ldots v,\ \ \{C_j^1, C_j^2\}\ j=1\ldots v-1)$$

$$= \text{Trinomial}(\ T_v^1+T_v^2\ ,\ \{\frac{f_v}{2\rho_v}\ ,\ \frac{f_v}{2\rho_v}\})$$

where $\rho_v = f_v + S_v f_{v+1} + \ldots + S_v S_{v+1} S_{v+2} \ldots \theta_l$ is the total probability of observing animals released in year v in post-stratum s under Model 1.

And:

$$P((R_v^1+R_v^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots v-1,\ \{C_j^1, C_j^2\}\ j=1\ldots v-1)$$

$$= \text{Binomial}(\ N_v\ ,\ \{2\rho_v\})$$

The denominator can be factored into slightly different, but similar, independent multinomial conditional distributions, or:

$$P(\{(C_j^1+C_j^2)\}\ j=k+1..l-1 \mid \{R_i^1+R_i^2\}\ i=1\ldots k,\ \{C_j^1+C_j^2\}\ j=1..k)$$

$$\times\ P((C_k^1+C_k^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \ \{(C_j^1+C_j^2)\}\ j=1\ldots k-1)$$

$$\times\ P((R_k^1+R_k^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k-1,\ \{(C_j^1+C_j^2)\}\ j=1\ldots k-1)$$

$$\vdots$$

$$\times\ P((C_1^1+C_1^2) \mid (R_1^1+R_1^2)\ \ )$$

$$\times\ P((R_1^1+R_1^2)\ ).$$

The individual distributions can now be identified:

$$P(\{(C_j^1+C_j^2)\}\ j=k+1..l-1 \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{(C_j^1+C_j^2)\}\ j=1..k)$$

$$= \text{Multinomial}(\ T_{k+1}^1+T_{k+1}^2,\ \{\frac{S_k S_{k+1} \ldots S_{v-1} f_v}{\sum_{j=k+1}^{l} S_k S_{k+1} \ldots S_{j-1} f_j^1}\}\ v=k+1\ldots l\ ).$$

And:

$$P\left((C_v^1+C_v^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots v,\ \{(C_j^1+C_j^2)\}\ j=1\ldots v-1\right)$$

$$= \text{Binomial}\left(T_v^1+T_v^2,\ \left\{\frac{f_v}{\rho_v}\right\}\right).$$

And:

$$P\left((R_v^1+R_v^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots v-1,\ \{(C_j^1+C_j^2)\}\ j=1\ldots v-1\right)$$

$$= \text{Binomial}\left(N_v,\ \{2\rho_v\}\right).$$

The ratio of the joint distributions of the two MSS can now be evaluated, and, as expected, all the nusiance parameters cancel. The test is based upon the conditional distribution:

$$\prod_{j=1}^{l} \begin{pmatrix} C_j^1 + C_j^2 \\ C_j^1\ ,\ C_j^2 \end{pmatrix} \times 2^{-\sum_{j=1}^{l} (C_j^1+C_j^2)}$$

The extension to m strata is obvious:

$$\prod_{j=1}^{l} \begin{pmatrix} C_j^1 +\ldots+ C_j^m \\ C_j^1\ ,\ldots,\ C_j^m \end{pmatrix} \times m^{-\sum_{j=1}^{l} (C_j^1+\ldots+C_j^m)}$$

The i^{th} term of the product is the distribution of the exact test for homogeneous multinomial proportions, and hence the contingency table test in Table 2.5 is clearly equivalent to the exact test in large samples.

Appendix 2.D
Derivation of the conditional distribution used in the test of Model 1 vs. Model 2b

The derivation will be illustrated using the case when k=3, l=4, and m=2. The extension to more than two post-strata will be obvious.

The conditional distribution is found as:

$$P_{\text{Model 1}}(\text{ MSS of Model 2b} \mid \text{MSS of Model 1})$$

$$= \frac{P_{\text{Model 1}}(\{(C_j^1+C_j^2)\}\ j=1\ldots k,\ \{C_j^1,C_j^2\}\ j=k+1..l,\ \{Z_i^1,Z_i^2\},\ i=1\ldots k-1)}{P_{\text{Model 1}}(\{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{(C_j^1+C_j^2)\},\ j=1\ldots l-1\ )}\ .$$

The distribution of the numerator is simplified by first transforming to an equivalent set of MSS:

$$\{\{(C_j^1+C_j^2)\}\ j=1\ldots k,\ \{(C_j^1,C_j^2)\}\ j=k+1\ldots l-1,\ \{Z_i^1\}\ i=1\ldots k,\ \{(R_i^1+R_i^2)\},\ i=1\ldots k\}$$

Then the numerator may be factored into conditionally independent multinomial distributions:

$$P(\{C_j^1,C_j^2\}\ j=k+1..l-1 \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{(C_j^1+C_j^2)\}\ j=1..k,\ \{Z_i^1\}i=1\ldots k)$$

$$\times\ P(Z_k^1 \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{(C_j^1+C_j^2)\}\ j=1\ldots k,\ \{Z_i^1\}\ i=1\ldots k-1\ )$$

$$\times\ P((C_k^1+C_k^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k,\ \{(C_j^1+C_j^2)\}\ j=1\ldots k-1,\ \{Z_i^1\}\ i=1\ldots k-1\ )$$

$$\times\ P((R_k^1+R_k^2) \mid \{(R_i^1+R_i^2)\}\ i=1\ldots k-1,\ \{(C_j^1+C_j^2)\}\ j=1\ldots k-1,\ \{Z_i^1\}\ i=1\ldots k-1\ )$$

$$\vdots$$

$$\times\ P(\ Z_1^1 \mid (R_1^1+R_1^2),\ (C_1^1+C_1^2)\ )$$

$$\times\ P((C_1^1+C_1^2) \mid (R_1^1+R_1^2)\ )$$

$$\times\ P((R_1^1+R_1^2)\ ).$$

The individual distributions can now be identified:

$$P(\{C_j^1,C_j^2\}\ j=k+1..l-1 \mid \{(R_i^1+R_i^2)\}\ i=1...k,\ \{C_j^1+C_j^2\}\ j=1...k,\ \{Z_i^1\}\ i=1...k)$$

$$= \text{Multinomial}\left(Z_k^s,\ \{\frac{s_k s_{k+1}..s_{v-1} f_v}{\sum_{j=k+1}^{l} s_k s_{k+1}..s_{j-1} f_j}\}\ v=k+1...l-1\right) \quad \text{for } s=1..2$$

And:

$$P(\{Z_v^1\} \mid \{(R_i^1+R_i^2)\}\ i=1...v,\ \{(C_j^1+C_j^2)\}\ j=1...v,\ \{Z_i^1\}\ i=1...v-1\ )$$

$$= \text{Binomial}(\ Z_v^1+Z_v^2,\ \{.5\}).$$

And:

$$P(\{(C_v^1+C_v^2)\} \mid \{(R_i^1+R_i^2)\}\ i=1...v,\ \{(C_j^1+C_j^2)\}\ j=1...v-1,\ \{Z_i^1\}\ i=1...v-1)$$

$= \text{Binomial}(\ T_v^1+T_v^2,\ \{\frac{f_v}{\rho_v}\})$ where ρ_v was defined in Appendic 2.C.

And:

$$P((R_v^1+R_v^2) \mid \{(R_i^1+R_i^2)\}\ i=1...v-1,\ (\{C_j^1+C_j^2\}\ j=1...v-1,\ \{Z_i^1\}\ i=1...v-1)$$

$$= \text{Binomial}(\ N_v,\ \{2\rho_v\}).$$

The denominator was expanded in Appendix 2.C. The ratio of the distributions of the two MSS can now be evaluated. The test is then based upon the conditional distribution:

$$\prod_{j=1}^{k-1} \frac{\binom{Z_j^1 + Z_j^2}{Z_j^1\ ,\ Z_j^2}}{2^{(Z_j^1+Z_j^2)}} \times \prod_{j=k+1}^{l} \frac{\binom{C_j^1 + C_j^2}{C_j^1\ ,\ C_j^2}}{2^{(C_j^1+C_j^2)}}$$

The extension to m strata is obvious:

$$\prod_{j=1}^{k-1} \frac{\binom{Z_j^1+\ldots+Z_j^m}{Z_j^1,\ldots,Z_j^m}}{m^{(Z_j^1+\ldots+Z_j^m)}} \times \prod_{j=k+1}^{l} \frac{\binom{C_j^1+\ldots+C_j^m}{C_j^1,\ldots,C_j^m}}{m^{(C_j^1+\ldots+C_j^m)}}$$

The i^{th} term of the product is the distribution of the exact test for homogeneous multinomial proportions, and hence the contingency table test in Table 2.5 is clearly equivalent to the exact test in large samples.

Appendix 2.E
Derivation of the conditional distribution used in the goodness-of-fit test for Model 3

The conditional distribution is found as:

$$P_{\text{Model 3}}(\text{ Data } \mid \text{ MSS of Model 3})$$

$$= \frac{P_{\text{Model 3}}(\ \{R^s_{ij}\}\ i=1\ldots k,\ j=i\ldots l,\ s=1\ldots m\ )}{P_{\text{Model 3}}(\ \{\{R^s_i\}\ i=1\ldots k,\ \{C^s_j\}\ j=1\ldots l-1\}\ s=1\ldots m)}$$

The numerator is the product of independent multinomial distributions (Section 1.3) and the denominator can be factored into conditionally independent multinomial distributions in much the same way as in Appendix 2.B. The test is based upon the conditional distribution:

$$\prod_{s=1}^{m} \frac{\displaystyle\prod_{i=1}^{k} \binom{R^s_i}{R^s_{ii},\ R^s_{i,i+1},\ldots,\ R^s_{il}}}{\displaystyle\prod_{j=1}^{k} \binom{T^s_j}{C^s_j} \times \binom{T^s_{k+1}}{C^s_{k+1}\ ,\ldots,\ C^s_l}} .$$

Noting that:

$$T^s_{i+1} - R^s_{i+1} = T^s_i - C^s_i$$

$$R^s_{ij+} = R^s_{i+1,j+} - R^s_{i+1,j}$$

the distribution may be rewritten as:

$$\prod_{s=1}^{m} \prod_{i=2}^{k} \frac{\binom{R^s_i}{R^s_{ii},\ R^s_{i,i+1},\ldots,\ R^s_{il}} \binom{T^s_i - R^s_i}{R^s_{ii+}-R^s_{ii},\ldots,\ R^s_{il+}-R^s_{il}}}{\binom{T^s_i}{R^s_{ii+}\ ,\ldots,\ R^s_{il+}}}$$

The $(s,i)^{\text{th}}$ term of the product is the distribution of the exact test for homogeneous multinomial proportions, and hence the contingency table test in Table 2.5 is clearly equivalent to the exact test in large samples.

Chapter 3

The Partial- and Complete-Fidelity Models

Summary

The models of Chapter 2 are generalized by explicitly modelling the migration process previously hidden in the 'band-recovery rates'. In the Partial-Fidelity Model, animals are assumed to be faithful to their pre-stratum of release but choose the post-stratum in each year of migration independently of that chosen in previous years. In the Complete-Fidelity Model, animals are assumed to be faithful to both the pre-stratum of release and the post-stratum of migration for all years the animal is alive. In both models, ordinary band-recovery data is shown to be inadequate for inferences about the fundamental and derived parameters - the migration rates are confounded with the band-recovery rates. A modification to the experimental design in both models involving additional live sightings of animals in the post-strata is shown to be sufficient to allow full inference on all parameters. A numerical example, using simulated data, is presented for each model using this modified design.

Chapter 3
The Partial- and Complete-Fidelity Models

3.1 INTRODUCTION

In this and subsequent chapters, the models of Chapter 2 are generalized by explicitly modelling the migration process. In the previous models, the post-stratum band-recovery rates included a hidden migration component in those cases where recoveries were stratified by area of recovery. Now the migration component will be explicitly modelled by introducing parameters representing the migration rates from the pre- to post-strata. Naturally, additional assumptions must be made about the migration process. Two models, the Partial- and Complete-Fidelity Models each making different assumptions about the fidelity of the animals to the seasonal migration routes, are considered.

In the Partial-Fidelity Model, it is assumed that the animal is faithful to the pre-stratum of release but chooses the post-stratum independently of the choice in previous years. For example, Anderson and Henny (1972, p.86) state that female redheads (*Aythya americana*) have fidelity to their breeding areas (pre-strata) but may choose a different wintering area (post-strata) each year perhaps based upon environmental conditions present during migration. Banding takes place in the breeding areas. Recoveries occur on the wintering areas. Interest lies in the migration patterns from the breeding areas to the wintering areas. (This model is also applicable if the animals are pre-stratified by, for example, sex, and interest lies on the different migration patterns to wintering areas by the different sexes. Here the animal is "faithful" to its sex at banding, rather than the breeding area at banding.)

In the Complete-Fidelity Model, it is instead assumed that the animal is faithful to both its pre-stratum of release and to its post-stratum of migration in all years between release and recovery. For example, some species of birds home precisely to both their breeding sites and wintering sites each year. Banding takes place in the breeding areas. Recoveries occur on the wintering areas. Interest again lies in the migration patterns from breeding areas to wintering areas.

Chapman and Junge (1956) and Darroch (1961) used capture-recapture models to examine migration patterns from pre-strata (where marked animals were released) to post-strata (where animals were recaptured). However, they did not extend their results to more than two sampling occasions, and so did not have to consider the fidelity assumption. Arnason (1972, 1973) and Seber (1982, p. 555) extended these results to more than two sampling times, but considered the special case of migrations among a constant set of strata from year to year, i.e., an Internal-Transfer Model (Chapter 5). As well, in capture-recapture models, the act of capturing an animal is assumed to occur at a point in time while in band-recovery models, recoveries occur over a period of time. For example, recoveries of bands from ducks occur primarily from hunters and occur over several months. For highly exploited species, the band-recovery formulation in this paper is more appropriate. The methods of Brownie *et al.* (1985) can be used when the animals are pre-stratified at the time of release and each pre-stratum has its own unique survival and band-recovery rates. An implicit assumption of these models is that the animals are faithful to their pre-stratum of release and it is further assumed that these pre-stratum specific rates are applicable to all animals in the pre-stratum. In the case of migration, this is doubtful since an animal's survival and band-recovery rates likely depend upon the migration destination. Hence, as shown in Chapter 2, a post-release stratification analysis is also needed.

Both the Partial- and Complete-Fidelity Models are discussed in this Chapter since the modelling process and methodology are similar for both models. I first discuss the Partial-Fidelity Model (since it is likely to be more useful than the Complete-Fidelity Model) and show that ordinary band-recovery data are inadequate for all but estimation of the survival rates over all post-strata and the harvest-derivation rates since not all parameters are identifiable. The assumptions required for parameter identification and for testing hypotheses about the parameters of the model are determined and their consequences examined. I then show that a change to the experimental design to include live re-sightings of the animals in addition to recoveries in each post-stratum, allows estimation of more parameters and testing of hypotheses about the parameters while making fewer assumptions. The Complete-Fidelity Model is then examined and again ordinary band-recovery data are found to be inadequate. The same modification to the experimental design is shown to allow for estimation and hypothesis testing. Finally, an illustration of the results of this Chapter is presented and discussed.

3.2 NOTATION

Let there be k years of releases, l years of recovery, a pre-strata where banding occurs, and b post-strata where recoveries occur. For completeness, all parameters and statistics required for the extended experiments involving live re-sightings, discussed in Sections 3.4 and 3.6, are also included.

Fundamental Parameters

A dot in a superscript or a subscript of a parameter indicates that the parameter is the same for all values of the index.

N_i^{s*} = true population size of pre-stratum s in year i

$M_i^{s\cdot}$ = total emigration rate in year i of animals that were released in pre-stratum s to any of the post-strata where recoveries occur.

$$0 \le M_i^{s\cdot} \le 1$$

m_i^{st} = relative emigration rate in year i to post-strata where recoveries occur of animals released in pre-stratum s to post-stratum t.

$$0 \le m_i^{st} \le 1, \sum_{t=1}^{b} m_i^{st}=1$$

f_i^{st} = band-recovery rate of animals released in pre-stratum s and recovered in post-stratum t in year i.

$$0 \le f_i^{st} \le 1$$

p_i^{st} = sighting rate of animals released in pre-stratum *s* and sighted in post-stratum *t* in year *i*.

$0 \le p_i^{st} \le 1$

λ_i^{st} = band-reporting rate of animals released in pre-stratum *s* and recovered in post-stratum *t* in year *i*.
(This is a component of the band-recovery rate as discussed by Brownie *et al.*, 1985, Section 2.1)

$0 \le \lambda_i^{st} \le 1$

S_i^{st} = post-stratum specific survival rate for animals released from pre-stratum *s* which migrate to post-stratum *t* between the time of banding in year *i* and the time of banding in year *i*+1.

$0 \le S_i^{st} \le 1$

Derived Parameters

$S_i^{s\cdot}$ = net survival rate for animals released from pre-stratum *s* over all post-strata between the time of banding in year *i* and the time of banding in year *i*+1.

$$S_i^{s\cdot} = \sum_{t=1}^{b} M_i^{st} m_i^{st} S_i^{st} + \begin{array}{l}\text{migration to and survival in} \\ \text{post-strata where no recoveries occur}\end{array}$$

I_i^{st} = the relative immigration rate of animals into post-stratum *t* from pre-stratum *s* in year *i*.

$$I_i^{st} = \frac{N_i^{s*} \cdot M_i^{s\cdot} m_i^{st}}{\sum_{s=1}^{a} N_i^{s*} \cdot M_i^{s\cdot} m_i^{st}}$$

D_i^{st} = the relative harvest-derivation rates of animals from pre-stratum *s* within post-stratum *t* in year *i*.

$$D_i^{st} = \frac{N_i^{s*} \cdot M_i^{s\cdot} m_i^{st} f_i^{st} \,/\, \lambda_i^{st}}{\sum_{s=1}^{a} N_i^{s*} \cdot M_i^{s\cdot} m_i^{st} f_i^{st} \,/\, \lambda_i^{st}}$$

ρ_i^{st} = total probability that a banded animal from pre-stratum *s* in year *i* will be recovered or sighted in post-stratum *t* in or after year *i*. The parametric form will depend upon the model considered and is presented in Appendix 3.A for the Partial-Fidelity Model and Appendix 3.D for the Complete-Fidelity Model.

Statistics

A dot in a superscript or a subscript of a statistic indicates a total summed over all values of the index.

N_i^s = number of animals banded and released from pre-stratum *s* in year *i*. It is assumed that the band used identifies at least the year of banding and the pre-stratum. In practice, individually labelled bands are often used.

R_{ij}^{st} = number of animals released in pre-stratum *s* in year *i* which are recovered in post-stratum *t* in year *j*.

R_{ij+}^{st} = number of animals released in pre-stratum *s* in year *i* or earlier which are recovered in post-stratum *t* in year *j*.

$$R_{ij+}^{st} = R_{1j}^{st} + R_{2j}^{st} + \ldots + R_{ij}^{st}$$

A_{ij}^{st} = number of animals released in pre-stratum *s* in year *i* that are recovered **AND** sighted in post-stratum *t* in year j.

B_{ij}^{st} = number of animals released in pre-stratum *s* in year *i* that are recovered **BUT** not sighted in post-stratum *t* in year *j*.

W_{ij}^{st} = number of animals released in pre-stratum *s* in year *i* that are sighted **WITHOUT** being recovered in post-stratum *t* in year *j*.

W_{ijv}^{stu} =number of animals released in pre-stratum *s* in year *i* that are sighted **WITHOUT** being recovered in post-stratum *t* in year *j* and are NEXT sighted or recovered in post-stratum *u* in year *v*.

T_i^{st} = total number of animals from pre-stratum *s* recovered in post-stratum *t* that were known to be alive at time *i* and were recovered or sighted at or after time *i*.

Z_i^{st} = total number of animals from pre-stratum *s* recovered in post-stratum *t* that were known to be alive at time *i* and were recovered or sighted after time *i*.

Chapter 2 illustrates examples of the computation of the *T* and *Z* statistics from recovery matrices. The following relationships also hold among these statistics:

$$R_{ij}^{st} = A_{ij}^{st} + B_{ij}^{st}$$

$$T_1^{st} = R_{1\cdot}^{st} + W_{1\cdot}^{st} - W_{1\cdot\cdot}^{st\cdot}$$

$$T_i^{st} = T_{i-1}^{st} + (R_{i\cdot}^{st} + W_{i\cdot}^{st} - W_{i\cdot\cdot}^{st\cdot}) - (R_{\cdot,i-1}^{st} + W_{\cdot,i-1}^{st} - W_{\cdot,i-1,\cdot}^{st\cdot})$$

$$Z_i^{st} = T_i^{st} - (R_{\cdot i}^{st} + W_{\cdot i}^{st} - W_{\cdot i\cdot}^{st\cdot}) = T_{i+1}^{st} - (R_{i+1,\cdot}^{st} + W_{i+1,\cdot}^{st} - W_{i+1,\cdot,\cdot}^{st\cdot})$$

3.3 THE PARTIAL-FIDELITY MODEL USING ORDINARY BAND-RECOVERY DATA

The Partial-Fidelity Model is applicable when animals are banded and released in pre-strata and migrate each year to post-strata from which some bands are recovered. The animals are assumed always to return to their pre-stratum of release, but may choose a different post-stratum each year. Interest focuses on the migration rates from the pre-strata to the post-strata.

In this section, the use of ordinary band-recovery data in the Partial-Fidelity Model will be examined since it is important to understand exactly what information can be extracted from past or future ordinary banding studies. The assumptions and model parameters (along with their interpretations) that are required in the Partial-Fidelity Model are first outlined. It is shown that, unfortunately, ordinary band-recovery data are inadequate except for inference on the net survival and harvest-derivation rates. Since it may not be feasible to collect additional data, I then indicate what further assumptions are required for inferences about the other parameters of the model while remaining in an ordinary band-recovery context. The validity of these assumptions can only be assessed on biological grounds.

3.3.1 ASSUMPTIONS

The usual assumptions of band-recovery models as outlined in Section 1.1.3 are made. As well, it is assumed that:

- the banding process selects a simple random sample of animals from each pre-stratum. In particular, the banding process is not post-stratum selective, i.e., the proportion of banded animals is expected to be the same within a given pre-stratum across the groups what will emigrate to the various post-strata.
- animals retain their pre-stratum identification. Hence, if the breeding areas are the pre-strata, it is assumed that the animals are faithful to their breeding areas. If the pre-strata are permanent attributes of an animal (e.g., sex), this assumption is clearly true.
- emigration is Markovian. Emigration rates depend only upon the calendar year and not upon the (unknown) past migrations of the animals.
- the post-stratum is unique and correctly identified for each recovered animal.

· the band-recovery rates may depend upon the pre-stratum, the post-stratum, and the year of recovery, but not upon an animal's (unknown) past migration pattern.

· independent estimates of the population sizes (or the relative population sizes) are available.

· independent estimates of the band-reporting rates are available.

· the same number of years of releases are performed in all pre-strata, and the same number of years of recovery are performed in all post-strata. This assumption may be relaxed, but the notation becomes complex.

3.3.2 MODEL AND INTERPRETATION OF PARAMETERS

The yearly recoveries from each years releases can be displayed as shown in Figure 3.3.2a. Under the assumptions of Section 3.3.1, the yearly recoveries from each year's releases from each pre-stratum can be modelled as independent multinomial distributions along the lines of Chapter 2. The expected number of band-recoveries under this model can be put into a matrix form, as shown (Figure 3.3.2b) in the case of k=3 years of banding, l=4 years of recoveries, a=2 pre-strata where banding occurred, and b=2 post-strata where recoveries occurred. The expected number of bands never recovered is not shown. A numerical example using the parameters of Table 1.5a, assuming that these rates are constant over time, is shown in Figure 3.3.2c and is discussed below. It is assumed that animals only from the first two pre-strata are banded, and that recoveries are obtained from only the first two post-strata; this corresponds to Case II of Table 1.5a.

Figure 3.3.2a

Illustration of the number of recoveries in the Partial-Fidelity Model using ordinary band-recovery data in the case of k=3 year of releases, l=4 years of recoveries, a=2 pre-strata, and b=2 post-strata

Recoveries of pre-stratum 1 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	N_1^1	R_{11}^{11}	R_{12}^{11}	R_{13}^{11}	R_{14}^{11}	R_{11}^{12}	R_{12}^{12}	R_{13}^{12}	R_{14}^{12}
2	N_2^1		R_{22}^{11}	R_{23}^{11}	R_{24}^{11}		R_{22}^{12}	R_{23}^{12}	R_{24}^{12}
3	N_3^1			R_{33}^{11}	R_{34}^{11}			R_{33}^{12}	R_{34}^{12}

Recoveries of pre-stratum 2 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	N_1^2	R_{11}^{21}	R_{12}^{21}	R_{13}^{21}	R_{14}^{21}	R_{11}^{22}	R_{12}^{22}	R_{13}^{22}	R_{14}^{22}
2	N_2^2		R_{22}^{21}	R_{23}^{21}	R_{24}^{21}		R_{22}^{22}	R_{23}^{22}	R_{24}^{22}
3	N_3^2			R_{33}^{21}	R_{34}^{21}			R_{33}^{22}	R_{34}^{22}

Figure 3.3.2b

Expected number of recoveries in the Partial-Fidelity Model using ordinary band-recovery data in the case of k=3 years of banding, l=4 years of recovery, a=2 pre-strata with banding, and b=2 post-strata with recoveries

Expected recoveries of pre-stratum 1 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year				Post-stratum 2 recoveries by year			
		1	2	3	4	1	2	3	4
1	N_1^1	$N_1^1 M_1^{1\cdot} m_1^{11} f_1^{11}$	$N_1^1 S_1^{1\cdot} M_2^{1\cdot} m_2^{11} f_2^{11}$	$N_1^1 S_1^{1\cdot} S_2^{1\cdot} M_3^{1\cdot} m_3^{11} f_3^{11}$	$N_1^1 S_1^{1\cdot} S_2^{1\cdot} S_3^{1\cdot} M_4^{1\cdot} m_4^{11} f_4^{11}$	$N_1^1 M_1^{1\cdot} m_1^{12} f_1^{12}$	$N_1^1 S_1^{1\cdot} M_2^{1\cdot} m_2^{12} f_2^{12}$	$N_1^1 S_1^{1\cdot} S_2^{1\cdot} M_3^{1\cdot} m_3^{12} f_3^{12}$	$N_1^1 S_1^{1\cdot} S_2^{1\cdot} S_3^{1\cdot} M_4^{1\cdot} m_4^{12} f_4^{12}$
2	N_2^1		$N_2^1 M_2^{1\cdot} m_2^{11} f_2^{11}$	$N_2^1 S_2^{1\cdot} M_3^{1\cdot} m_3^{11} f_3^{11}$	$N_2^1 S_2^{1\cdot} S_3^{1\cdot} M_4^{1\cdot} m_4^{11} f_4^{11}$		$N_2^1 M_2^{1\cdot} m_2^{12} f_2^{12}$	$N_2^1 S_2^{1\cdot} M_3^{1\cdot} m_3^{12} f_3^{12}$	$N_2^1 S_2^{1\cdot} S_3^{1\cdot} M_4^{1\cdot} m_4^{12} f_4^{12}$
3	N_3^1			$N_3^1 M_3^{1\cdot} m_3^{11} f_3^{11}$	$N_3^1 S_3^{1\cdot} M_4^{1\cdot} m_4^{11} f_4^{11}$			$N_3^1 M_3^{1\cdot} m_3^{12} f_3^{12}$	$N_3^1 S_3^{1\cdot} M_4^{1\cdot} m_4^{12} f_4^{12}$

Expected recoveries of pre-stratum 2 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year				Post-stratum 2 recoveries by year			
		1	2	3	4	1	2	3	4
1	N_1^2	$N_1^2 M_1^{2\cdot} m_1^{21} f_1^{21}$	$N_1^2 S_1^{2\cdot} M_2^{2\cdot} m_2^{21} f_2^{21}$	$N_1^2 S_1^{2\cdot} S_2^{2\cdot} M_3^{2\cdot} m_3^{21} f_3^{21}$	$N_1^2 S_1^{2\cdot} S_2^{2\cdot} S_3^{2\cdot} M_4^{2\cdot} m_4^{21} f_4^{21}$	$N_1^2 M_1^{2\cdot} m_1^{22} f_1^{22}$	$N_1^2 S_1^{2\cdot} M_2^{2\cdot} m_2^{22} f_2^{22}$	$N_1^2 S_1^{2\cdot} S_2^{2\cdot} M_3^{2\cdot} m_3^{22} f_3^{22}$	$N_1^2 S_1^{2\cdot} S_2^{2\cdot} S_3^{2\cdot} M_4^{2\cdot} m_4^{22} f_4^{22}$
2	N_2^2		$N_2^2 M_2^{2\cdot} m_2^{21} f_2^{21}$	$N_2^2 S_2^{2\cdot} M_3^{2\cdot} m_3^{21} f_3^{21}$	$N_2^2 S_2^{2\cdot} S_3^{2\cdot} M_4^{2\cdot} m_4^{21} f_4^{21}$		$N_2^2 M_2^{2\cdot} m_2^{22} f_2^{22}$	$N_2^2 S_2^{2\cdot} M_3^{2\cdot} m_3^{22} f_3^{22}$	$N_2^2 S_2^{2\cdot} S_3^{2\cdot} M_4^{2\cdot} m_4^{22} f_4^{22}$
3	N_3^2			$N_3^2 M_3^{2\cdot} m_3^{21} f_3^{21}$	$N_3^2 S_3^{2\cdot} M_4^{2\cdot} m_4^{21} f_4^{21}$			$N_3^2 M_3^{2\cdot} m_3^{22} f_3^{22}$	$N_3^2 S_3^{2\cdot} M_4^{2\cdot} m_4^{22} f_4^{22}$

Figure 3.3.2c

Numerical illustration of the expected recoveries in the Partial-Fidelity Model using ordinary band-recovery data assuming the parameters in Table 1.5a are constant over time

Expected recoveries of pre-stratum 1 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	1000	20.00	12.00	7.20	4.32	20.00	12.00	7.20	4.32
2	1000		20.00	12.00	7.20		20.00	12.00	7.20
3	1000			20.00	12.00			20.00	12.00

Expected recoveries of pre-stratum 2 animals

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	1000	32.00	16.00	8.00	4.00	36.00	18.00	9.00	4.50
2	1000		32.00	16.00	8.00		36.00	18.00	9.00
3	1000			32.00	16.00			36.00	18.00

The row-wise similarities in each table are a result of assuming that the parameters of Table 1.5a are constant over time.

It is important for the proper interpretation of the parameters that the assumptions of the timing of the migration process and recovery process be clearly stated. In these models, it is assumed that banding in year i takes place at a point in time t_i. Then the "decision" of choice of post-stratum by the animal is assumed to take place immediately afterwards at time t_i^+. Recoveries occur until just before banding in the next year, i.e., from time t_i^+ to t_{i+1}^-. Some of these recoveries may not indicate the post-stratum chosen by the animal and are discarded. For example, if the post-strata are flyways, recoveries that occur before the choice of flyway is clear are uninformative about the post-stratum to be chosen and are discarded. Similarly, recoveries that occur after the bird has returned from the flyway are uninformative on which flyway was chosen and are also discarded. However, these recoveries do contain information about the net survival rate over all post-strata since the bird is known to have survived until the year of recovery. If the number of such animals is small, the loss of efficiency in the estimates of the survival rates will be small. Incorporating information from these discarded recoveries is straightforward (along the lines of Section 3.4), but tedious and is not pursued further.

Note that by placing the migration "decision" immediately after the time of banding, it is not implied that migration choices are actually made at this time. In reality, the choice of migration route depends upon many factors and may take place some time after banding. However, this decision is projected back to the time of banding so that any mortality between banding and migration is incorporated into the band-recovery rate, and not in the migration rates. In a sense, the migration rates are conditional upon all animals surviving to the time of migration. The band-recovery rates will, of course, contain a hidden survival component, as they do in ordinary band-recovery models.

The parameters $M_i^{s\cdot}$ represent the total emigration rate of animals released from pre-stratum *s*, to any of the post-strata where recoveries occurred in year *i*. The parameter allows animals to migrate in year *i* to post-strata without recoveries (with probability $1-M_i^{s\cdot}$) and is assumed invariant to the intermediate (unknown) migration history of the animal. For example, in Figure 3.3.2c, $M_1^{2\cdot}$ (the total emigration rate of pre-stratum 2 animals to the post-strata where recoveries occurred in year 1, taken from Table 1.5a) equals 70% being the sum of 40% from pre-stratum 2 to post-stratum 1 and 30% from pre-stratum 2 to post-stratum 2. The rate is less than 100%, since post-stratum 3, by assumption, had no recoveries.

The parameters m_i^{st} represent the relative emigration rates of animals released in pre-stratum *s*, to post-stratum *t* in year *i*, conditional upon the animal migrating to one of the post-strata where recoveries occurred; again independent of the intermediate (unknown) migration history of the animal. For example, in Figure 3.3.2c, m_1^{21} (the relative emigration rate from pre-stratum 2 to post-stratum 1 in year 1) equals 57.14% = 40%/70% (taken from Table 1.5a).

The parameters f_i^{st} represent the band-recovery rates of animals released in pre-stratum *s* and recovered in post-stratum *t* in year *i*.

These recovery rates are based upon the animals alive at banding time in year *i*, and include a mortality component, a band-retrieval component, and a band-reporting component. For example, in Figure 3.3.2c, f_1^{21} (the band-recovery rate for animals from pre-stratum 2 recovered in post-stratum 1 in year 1) equals 8% which equals the (unknown in practice) harvest rate of pre-stratum 2 animals in post-stratum 1 in year 1 (20%) times the band-reporting rate for bands from animals from pre-stratum 2 harvested in post-stratum 1 in year 1 (40%), taken from Table 1.5a.

Thus the expected number of bands returned from animals released from pre-stratum 2 in year 1 and recovered in post-stratum 1 in year 1, $E(R_{11}^{21})$, will be equal to the product of the number of animals banded, the total emigration rate, the relative emigration rate, and the band-recovery rate:

$$E(R_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times f_1^{21} \qquad \text{(or)}$$

$$E(R_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.08 = 32.00$$

The parameters $S_i^{s\cdot}$ represent the pre-stratum specific net survival rates of animals released in pre-stratum *s* over all post-strata (including those without recoveries) from the time of banding in year *i* to the time of banding in year *i*+1. In the numerical example of Chapter 1, the value of $S_1^{2\cdot}$ was found to be 0.50 which would imply that 0.50 of the animals released in pre-stratum 2 will return to this pre-stratum a year later and be available to migrate in the next year.

The pre-stratum specific net survival rates will be a component of the expected number of recoveries in all years after the year of release. For example, the expected number of bands returned from animals released in pre-stratum 2 in year 1, and recovered in post-stratum 1 in year 2, $E(R_{12}^{21})$, will be equal to the product of the number of animals banded, the net survival rate between years 1 and 2, the total emigration in year 2, the relative emigration rate in year 2, and the band-recovery rate in year 2, or

$$E(R_{12}^{21}) = N_1^2 \times S_1^{2\cdot} \times M_2^{2\cdot} \times m_2^{21} \times f_2^{21}.$$

Assuming the rates in Table 2a are constant over time, this can be computed as:

$$E(R_{12}^{21}) = 1000 \times 0.50 \times 0.70 \times 0.5714 \times 0.08 = 16.00$$

Without further assumptions, it is not possible to factor out the individual post-stratum specific survival rates from the net survival rate, since there is no information about these rates for animals that may temporarily emigrate to post-strata without recoveries (in this case, post-stratum 3), but then return to their pre-stratum and are available to emigrate to post-strata in later years. This is apparent from Figure 3.3.2b where all the expected results can be expressed as a function of the net survival rates alone. Note that in the models considered by Arnason (1972, 1973), it was assumed that if emigration to other post-strata took place, the animals permanently leave the experiment and such emigration was treated as another form of "mortality". No such assumption is made here.

3.3.3 ESTIMATION

There are al total emigration parameters ($M_i^{s\cdot}$), $a(b-1)l$ relative emigration parameters (m_i^{st}), abk band-recovery parameters (f_i^{st}), $a(k-1)$ net survival parameters ($S_i^{s\cdot}$), and $ab(l-k)$ "product" parameters of the form $S_k^{s\cdot}S_{k+1}^{s\cdot}\ldots S_{i-1}^{s\cdot}f_i^{st}$ for recoveries occurring after year k, for a total of $a(2bl+k-1)$ parameters.

Since the yearly recoveries from each year's releases from each pre-stratum can be modelled as independent multinomial distributions, the likelihood function is easily constructed. For example, the likelihood function in the case of k=3 years of releases, l=4 years of recoveries, a=2 pre-strata where banding occurs and b=2 post-strata where recoveries occur can be written as:

$$L = \prod_{s=1}^{a} \binom{N_1^{s}}{R_{11}^{s1},\ R_{12}^{s1},\ R_{13}^{s1},\ R_{14}^{s1},\ R_{11}^{s2},\ R_{12}^{s2},\ R_{13}^{s2},\ R_{14}^{s2}}$$

$$\times\ (M_1^{s\cdot}m_1^{s1}f_1^{s1})^{R_{11}^{s1}}\ (S_1^{s\cdot}M_2^{s\cdot}m_2^{s1}f_2^{s1})^{R_{12}^{s1}}\ (S_1^{s\cdot}S_2^{s\cdot}M_3^{s\cdot}m_3^{s1}f_3^{s1})^{R_{13}^{s1}}\ (S_1^{s\cdot}S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1})^{R_{14}^{s1}}$$

$$\times\ (M_1^{s\cdot}m_1^{s2}f_1^{s2})^{R_{11}^{s2}}\ (S_1^{s\cdot}M_2^{s\cdot}m_2^{s2}f_2^{s2})^{R_{12}^{s2}}\ (S_1^{s\cdot}S_2^{s\cdot}M_3^{s\cdot}m_3^{s2}f_3^{s2})^{R_{13}^{s2}}\ (S_1^{s\cdot}S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{R_{14}^{s2}}$$

$$\times\ (1-M_1^{s\cdot}m_1^{s1}f_1^{s1}-S_1^{s\cdot}M_2^{s\cdot}m_2^{s1}f_2^{s1}-S_1^{s\cdot}S_2^{s\cdot}M_3^{s\cdot}m_3^{s1}f_3^{s1}-S_1^{s\cdot}S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1}-$$

$$M_1^{s\cdot}m_1^{s2}f_1^{s2}-S_1^{s\cdot}M_2^{s\cdot}m_2^{s2}f_2^{s2}-S_1^{s\cdot}S_2^{s\cdot}M_3^{s\cdot}m_3^{s2}f_3^{s2}-S_1^{s\cdot}S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{N_1^{s}-R_{1\cdot}^{s\cdot}}$$

$$\times \binom{N_2^{s}}{R_{22}^{s1},\ R_{23}^{s1},\ R_{24}^{s1},\ R_{22}^{s2},\ R_{23}^{s2},\ R_{24}^{s2}}$$

$$\times\ (M_2^{s\cdot}m_2^{s1}f_2^{s1})^{R_{22}^{s1}}\ (S_2^{s\cdot}M_3^{s\cdot}m_3^{s1}f_3^{s1})^{R_{23}^{s1}}\ (S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1})^{R_{24}^{s1}}$$

$$\times\ (M_2^{s\cdot}m_2^{s2}f_2^{s2})^{R_{22}^{s2}}\ (S_2^{s\cdot}M_3^{s\cdot}m_3^{s2}f_3^{s2})^{R_{23}^{s2}}\ (S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{R_{24}^{s2}}$$

$$\times\ (1-M_2^{s\cdot}m_2^{s1}f_2^{s1}-S_2^{s\cdot}M_3^{s\cdot}m_3^{s1}f_3^{s1}-\ \ldots\ -M_2^{s\cdot}m_2^{s2}f_2^{s2}-S_2^{s\cdot}M_3^{s\cdot}m_3^{s2}f_3^{s2}-S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{N_2^{s}-R_{2\cdot}^{s\cdot}}$$

$$\times \binom{N_3^{s}}{R_{33}^{s1},\ R_{34}^{s1},\ R_{33}^{s2},\ R_{34}^{s2}}$$

$$\times\ (M_3^{s\cdot}m_3^{s1}f_3^{s1})^{R_{33}^{s1}}\ (S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1})^{R_{34}^{s1}}\ (M_3^{s\cdot}m_3^{s2}f_3^{s2})^{R_{33}^{s2}}\ (S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{R_{34}^{s2}}$$

$$\times\ (1-M_3^{s\cdot}m_3^{s1}f_3^{s1}-S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1}-M_3^{s\cdot}m_3^{s2}f_3^{s2}-S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{N_3^{s}-R_{3\cdot}^{s\cdot}}\ .$$

Not all parameters are identifiable, since, for example, m_i^{st} and f_i^{st} always occur together in product form. After simplification, the likelihood reduces to:

$$L = \text{constant}\ \times \prod_{s=1}^{a}\ (M_1^{s\cdot}m_1^{s1}f_1^{s1})^{R_{\cdot 1}^{s1}}\ (M_1^{s\cdot}m_1^{s2}f_1^{s2})^{R_{\cdot 1}^{s2}}$$

$$\times\ (M_2^{s\cdot}m_2^{s1}f_2^{s1})^{R_{\cdot 2}^{s1}}\ (M_2^{s\cdot}m_2^{s2}f_2^{s2})^{R_{\cdot 2}^{s2}}$$

$$\times\ (M_3^{s\cdot}m_3^{s1}f_3^{s1})^{R_{\cdot 3}^{s1}}\ (M_3^{s\cdot}m_3^{s2}f_3^{s2})^{R_{\cdot 3}^{s2}}$$

$$\times\ (S_3^{s\cdot}M_4^{s\cdot}m_4^{s1}f_4^{s1})^{R_{\cdot 4}^{s1}}\ (S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{R_{\cdot 4}^{s2}}$$

$$\times\ (S_1^{s\cdot})^{Z_1^{s\cdot}}\ \ (S_2^{s\cdot})^{Z_2^{s\cdot}}$$

$$\times\ (1-M_1^{s\cdot}m_1^{s1}f_1^{s1}-S_1^{s\cdot}M_2^{s\cdot}m_2^{s1}f_2^{s1}-\ \ldots\ -\ S_1^{s\cdot}S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{N_1-R_{1\cdot}^{s\cdot}}$$

$$\times\ (1-M_2^{s\cdot}m_2^{s1}f_2^{s1}-S_2^{s\cdot}M_3^{s\cdot}m_3^{s1}f_3^{s1}-\ \ldots\ -\ S_2^{s\cdot}S_3^{s\cdot}M_4^{s\cdot}m_4^{s2}f_4^{s2})^{N_2-R_{2\cdot}^{s\cdot}}$$

$$\times\ (1-M_3^{s\cdot} m_3^{s1} f_3^{s1} - S_3^{s\cdot} M_4^{s\cdot} m_4^{s1} f_4^{s1} - \ \dots\ - S_3^{s\cdot} M_4^{s\cdot} m_4^{s2} f_4^{s2})^{N_3 - R_{3\cdot}^{s\cdot}}$$

from which the MSS can be identified.

Two questions are considered. First, exactly what fundamental or derived parameters can be estimated using ordinary band-recovery data? Second, since it may not be feasible to collect additional data, what further assumptions are required in order to estimate the remaining fundamental or derived parameters?

3.3.3.1 Estimation without further assumptions

The MSS has dimension a(bl+k-1) and one representation of its components is found to be:

$$R_{i\cdot}^{s\cdot} \quad \begin{array}{l} s=1\dots a \\ i=1\dots(k-1) \end{array} \qquad \text{and} \qquad R_{\cdot i}^{st} \quad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=1\dots l \end{array} \quad .$$

One set of identifiable functions of the parameters can be estimated using the methods outlined in Chapter 1 as:

$$\widehat{M_i^{s\cdot} m_i^{st} f_i^{st}} = \frac{R_{i\cdot}^{s\cdot} R_{\cdot i}^{st}}{N_i^s T_i^{s\cdot}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=1\dots k \end{array}$$

$$\widehat{S_k^{s\cdot} \dots S_{i-1}^{s\cdot} M_i^{s\cdot} m_i^{st} f_i^{st}} = \frac{R_{k\cdot}^{s\cdot} R_{\cdot i}^{st}}{N_k^s T_k^{s\cdot}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=(k+1)\dots l \end{array}$$

$$\widehat{S_i^{s\cdot}} = \frac{R_{i\cdot}^{s\cdot} Z_i^{s\cdot} N_{i+1}^{s\cdot}}{N_i^s T_i^{s\cdot} R_{i+1,\cdot}^{s\cdot}} \qquad \begin{array}{l} s=1\dots a \\ i=1\dots(k-1) \end{array} \quad .$$

Note that the Partial-Fidelity Model with ordinary band-recovery data is simply a reparameterization of Model 2a of Chapter 2 for each pre-stratum as follows:

Parameter of Model 2a of Chapter 2 for a single pre-stratum	Identifiable function of the parameters of the Partial-Fidelity Model
f_i^t	$M_i^{s\cdot} m_i^{st} f_i^{st}$
$S_k \ldots S_{i-1} f_i^t$	$S_k^{s\cdot} \ldots S_{i-1}^{s\cdot} M_i^{s\cdot} m_i^{st} f_i^{st}$
S_i	$S_i^{s\cdot}$

(Note that the post-stratum is designated here by superscript t whereas it was designated by superscript s in Chapter 2.) As noted in Chapter 2, f_i^t, the "gross band-recovery rate" is a function of the total emigration rate ($M_i^{s\cdot}$), the relative emigration rate (m_i^{st}), and the true band-recovery rate (f_i^{st}). The emigration and band-recovery rates cannot be separately estimated without further assumptions (Section 3.3.3.2). The pre-stratum specific net survival rates over all post-strata ($S_i^{s\cdot}$) can be estimated even though recoveries are not received from all post-strata since it is assumed that if an animal migrates to another post-stratum, it will return in the next year to its pre-stratum of release and will "forget" where it migrated in previous years. The animals will again migrate and may be recovered in subsequent years. The variance of this estimator was presented in Chapter 2.

The close relationship between the Partial-Fidelity Model and Model 2a of Chapter 2 may, at first glance, be surprising. In all of the models of Chapter 2, it was implicitly assumed that all animals were faithful to one and only one post-stratum which appears to contradict the assumption of the Partial-Fidelity Model of Markovian behaviour in choosing the post-stratum each year. However, in

Model 2a, all animals, regardless of post-stratum, were assumed to have a common survival rate, and so it is immaterial to the model formulation if the animal remains faithful to its eventual post-stratum of recovery, or freely migrates to other post-strata; the yearly survival rates are the same in both cases. In the Partial-Fidelity Model, the post-stratum survival rates are allowed to differ, but in the absence of information about where an animal migrates, the only survival rate that is applicable is the net survival rate over all post-strata ($S_i^{s\cdot}$) being a convolution of the post-stratum specific survival rates and the migration rates. This survival rate will apply to all animals in the years between release and recovery. Both models then model survival in the same fashion. The connection between the band-recovery rates of Model 2a and the migration and band-recovery components of the Partial-Fidelity Model is expected since, as noted in Chapter 2, the band-recovery rates of Model 2a contain migration and band-recovery components.

Since the net survival rate over all post-strata ($S_i^{s\cdot}$) is a convolution of the post-stratum specific survival rates (S_i^{st}) and the absolute emigration rates ($M_i^{s\cdot} m_i^{st}$) (including those of post-strata where no recoveries occur), the individual post-stratum survival rates cannot be estimated since the emigration rates cannot be estimated individually. Even if estimates of the emigration rates were available, there are many different sets of post-stratum survival rates that would give rise to the same net survival rate. For example, if the absolute emigration rates to three post-strata were known to be 0.40, 0.40, and 0.20 respectively, then each of the following sets of post-stratum survival rates all lead to the same net survival rate over all post-strata:

Post-stratum survival rates			Computation of net survival rate over all post-strata
1.00	0.00	0.00	1.00(0.40) + 0.00(0.40) + 0.00(0.20) = 0.40
0.50	0.50	0.00	0.50(0.40) + 0.50(0.40) + 0.00(0.20) = 0.40
0.00	0.50	0.67	0.00(0.40) + 0.50(0.40) + 1.00(0.20) = 0.40

It is impossible to estimate the absolute or total immigration rates unless all possible pre-strata are included in the banding-program. Furthermore, since the relative immigration rates are computed by first weighting the absolute emigration rates by the pre-stratum population sizes, and since the band-recovery rates are confounded with the absolute emigration rates, the relative immigration rates cannot be estimated without further assumptions.

It is also impossible to estimate the absolute harvest-derivation rates unless all possible pre-strata are included in the banding program. However, the relative harvest-derivation rates can be estimated by weighting the gross recovery rates (product of total emigration, relative emigration and band-recovery rates, $M_i^{s\cdot} m_i^{st} f_i^{st}$) by the external estimates of the absolute or relative population size (N_i^{s*}) and the inverse of the band-reporting rate (λ_i^{st}):

$$\hat{D}_i^{st} = \frac{\hat{N}_i^{s*} \cdot \hat{M}_i^{s\cdot} \hat{m}_i^{st} f_i^{st} \,/\, \hat{\lambda}_i^{st}}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot \hat{M}_i^{s\cdot} \hat{m}_i^{st} f_i^{st} \,/\, \hat{\lambda}_i^{st}} = \frac{\hat{N}_i^{s*} \cdot R_{i\cdot}^{s\cdot} R_{\cdot i}^{st} / (N_i^s T_i^{s\cdot} \cdot \hat{\lambda}_i^{st})}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot R_{i\cdot}^{s\cdot} R_{\cdot i}^{st} / (N_i^s T_i^{s\cdot} \cdot \hat{\lambda}_i^{st})} \qquad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{array}$$

Variances may be estimated using the delta-method. In some circumstances, it is reasonable to assume that the band-reporting rates within post-stratum *t* in year *i* are homogeneous among the pre-strata, i.e., $\lambda_i^{st} = \lambda_i^{\cdot t}$, even if the band-recovery rates are not. In these cases, the band-reporting rates are not required, and the harvest-derivation estimators simplify to:

$$\hat{D}_i^{st} = \frac{\hat{N}_i^{s*} \cdot M_i^{s\cdot} \hat{m}_i^{st} f_i^{st}}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot M_i^{s\cdot} \hat{m}_i^{st} f_i^{st}} = \frac{\hat{N}_i^{s*} \cdot R_{i\cdot}^{s\cdot} R_{\cdot i}^{st} / (N_i^s T_i^{s\cdot})}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot R_{i\cdot}^{s\cdot} R_{\cdot i}^{st} / (N_i^s T_i^{s\cdot})}$$

3.3.3.2 Assumptions necessary to estimate the confounded parameters

If the band-recovery rates were known exactly, then it is a simple matter to estimate the emigration rates. This rarely (if ever) occurs in practice and is not discussed further. However, in some cases, certain reasonable assumptions about the band-recovery rates allow the relative emigration and relative immigration rates to be estimated.

If external estimates of the relative ratio of the band-recovery rates among post-strata for each pre-stratum are available or are known exactly, i.e., if $f_i^{st} = \alpha_i^{\cdot t} f_i^{s1}$ for known or estimated $\alpha_i^{\cdot t}$ but unknown f_i^{s1}, then it is possible to estimate the relative emigration rates (m_i^{st}). It is not necessary that the actual recovery rates be estimated; only their relative magnitudes. This could be done by using a proportional-hazards type model. For example, two post-strata may be similar so that the band-recovery rates are felt to be proportional to the hunter-days of effort expended in each post-stratum. The relative ratio of the band-recovery rates would correspond to the ratio of the hunting efforts, but the exact relationship between hunting effort and recovery rates would remain unknown. Then:

$$\frac{M_i^{s\cdot}\hat{m}_i^{st} f_i^{st}/\hat{\alpha}_i^{\cdot t}}{\sum_{t=1}^{b} M_i^{s\cdot}\hat{m}_i^{st} f_i^{st}/\hat{\alpha}_i^{\cdot t}} = \frac{R_{i\cdot}^{s\cdot}R_{\cdot i}^{st}/(N_i^{s}T_i^{s\cdot}\hat{\alpha}_i^{\cdot t})}{\sum_{t=1}^{b} R_{i\cdot}^{s\cdot}R_{\cdot i}^{st}/(N_i^{s}T_i^{s\cdot}\hat{\alpha}_i^{\cdot t})}$$

is the MLE for

$$\frac{M_i^{s\cdot}m_i^{st} f_i^{st}/\alpha_i^{\cdot t}}{\sum_{t=1}^{b} M_i^{s\cdot}m_i^{st} f_i^{st}/\alpha_i^{\cdot t}} = \frac{M_i^{s\cdot}m_i^{st} f_i^{s1}\alpha_i^{\cdot t}/\alpha_i^{\cdot t}}{\sum_{t=1}^{b} M_i^{s\cdot}m_i^{st} f_i^{s1}\alpha_i^{\cdot t}/\alpha_i^{\cdot t}} = m_i^{st} \ .$$

The total emigration rates still remain confounded with the band-recovery rates and cannot be estimated under any reasonable assumptions. This is not unexpected, since it is impossible to distinguish between a high total emigration rate and low band-recovery rate, and a low total emigration rate and a high band-recovery rate.

If the band-recovery rates in year i are assumed to be homogeneous among the pre-strata within post-stratum t (i.e., $f_i^{st} = f_i^{\cdot t}$) then the relative immigration rates can be estimated. For example, if the pre-strata are breeding areas relatively close together, the animals may migrate at similar times and face similar harvesting pressures. Since the animals are otherwise indistinguishable, there is no reason to believe their band-recovery rates would differ. This assumption would be suspect if the breeding areas are far apart, had markedly different age or sex structures, or if the animals migrated at different times. Then the relative immigration rates can be estimated by:

$$\hat{I}_i^{st} = \frac{\hat{N}_i^{s*}\cdot M_i^{s\cdot}\hat{m}_i^{st} f_i^{st}}{\sum_{s=1}^{a} \hat{N}_i^{s*}\cdot M_i^{s\cdot}\hat{m}_i^{st} f_i^{st}} = \frac{\hat{N}_i^{s*}\cdot R_{i\cdot}^{s\cdot}R_{\cdot i}^{st}/(N_i^{s}T_i^{s\cdot})}{\sum_{s=1}^{a} \hat{N}_i^{s*}\cdot R_{i\cdot}^{s\cdot}R_{\cdot i}^{st}/(N_i^{s}T_i^{s\cdot})} \quad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{array} \ .$$

3.3.3.3 Summary of results on estimation

The major problem in using ordinary band-recovery data for estimation purposes in the Partial-Fidelity Model is that the emigration rates are confounded with the band-recovery rates. Use of this type of data implies that:

- total emigration rates and band-recovery rates can not be estimated separately under any reasonable restriction; but their product may be estimated.
- net survival rates over all post-strata can be estimated.
- post-stratum specific survival rates cannot be estimated.
- relative harvest-derivation rates can be estimated if independent estimates of the pre-stratum population sizes and band-reporting rates are available.
- relative emigration rates can be estimated if the relative magnitudes of the band-recovery rates among post-strata are known or can be estimated from other studies ($f_i^{st} = \alpha_i^{\cdot t} f_i^{s1}$).
- relative immigration rates can be estimated if it is assumed that the band-recovery rates are homogeneous among pre-strata within a post-stratum ($f_i^{st} = f_i^{\cdot t}$)

Unfortunately, the assumptions necessary for parameter estimation cannot be tested using the data from the experiment and must be assessed on biological grounds.

3.3.4 TESTING

Since ordinary band-recovery data are not sufficient for estimation of many of the parameters of interest, it is not surprising, that they are also not sufficient for testing hypotheses about the parameters.

However, many meaningful tests can be constructed if additional assumptions are made.

I first discuss a partial goodness-of-fit test based upon the results of Chapter 2. I then discuss "model-reduction" tests that examine the homogeneity of the parameters over strata or over time. A set of hierarchical models (as in Chapter 2) is not developed since the data from ordinary band-recovery data are so inadequate for this purpose.

Note that the tests developed in Chapter 2 of homogeneous gross "band-recovery rates" are really tests that the product of emigration and the band-recovery rates are homogeneous among post-strata, i.e., a test if $M_i^{s\cdot} m_i^{st} f_i^{st}$ are homogeneous among post-strata, and consequently, may be inappropriate.

3.3.4.1 A partial goodness-of-fit test

Since the Partial-Fidelity Model using ordinary band-recovery data is a reparameterization of Model 2a of Chapter 2, a non-specific, partial goodness-of-fit test can be constructed using the goodness-of-fit test for Model 2a. Since some parameters are confounded, not all aspects of the model can be examined. If the goodness-of-fit indicates that the Partial-Fidelity Model is not appropriate, no single alternative is suggested.

The partial goodness-of-fit test may be subdivided into two components:

- a component to test if the product of the relative emigration rates and band-recovery rates in year j are the same for all animals from a given pre-stratum regardless of when released.
- a component to test if the net survival rates in year j are the same for all animals from a given pre-stratum regardless of when released conditional upon the test of the first component not rejecting its null hypothesis.

A large-sample contingency table that can be used in the test of the hypothesis of the first component is shown in Table 3.3.4.1a. If this hypothesis is rejected, either the relative migration rates or the band-recovery rates or both depend upon the year of release. This might occur if the assumption that animals "forget" their previous migration routes is not valid. Then the animals would tend to migrate in subsequent years to the post-stratum of previous years, and there will be a gradual shift in the relative migration ratio of the banded-cohort to the post-strata with the highest post-stratum survival rates. Newly banded cohorts, since they are a random sample of the population, may include younger animals who have not yet had a chance to develop these patterns.

A large sample contingency table that can be used in the test of the hypothesis of the second component is shown in Table 3.3.4.1b and should only be performed if the hypothesis in the first component is not rejected; otherwise, interpretation of the second test is unclear. Since estimation of the net survival rates may be performed by combining the data over post-strata and treating the data as if they

Table 3.3.4.1a

A large sample contingency table that can be used for the first component of the partial goodness-of-fit test in the Partial-Fidelity Model using ordinary band-recovery data

H: $m_{ij}^{st} f_{ij}^{st} = m_{j}^{st} f_{j}^{st}$

A: product terms are year-of-release specific

where m_{ij}^{st} = relative migration rate of animals released in pre-stratum *s* in year *i* to post-stratum *t* in year *j*.

f_{ij}^{st} = band-recovery rate of animals released in pre-stratum *s* in year *i* when recovered in post-stratum *t* in year *j*.

	MSS	Dimension
H	$R_{ij}^{s\cdot}$, $R_{\cdot j}^{st}$	$a(kl-(k-1)k/2)+a(b-1)l$
A	R_{ij}^{st}	$ab(kl-(k-1)k/2)$

Contingency Table for each (s,j) pair

R_{1j}^{s1}	R_{1j}^{s2}	...	R_{1j}^{sb}	$R_{1j}^{s\cdot}$
		⋮		
R_{mj}^{s1}	R_{mj}^{s2}	...	R_{mj}^{sb}	$R_{mj}^{s\cdot}$
$R_{\cdot j}^{s1}$	$R_{\cdot j}^{s2}$	...	$R_{\cdot j}^{sb}$	$R_{\cdot j}^{s\cdot}$

where m=min(j,k)

There are (min(j,k)-1)(b-1) degrees of freedom for each (s,j) pair. The overall test is computed by summing the component chi-square test statistics and degrees of freedom for a total of $a(b-1)(l(k-1)-(k-1)k/2)$ degrees of freedom.

Intuitively, if the null hypothesis is true, the recoveries of pre-stratum *s* animals in year *j (columns)* should occur in the same proportions among the post-strata regardless of year of release (rows)

This test will not detect changes in the total migration rate among releases.

Table 3.3.4.1b

A large sample contigency table that can be used for the second component of the partial goodness-of-fit test in the Partial-Fidelity Model using ordinary band-recovery data

H : $S^{s\cdot}_{ij-1} = S^{s\cdot}_{i} S^{s\cdot}_{i+1} \ldots S^{s\cdot}_{j-1}$ assuming that the first component did not reject its null hypothesis.

A : survival in years *i...j*-1 is not the same for all releases

where $S^{s\cdot}_{ij-1}$ = net survival rate of animals from pre-stratum *s* released in year i over all post-strata in years *i...j*-1.

	MSS	Dimension
H	$R^{s\cdot}_{i\cdot}$	a(bl+k-1)
	$R^{st}_{\cdot j}$	
A	$R^{s\cdot}_{ij}$	a(kl-k(k-1)/2)+ a(b-1)l
	$R^{st}_{\cdot j}$	

Contingency Table for (s,i) pair

$R^{s\cdot}_{ii+}-R^{s\cdot}_{ii}$	...	$R^{s\cdot}_{il+}-R^{s\cdot}_{il}$	$Z^{s\cdot}_{i-1}$
$R^{s\cdot}_{ii}$	...	$R^{s\cdot}_{il}$	$R^{s\cdot}_{i\cdot}$
$R^{s\cdot}_{ii+}$	$R^{s\cdot}_{i,i+1,+}\ldots$	$R^{s\cdot}_{il+}$	$T^{s\cdot}_{i}$

where $R^{s\cdot}_{ij+} = \sum_{k=1}^{i} R^{s\cdot}_{kj}$

There are (*l*-*i*) degrees of freedom for each (*s*,*i*) pair, i=2...k. The overall test is computed by summing the component chi-square test statistics and degrees of freedom for a total of *a*((*k*-1)(*l*-1)-(*k*-1)*k*/2) degrees of freedom.

Intuitively, under both H and A, we may combine post-strata and treat the data as coming from an ordinary band-recovery experiment. Under H, the combined data can be fit by Model 1 of Brownie *et al.* (1985, Section 2.2). Under A, Model 1 is not appropriate. Hence the test is the exact goodness-of-fit test to model M_1.

This test should only be performed if the test of the first component does not reject the null hypothesis; otherwise the interpretation of this test is not clear.

came from an ordinary band-recovery experiment (Model M_1 of Brownie *et al.*, 1985, Section 2.2), the test reduces to the exact goodness-of-fit test of Robson and Youngs (1971). If this test rejects, survival may be age related rather than year specific.

3.3.4.2 Tests of the emigration rates

Recall that estimation of emigration rates was possible if the ratio of band-recovery rates among the post-strata was known or could be estimated. In order to test if the relative emigration rates are homogeneous among pre-strata or over time, similar assumptions about the band-recovery rates are required. No tests are possible for the absolute or total emigration rates unless the band-recovery rates are assumed (unrealistically) to be known exactly.

Testing for homogeneous relative emigration rates among pre-strata:
A test for homogeneous relative emigration rates among pre-strata is possible if it is assumed that the post-stratum band-recovery rates are proportional among the pre-strata, i.e., that $f_j^{st} = \alpha_j^{s\cdot} f_j^{1t}$. This assumption includes, as a special case, the assumption often made that the post-stratum specific band-recovery rates are homogeneous among all pre-strata, i.e., that $f_j^{st} = f_j^{\cdot t}$. For example, if the pre-strata are the sex of an animal, then the sexes may exhibit distinct characteristics or behaviours (e.g., coloration) such that males are about twice as likely to be spotted and harvested in all post-strata. If the band-reporting rate within each post-stratum is the same for both sexes, then the band-recovery rate for males will be twice that of females in each post-stratum. Or there may be no discernable

differences between the sexes and the band-recovery rates are assumed to be equal.

A large sample contingency table can then be constructed and is shown in Table 3.3.4.2a. This contingency table is actually used to test if the parametric functions in year j:

$$\frac{M_j^{s\cdot} m_j^{st} f_j^{st}}{\sum_{v=1}^{b} M_j^{s\cdot} m_j^{sv} f_j^{sv}} = \frac{m_j^{st} f_j^{st}}{\sum_{v=1}^{b} m_j^{sv} f_j^{sv}}$$

are homogeneous among pre-strata, which (under the stated assumption) reduces to examining if:

$$\frac{m_j^{st} f_j^{1t} \alpha_j^{s\cdot}}{\sum_{v=1}^{b} m_j^{sv} f_j^{1v} \alpha_j^{s\cdot}} = \frac{m_j^{st} f_j^{1t}}{\sum_{v=1}^{b} m_j^{sv} f_j^{1v}}$$

are homogeneous among pre-strata. Since the weights applied to the relative emigration rates now do not depend upon the pre-stratum, this is equivalent to testing if the relative emigration rates are homogeneous among pre-strata. Of course, the test can be viewed either as a:

- test if $m_j^{st} = m_j^{\cdot t}$ assuming that $f_j^{st} = \alpha_j^{s\cdot} f_j^{1t}$ (or)
- test if $f_j^{st} = \alpha_j^{s\cdot} f_j^{1t}$ assuming that $m_j^{st} = m_j^{\cdot t}$.

The latter interpretation may be of interest in testing if different types of bands are returned proportionally in all post-strata when the pre-stratum is defined as the type of band, and by doing so, it is reasonable to assume that the migration patterns of the pre-stratum are equal.

Table 3.3.4.2a

A large sample contingency table that can be used to test for homogeneous relative emigration rates among pre-strata in the Partial-Fidelity Model using ordinary band-recovery data

H: $m_{\cdot j}^{st} = m_{\cdot j}^{\cdot t}$ assuming $f_{\cdot j}^{st} = \alpha_{\cdot j}^{s\cdot} f_{\cdot j}^{1t}$ and $\alpha_{\cdot j}^{s\cdot}$ unknown

A: relative emmigration rates are pre-stratum specific under the same assumption

	MSS	Dimension
H	$Z_{\cdot j}^{s\cdot}$	$a(l+k-1)+(b-1)l$
	$R_{\cdot j}^{\cdot t}$	
	$R_{\cdot j}^{s\cdot}$	
A	$Z_{\cdot j}^{s\cdot}$	$a(bl+k-1)$
	$R_{\cdot j}^{st}$	

Contingency Table for year j

$R_{\cdot j}^{11}$	$R_{\cdot j}^{12}$	...	$R_{\cdot j}^{1b}$	$R_{\cdot j}^{1\cdot}$
	⋮			
$R_{\cdot j}^{a1}$	$R_{\cdot j}^{a2}$	...	$R_{\cdot j}^{ab}$	$R_{\cdot j}^{a\cdot}$
$R_{\cdot j}^{\cdot 1}$	$R_{\cdot j}^{\cdot 2}$	...	$R_{\cdot j}^{\cdot b}$	$R_{\cdot j}^{\cdot\cdot}$

There are $(a-1)(b-1)$ degrees of freedom for year j. The overall test is computed by summing the component chi-square test statistics and degrees of freedom for a total of $(a-1)(b-1)l$ degrees of freedom.

Intuitively, when the null hypothesis is true and the assumption is valid, the total number of recoveries in year j in each post-stratum (columns) should occur in the same proportions for every pre-stratum (rows) and will reflect the homogeneous migration rates in year j.

Testing for homogeneous relative emigration rates over time:

A test for homogeneous relative emigration rates over time within a pre-stratum is possible if it is assumed that the band-recovery rates are proportional over time, i.e., that $f_j^{st} = \alpha_j^{s\cdot} f_1^{st}$. For example, if harvest regulations do not change over time in all the post-strata, it may be reasonable to assume that the band-recovery rates, while changing from year to year, occur in the same proportion (e.g., the band-recovery rate in post-stratum 1 is always twice that of post-stratum 2 in any year).

A large sample contingency table can be constructed and is shown in Table 3.3.4.2b. This contingency table is actually used to test if the parametric functions:

$$\frac{M_j^{s\cdot} m_j^{st} f_j^{st}}{\sum_{v=1}^{b} M_j^{s\cdot} m_j^{sv} f_j^{sv}} = \frac{m_j^{st} f_j^{st}}{\sum_{v=1}^{b} m_j^{sv} f_j^{sv}}$$

are homogeneous over time which (under the stated assumption) reduces to examining if:

$$\frac{m_j^{st} f_1^{st} \alpha_j^{s\cdot}}{\sum_{v=1}^{b} m_j^{sv} f_1^{sv} \alpha_j^{s\cdot}} = \frac{m_j^{st} f_1^{st}}{\sum_{v=1}^{b} m_j^{sv} f_1^{sv}}$$

are homogeneous over time. Since the weights applied to the relative emigration rates do not depend upon the year of recovery, this is equivalent to examining if the relative emigration rates are homogeneous over time. Of course the test can be viewed as either as a:

- test if $m_j^{st} = m_{\cdot}^{st}$ assuming that $f_j^{st} = \alpha_j^{s\cdot} f_1^{st}$ (or)

Table 3.3.4.2b

A large sample contingency table that can be used to test for homogeneous relative emmigration rates over time in the Partial-Fidelity Model using ordinary band-recovery data

H: $m_{j}^{st} = m_{\cdot}^{st}$ assuming $f_{j}^{st} = \alpha_{j}^{s\cdot} f_{1}^{st}$

A: relative emmigration rates vary over time under the same assumption

	MSS	Dimension
H	$z_{j\cdot}^{s\cdot}$ $R_{\cdot\cdot}^{st}$ $R_{\cdot j}^{s\cdot}$	$a(l+k+b-2)$
A	$z_{j\cdot}^{s\cdot}$ $R_{\cdot j}^{st}$	$a(bl+k-1)$

Contingency Table for pre-stratum *s*

$R_{\cdot 1}^{s1}$	$R_{\cdot 1}^{s2}$	...	$R_{\cdot 1}^{sb}$	$R_{\cdot 1}^{s\cdot}$
		⋮		
$R_{\cdot l}^{s1}$	$R_{\cdot l}^{s2}$	...	$R_{\cdot l}^{sb}$	$R_{\cdot l}^{s\cdot}$
$R_{\cdot\cdot}^{s1}$	$R_{\cdot\cdot}^{s2}$	...	$R_{\cdot\cdot}^{sb}$	$R_{\cdot\cdot}^{s\cdot}$

There are $(b-1)(l-1)$ degrees of freedom for each pre-stratum. The overall test is computed by summing the component chi-square test statistics and degrees of freedom for a total of $a(b-1)(l-1)$ degrees of freedom.

Intuitively, when the null hypothesis is true and the assumption is valid, the total recoveries over all years in each post-stratum (columns) should occur in the same proportion for every year of recovery (rows) and will reflect the homogeneous migration rates over time.

- test if $f_j^{st} = \alpha_j^{s\cdot} f_1^{st}$ assuming that $m_j^{st} = m_\cdot^{st}$.

The latter test is not likely to be of much interest since it is usually unrealistic to assume that migration rates are not changing over time.

3.3.4.3 Tests of the immigration rates

As in the estimation of the immigration rates, it is impossible to examine the absolute immigration rates unless the post-strata are exhaustive. In this case, the relative immigration rates would equal the absolute immigration rates. As well, further assumptions are required about the band-recovery rates in order to examine the relative immigration rates.

Testing for homogeneous relative immigration rates among post-strata:

A test for homogeneous relative immigration rates among the post-strata is equivalent to a test if the ratios:

$$(I_j^{st})^* = \frac{m_j^{st}}{\sum_{u=1}^{a} m_j^{ut}}$$

are homogeneous among the post-strata, since I_j^{st} can be obtained from I_j^{st*} by using weights that are independent of the post-strata, i.e., $N_j^{s*} M_j^{s\cdot}$ does not depend upon the post-strata. This in turn can be shown to be equivalent to testing for homogeneous relative emigration rates among pre-strata for which a large sample contingency table was presented in Table 3.3.4.2a. For example, consider the array of values:

$$\begin{array}{ccc} a & b & c \\ a' & b' & c' \end{array}$$

Then testing if:

$$\frac{a}{a + a'} = \frac{b}{b + b'} = \frac{c}{c + c'}$$

(a test of the relative immigration rates) is equivalent to testing if

$$\frac{a}{a + b + c} = \frac{a'}{a' + b' + c'}, \quad \text{and} \quad \frac{b}{a + b + c} = \frac{b'}{a' + b' + c'}$$

(a test of the relative emigration rates). Hence the test for homogeneous relative immigration rates among post-strata is exactly the same as the test for homogeneous relative emigration rates among pre-strata, and the same assumptions are required. Note that the test is only valid for recovery years $1...k$ since after this point band-recovery, migration, and survival parameters are now confounded and are not biologically meaningful for use in determining immigration rates.

Testing for homogeneous immigration rates over time:

Since the definition of the immigration rates involves the (unknown) population size at each time, a test cannot be constructed (under any assumptions about the band-recovery rates) to examine if the immigration rates change over time based upon the data only from an ordinary band-recovery study. (This differs from the previous section, where the unknown population size was the same for all post-strata, and where a test could be constructed). An *ad hoc* test can be constructed using external estimates of the population size and its variance, but is not pursued further. An example of the derivation of such an *ad hoc* test when sightings are also present is given in Appendix 3.F and illustrated in the numerical example of Section 3.7.

3.3.4.4 Tests of the harvest-derivation rates

As in the estimation of the harvest-derivation rate, it is impossible to construct a test about the absolute harvest-derivation rates unless the pre-strata are exhaustive in which case the relative harvest-derivation rates will equal the absolute harvest-derivation rates. Since the harvest-derivation rates may be estimated without further assumptions, one would expect that tests about these rates could be constructed without further assumptions; however this is not the case.

Testing for homogeneous relative harvest-derivation rates among post-strata:

Since the band-reporting rates used in computing the harvest-derivation rates vary among the post-strata and must be estimated from outside the study, no test of the homogeneity of the derivation rates among post-strata can be constructed using only ordinary band-recovery data. An *ad hoc* test using the external estimates and their estimated variances can be constructed, but is not pursued further. In some cases, the band-reporting rates are homogeneous among the pre-strata within a post-stratum, i.e., $\lambda_j^{st} = \lambda_j^{\cdot t}$. Following a similar argument to that in testing if the relative immigration rates are independent of post-strata, the contingency table used to test for homogeneous relative harvest-derivation among post-strata in the presence of homogeneous band-reporting rates reduces to the contingency table presented in Section 3.3.4.2a, with the proviso that testing takes place only in years $1 \ldots k$. However, no further assumptions need to be made about the band-recovery rates since these rates are part of the harvest-derivation rates.

Testing for homogeneous relative harvest-derivation rates over time: Since the pre-stratum population sizes and the post-stratum band-reporting rates used in estimating the harvest-derivation rates vary over time and must be estimated outside the band-recovery study, a test cannot be constructed for homogenous harvest-derivation rates over time based only upon the data from an ordinary band-recovery study. (This differs from the previous section, where the unknown population sizes used in computing the derivation rates are the same for all post-strata within a pre-stratum and are essentially ignored). If the population sizes and band-reporting rates are estimated from an independent study with estimates of their precision, then an *ad hoc* test can be constructed but is not pursued further. An example of the derivation of an *ad hoc* test when sightings are employed is given in Appendix 3.F and a numerical example illustrating the test is found in Section 3.7.

3.3.4.5 Tests of the net survival rate over all post-strata

Tests for homogeneous net survival rates among pre-strata or over time can be constructed, but are not in closed form. Since the band-recovery data in the Partial-Fidelity Model can be combined over post-strata and treated as the simple band-recovery model M_1 of Brownie *et al.* (1985, Section 2.2) for the purposes of estimating and testing the net survival rate, techniques such as those in Brownie, Hines, and Nichols (1985) can be used.

3.3.4.6 Summary of results on testing

The confounding of the band-recovery and migration rates causes numerous problems when testing hypotheses about the parameters in the

Partial-Fidelity Model. In some cases further assumptions may be necessary. In summary:

· a partial goodness-of-fit test can be constructed and partitioned.

· a test for homogenous relative emigration rates among pre-strata is possible if it is assumed that the post-stratum band-recovery rates are proportional among pre-strata ($f_j^{st} = \alpha_j^{s\cdot} f_j^{1t}$).

· a test for homogeneous relative emigration rates over time is possible if it is assumed that the band-recovery rates are proportional over time ($f_j^{st} = \alpha_j^{s\cdot} f_1^{st}$).

· a test for homogenous relative immigration rates among post-strata is equivalent to a test for homogenous relative emigration rates among pre-strata.

· an *ad hoc* test may be constructed to test for homogeneous relative immigration rates over time when external estimates of the yearly pre-stratum population sizes and estimates of their precision are available and further assumptions are made about the band-reporting rate.

· an *ad hoc* test can be constructed to test for homogeneous relative harvest-derivation rates among post-strata when external estimates of the band-reporting rates and estimates of their precision are available. However, if the band-reporting rates are assumed to be homogeneous among the pre-strata within a post-stratum ($\lambda_j^{st} = \lambda_j^{\cdot t}$), a large sample contingency table is identical in form to that used in the test for homogeneous relative emigration rates over pre-strata.

· an *ad hoc* test for homogeneous relative harvest-derivation rates over time can be constructed when external estimates of the yearly pre-stratum population sizes and band-reporting rates and estimates of their precision are available.

· tests for homogeneous net survival rates among pre-strata or over time are not available in closed form, but can be obtained from the results of ordinary band-recovery models after combining the data over post-strata.

3.3.5 SUMMARY OF THE PARTIAL-FIDELITY MODEL WITH ORDINARY BAND-RECOVERY DATA

The major problem in using ordinary band-recovery data in the Partial-Fidelity Model is that the band-reporting rate is irretrievably confounded with the emigration rate. This implies that estimation and tests of the emigration or immigration rates are not possible unless further assumptions about the band-recovery rates are made. These assumptions are not testable using the data at hand, and must be assessed on biological grounds alone.

Estimation and tests of the harvest-derivation may be possible if independent estimates of the pre-stratum population sizes and band-reporting rates and estimates of their precision are available.

The net survival rate over all post-strata may be estimated and tested without further assumptions by combining the data over post-strata and using Model M_1 of Brownie *et al.* (1985, Section 2.2).

In short, there are numerous shortcomings in using ordinary band-recovery data with the Partial-Fidelity Model. Estimation and hypothesis testing is possible under various restrictions, but these restrictions must be assessed on biological grounds.

3.4 A MODIFICATION TO THE EXPERIMENTAL DESIGN IN THE PARTIAL-FIDELITY MODEL

The major problem in using ordinary band-recovery data in the Partial-Fidelity Model is the confounding of the band-recovery rates with the emigration rates. This can be resolved if an estimate can be obtained of the band-recovery rates.

In some cases, it is possible to obtain sightings of the animals in the post-strata, in addition to the band-recoveries. For example, if birds are banded, it may be possible to identify the individual banded birds as they fly overhead, or congregate in staging areas along the migration route. If the act of sighting has no effect on subsequent survival, harvest, band-recovery, or future sightings, then many of the previously confounded parameters become separately identifiable. Live recaptures may also be used to obtain sightings provided there is no subsequent loss on capture or subsequent handling-induced mortality. The use of sightings in the post-strata transform this model into a hybrid of band-recovery and capture-recapture models since sightings may be interpreted as a simultaneous capture and release. However, no attempt is made to estimate animal abundances as in capture-recapture studies.

Sightings of the animals in the pre-strata may also occur. Unfortunately, these provide no information on the migration rates from pre- to post-strata. They do provide information about the net survival rate over all post-strata and the post-stratum specific survival rates. Such information can be incorporated into the models in a straightforward (but tedious) fashion; since the information is not useful for estimating the migration rates, this generalization is not pursued further.

3.4.1 ASSUMPTIONS

The additional assumptions over those made in the Partial-Fidelity Model with ordinary band-recovery data are:

- tags are unique so that the sighting and recovery history of each individual animal can be followed;
- sighting an animal in a post-stratum is independent of recovering the band from an animal;
- sighting an animal has no effect on subsequent mortality or migration patterns;
- if an animal is sighted in a post-stratum, it implies that the animal has chosen to migrate to this post-stratum;
- multiple sightings or captures within a year are considered as a single sighting. By the previous assumption, such multiple sightings must take place within a single post-stratum;
- for simplicity, all post-strata where recoveries occurred are assumed to have sightings.

It is not necessary to assume that the sighting periods in a year are the same for all post-strata.

The assumption of independence between recoveries and sightings is the most crucial. This assumption implies that sightings must take place before or at the same time as recoveries; otherwise, the probability of sighting and recovering an animal will be zero and is not equal to the product of the two rates. As well, the sighting and recovery efforts must be applied either to the entire set of animals choosing a post-stratum, or to the same subset. For example, if post-strata are flyways, the independence assumption will be violated if recoveries and sightings take place in separate geographical areas within the flyway. If sightings and recoveries are separated by time, then the study must be designed so that the subset of animals that were sighted will also be subject to recoveries. A common violation would occur if the animals that were sighted have left the recovery area before the start of the hunting season.

3.4.2 MODEL AND INTERPRETATION OF THE PARAMETERS

As shown in Appendix 3.A, the set of sighting and recovery histories from a release can be modelled using multinomial distributions; however the data representation required for it is complex. A reduced-data array can be constructed that contains all the necessary information required for estimation and hypothesis testing (except for the complete goodness-of-fit test which requires the original data), and whose form assists in an intuitive understanding of the results that follow.

A symbolic representation of the reduced-data array in the case of k=3 years of releases, and l=4 years of recoveries is shown in Figure 3.4.2a. In the reduced-data array, the number of animals released from pre-stratum s in year i and whose band is recovered in post-stratum t in year j (R_{ij}^{st}) is split into two components:

- those recovered **AND** sighted in post-stratum t in year j (A_{ij}^{st})
- those recovered **BUT** not sighted in post-stratum t in year j (B_{ij}^{st}).

Figure 3.4.2a

Symbolic representation of the reduced-data array in the Partial-Fidelity Model with sightings in the post-strata in the case of k=3 years of release and l=4 years of recoveries

Year Released	Number Banded	Year of recovery or sighting of animals in post-stratum t[a] 1	2	3	4
1	N^s_1	A^{st}_{11}	A^{st}_{12}	A^{st}_{13}	A^{st}_{14}
		B^{st}_{11}	B^{st}_{12}	B^{st}_{13}	B^{st}_{14}
		W^{st}_{11}	W^{st}_{12}	W^{st}_{13}	W^{st}_{14}
		$W^{st\cdot}_{11\cdot}$	$W^{st\cdot}_{12\cdot}$	$W^{st\cdot}_{13\cdot}$	b
2	N^s_2		A^{st}_{22}	A^{st}_{23}	A^{st}_{24}
			B^{st}_{22}	B^{st}_{23}	B^{st}_{24}
			W^{st}_{22}	W^{st}_{23}	W^{st}_{24}
			$W^{st\cdot}_{22\cdot}$	$W^{st\cdot}_{23\cdot}$	b
3	N^s_3			A^{st}_{33}	A^{st}_{34}
				B^{st}_{33}	B^{st}_{34}
				W^{st}_{33}	W^{st}_{34}
				$W^{st\cdot}_{33\cdot}$	b

Statistics

A^{st}_{ij} = number of animals released from pre-stratum s in year i that are recovered **AND** sighted in post-stratum t in year j

B^{st}_{ij} = number of animals released from pre-stratum s in year i that are recovered **BUT** not sighted in post-stratum t in year j

W^{st}_{ij} = number of animals released from pre-stratum s in year i that are sighted **WITHOUT** being recovered in post-stratum t in year j.

$W^{st\cdot}_{ij\cdot}$ = number of animals released in pre-stratum s in year i that are sighted without being recovered in post-stratum t in year j and are subsequently sighted or recovered in any post-stratum.

[a] There will one such array for every combination of pre- and post-stratum as laid out in Figure 3.3.2a

[b] Must be 0 since experiment is terminated in year 4.

The number of animals released from pre-stratum *s* in year *i* and whose band is sighted **WITHOUT** being recovered in post-stratum *t* in year *j* (W_{ij}^{st}) is also required. Since the band was not recovered from these animals, they may be sighted or recovered at a later time, in a different post-stratum. The number of animals from W_{ij}^{st} that are subsequently recovered or sighted at any later time in any post-stratum ($W_{ij\cdot}^{st\cdot}$) is also tabulated. There are $W_{ij}^{st}-W_{ij\cdot}^{st\cdot}$ animals released from pre-stratum *s* in year *i* that were sighted without being recovered in post-stratum *t* in year *j* and were never sighted or recovered after year *j*.

The number of animals never recovered nor sighted at any time after release is not shown. It is easily computed since the total number of unique animals released from pre-stratum *s* in year *i* that are subsequently recovered or sighted during the rest of the experiment is computed as:

$$\sum_{j=i}^{l}\sum_{t=1}^{b}(A_{ij}^{st}+B_{ij}^{st}+(W_{ij}^{st}-W_{ij\cdot}^{st\cdot})) = A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+(W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot})$$

Note that an animal may contribute to several elements of the reduced-data array. For example, an animal with a history of:

- released from pre-stratum 1 in year 1;
- sighted **WITHOUT** being recovered in post-stratum 2 in year 2;
- sighted **WITHOUT** being recovered in post-stratum 1 in year 3;
- recovered **AND** sighted in post-stratum 2 in year 4;

will contribute to the terms:

$$W_{12}^{12},\quad W_{12\cdot}^{12\cdot},\ W_{13}^{11},\ W_{13\cdot}^{11\cdot},\ \text{and } A_{14}^{12}.$$

The general expression for the expected number of animals observed for each element of the reduced-data array is shown in Figure 3.4.2b in the case of k=3 years of releases, and l=4 years of recoveries. Figure 3.4.2b should be compared with Figure 3.4.2a to see the correspondence between the elements of the reduced-data array and the general formulae. A numerical example using the parameters of Table 1.5a, assuming they are constant over time, and assuming a uniform sighting rate of 30% among all pre-strata within each post-stratum in all years, is shown in Figure 3.4.2c and discussed below. It is assumed that banding occurred only in the first two pre-strata from Table 1.5a, and that recoveries and sightings are obtained from only the first two post-strata.

The parameters $M_i^{s\cdot}$, m_i^{st}, and f_i^{st} were discussed in Section 3.3.2 and retain their interpretations.

The parameters p_i^{st} represent the rate at which banded animals released from pre-stratum s are sighted in post-stratum t in year i. As noted earlier, it is important that the study be designed carefully so that the sighting of a band is independent of the recovery of the band, and that a sighting does not affect the subsequent recovery, survival, or migration patterns. The sighting rate is allowed to vary with pre-stratum within a post-stratum for the very reasons permitting the variation in the band-recovery rates (Section 3.3.2). However, in the numerical example of Figure 3.4.2c, a constant sighting rate of 30% among all pre-strata within all post-strata at all times was assumed.

Figure 3.4.2b

Expected values of the reduced-data array in the Partial-Fidelity Mmodel with sightings in the post-strata in the case of k=3 year of releases and l=4 years of recoveries.

Year	Number Banded	Expected number of animals recovered or sighted in post-stratum t[a] by year 1	2	3	4
1	N_1^s	$N_1^s M_1^{s\cdot} m_1^{st} \times p_1^{st} f_1^{st}$	$N_1^s S_1^{s\cdot} M_2^{s\cdot} m_2^{st} \times p_2^{st} f_2^{st}$	$N_1^s S_1^{s\cdot} S_2^{s\cdot} M_3^{s\cdot} m_3^{st} \times p_3^{st} f_3^{st}$	$N_1^s S_1^{s\cdot} S_2^{s\cdot} S_3^{s\cdot} M_4^{s\cdot} m_4^{st} \times p_4^{st} f_4^{st}$
		" $\times (1-p_1^{st}) f_1^{st}$	" $\times (1-p_2^{st}) f_2^{st}$	" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
		" $\times p_1^{st} (1-f_1^{st})$	" $\times p_2^{st} (1-f_2^{st})$	" $\times p_3^{st} (1-f_3^{st})$	" $\times p_4^{st} (1-f_4^{st})$
		" $\times p_1^{st} S_1^{st} \rho_2^{s\cdot}$	" $\times p_2^{st} S_2^{st} \rho_3^{s\cdot}$	" $\times p_3^{st} S_3^{st} \rho_4^{s\cdot}$	b
2	N_2^s		$N_2^s M_2^{s\cdot} m_2^{st} \times p_2^{st} f_2^{st}$	$N_2^s S_2^{s\cdot} M_3^{s\cdot} m_3^{st} \times p_3^{st} f_3^{st}$	$N_2^s S_2^{s\cdot} S_3^{s\cdot} M_4^{s\cdot} m_4^{st} \times p_4^{st} f_4^{st}$
			" $\times (1-p_2^{st}) f_2^{st}$	" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
			" $\times p_2^{st} (1-f_2^{st})$	" $\times p_3^{st} (1-f_3^{st})$	" $\times p_4^{st} (1-f_4^{st})$
			" $\times p_2^{st} S_2^{st} \rho_3^{s\cdot}$	" $\times p_3^{st} S_3^{st} \rho_4^{s\cdot}$	b
3	N_3^s			$N_3^s M_3^{s\cdot} m_3^{st} \times p_3^{st} f_3^{st}$	$N_3^s S_3^{s\cdot} M_4^{s\cdot} m_4^{st} \times p_4^{st} f_4^{st}$
				" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
				" $\times p_3^{st} (1-f_3^{st})$	" $\times p_4^{st} (1-f_4^{st})$
				" $\times p_3^{st} S_3^{st} \rho_4^{s\cdot}$	b

[a] There will one such array for every combination of pre- and post-strata laid out as in Figure 3.3.2a. Refer to Figure 3.4.2a for the correspondence between these formulae and the reduced-data array components.

[b] Must be 0 since experiment is terminated in year 4.

Figure 3.4.2c
Expected reduced-data array in the Partial-Fidelity Model with sightings in the post-strata using the parameters of Table 1.5a and assuming a constant sighting rate of 0.30 for all pre-strata within each post-stratum in all years.

Releases from pre-stratum 1

Year	Number Banded	Expected sightings or recoveries in post-stratum 1 by year: 1	2	3	4	Expected sightings or recoveries in post-stratum 2 by year: 1	2	3	4
1	1000	6.00	3.60	2.16	1.30	6.00	3.60	2.16	1.30
		14.00	8.40	5.04	3.02	14.00	8.40	5.04	3.02
		114.00	68.40	41.04	24.62	114.00	68.40	41.04	24.62
		27.12	14.15	5.79		32.54	16.98	6.95	
2	1000		6.00	3.60	2.16		6.00	3.60	2.16
			14.00	8.40	5.04		14.00	8.40	5.04
			114.00	68.40	41.04		114.00	68.40	41.04
			23.58	9.65			28.30	11.58	
3	1000			6.00	3.60			6.00	3.60
				14.00	8.40			14.00	8.40
				114.00	68.40			114.00	68.40
				16.08				19.30	

Figure 3.4.2c (continued)

Releases from pre-stratum 2

Year	Number Banded	Expected sightings or recoveries in post-stratum 1 by year: 1	2	3	4	Expected sightings or recoveries in post-stratum 2 by year: 1	2	3	4
1	1000	9.60	4.80	2.40	1.20	10.80	5.40	2.70	1.35
		22.40	11.20	5.60	2.80	25.20	12.60	6.30	3.15
		110.40	55.20	27.60	13.80	79.20	39.60	19.80	9.90
		23.72	10.71	3.86		21.33	9.64	3.48	
2	1000		9.60	4.80	2.40		10.80	5.40	2.70
			22.40	11.20	5.60		25.20	12.60	6.30
			110.40	55.20	27.60		79.20	39.60	19.80
			21.42	7.73			19.28	6.96	
3	1000			9.60	4.80			10.80	5.40
				22.40	11.20			25.20	12.60
				110.40	55.20			79.20	39.60
				15.46				13.91	

The row-wise similarities in each table are a result of assuming that the parameters of Table 1.5a are constant over time and assuming that the sighting rate is 30% for all pre-strata within each post-stratum in all years.

Then, for example, in Figure 3.4.2c the expected number of animals released from pre-stratum 2 in year 1, and whose band is recovered **AND** sighted in post-stratum 1 in year 1, $E(A_{11}^{21})$, is computed as:

$$E(A_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times p_1^{21} \times f_1^{21} \qquad \text{(or)}$$

$$E(A_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.30 \times 0.08 = 9.60.$$

In a similar way, the expected number of animals released from pre-stratum 2 in year 1 and whose band is recovered **BUT** not sighted in post-stratum 1 in year 1, $E(B_{11}^{21})$, Figure 3.4.2c, is computed as:

$$E(B_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times (1-p_1^{21}) \times f_1^{21} \qquad \text{(or)}$$

$$E(B_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times (1.00-0.30) \times 0.08 = 22.40.$$

Note that the expected number of animals released from pre-stratum 2 in year 1 and whose band is recovered in post-stratum 1 in year 1 (whether sighted or not), $E(R_{11}^{21})$, is computed as the sum of these two components, and equals that shown in Figure 3.3.2b, i.e.:

$$E(R_{11}^{21}) = 32.00 = E(A_{11}^{21}) + E(B_{11}^{21}) = 9.60 + 22.40 \quad .$$

The expected number of animals released from pre-stratum 2 in year 1 and whose band is sighted **WITHOUT** being recovered in post-stratum 1 in year 1, ($E(W_{11}^{21})$, Figure 3.4.2c), is computed as:

$$E(W_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times p_1^{21} \times (1-f_1^{21}) \qquad \text{(or)}$$

$$E(W_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.30 \times (1.00-0.08) = 110.40.$$

As before, the parameter $S_i^{s\cdot}$ represents the net survival rate of animals released from pre-stratum *s* over all the post-strata (including those without recoveries) from the time of banding in year *i* to the time of banding in year *i*+1. Since it is assumed that sighting has no effect on survival, all the sightings of an animal prior to the current sighting or recovery can be "ignored" when computing the expected values of the recovery statistics. For example, in Figure 3.4.2c the expected number of animals released from pre-stratum 2 in year 1 and whose bands are either: recovered **AND** sighted; recovered **BUT** not sighted; or sighted **WITHOUT** being recovered in post-stratum 1 in year 2 are computed as:

$$E(A_{12}^{21}) = N_1^2 \times S_1^{2\cdot} \times M_2^{2\cdot} \times m_2^{21} \times p_2^{21} \times f_2^{21} \qquad \text{(or)}$$

$$E(A_{12}^{21}) = 1000 \times 0.50 \times 0.70 \times 0.5714 \times 0.30 \times 0.08 = 4.80 \quad ,$$

$$E(B_{12}^{21}) = N_1^2 \times S_1^{2\cdot} \times M_2^{2\cdot} \times m_2^{21} \times (1-p_2^{21}) \times f_2^{21} \qquad \text{(or)}$$

$$E(B_{12}^{21}) = 1000 \times 0.50 \times 0.70 \times 0.5714 \times (1.00-0.30) \times 0.08 = 11.20,$$

and

$$E(W_{12}^{21}) = N_1^2 \times S_1^{2\cdot} \times M_2^{2\cdot} \times m_2^{21} \times p_2^{21} \times (1-f_2^{21}) \qquad \text{(or)}$$

$$E(W_{12}^{21}) = 1000 \times 0.50 \times 0.70 \times 0.5714 \times 0.30 \times (1.00-0.08) = 55.20$$

respectively.

The remaining type of statistic in the reduced-data array is the number of animals released from pre-stratum *s* in year *i*, and whose bands are sighted without being recovered in post-stratum *t* in year *j*, and are recovered or sighted in later years in any post-stratum ($W_{ij\cdot}^{st\cdot}$).

In order for a band to be sighted or recovered subsequent to being sighted without being recovered in post-stratum t in year j, the animal must survive in post-stratum t in year j (conditional upon the band not being recovered). Then, by the assumptions of the Partial-Fidelity Model, the animal will return to its pre-stratum and, because of the assumption of Markovian migrations and survival, it will be subject to the same "forces" of migration, band-recovery, sighting, and survival as newly released animals in pre-stratum s in year j+1. Since the animal was sighted in post-stratum t in year j and is known to have survived (since its band is recovered or sighted later), the post-stratum specific survival rate (S_j^{st}) can be entered into the model.

Because animals may migrate to post-strata where no recoveries occurred, both the net survival rates over all post-strata ($S_i^{s\cdot}$), and the post-stratum specific survival rates (S_i^{st}) enter into the model. However, in the special case that $M_i^{s\cdot} = 1$, i.e., the experimenter is sure that all possible post-strata are included in the experiment, the inclusion of $S_i^{s\cdot}$ will be redundant since the net survival rates over all post-strata is computed as the convolution of the emigration rates and the post-stratum specific survival rates as given in Section 3.2.

Then for example, in Figure 3.4.2c the expected number of animals released from pre-stratum 2 in year 1 whose bands were sighted without being recovered in post-stratum 1 in year 2, and whose bands are subsequently recovered or sighted during the remainder of the experiment is computed as:

$$E(W_{12\cdot}^{21\cdot}) = N_1^2 \times S_1^{2\cdot} \times M_2^{2\cdot} \times m_2^{21} \times p_2^{21} \times S_2^{21} \times \rho_3^{2\cdot}$$

where $\rho_3^{2\cdot}$ is the probability than an animal will be recovered or sighted when released in pre-stratum 2 in year 3. Or,

$$E(W_{12\cdot}^{21\cdot}) = 1000 \times 0.50 \times 0.70 \times 0.5714 \times 0.30 \times 0.50 \times \rho_3^{2\cdot}$$

$$= 30.00 \times \rho_3^{2\cdot} \quad .$$

(Note that the band-recovery rate does not enter into the computation since, by definition, the post-stratum specific survival rate includes, as a hidden component, the probability of not being recovered).

Now $\rho_3^{2\cdot}$ is tedious to compute but, using Formula 3.A.2 presented in Appendix 3.A, $\rho_3^{2\cdot} = 0.357$, and so

$$E(W_{12\cdot}^{21\cdot}) = 30.00 \times 0.357 = 10.71.$$

Hence, of the 1000 animals banded and released in pre-stratum 2 in year 1, it is expected that 55.20 animals will be sighted without being recovered in post-stratum 1 in year 2 (W_{12}^{21}), and of these, 10.71 animals will be subsequently sighted or recovered during the remainder of the experiment ($W_{12\cdot}^{21\cdot}$). As well,

$$E(W_{12}^{21})-E(W_{12\cdot}^{21\cdot}) = 55.20-10.71 = 44.49$$

is the expected number of animals released from pre-stratum 2 in year 1 whose bands were sighted for the last time in post-stratum 1 in year 2.

The expected total number of animals banded and released in pre-stratum 2 in year 1 that are sighted or recovered during the entire experiment, ignoring duplicate sightings, is computed as:

$$E(\sum_{j=1}^{4} \sum_{t=1}^{2} (A_{1j}^{2t}+B_{1j}^{2t}+(W_{1j}^{2t}-W_{1j\cdot}^{2t\cdot})))$$

or, from Figure 3.4.2c,

$9.60 + 22.40 + (110.40 - 23.72) +$	(Post-stratum 1)
$4.80 + 11.20 + (\ 55.20 - 10.71) +$	
$2.40 + \ 5.60 + (\ 27.60 - \ 3.86) +$	
$1.20 + \ 2.80 + (\ 13.80 - \ 0.00) +$	
$10.80 + 25.20 + (\ 79.20 - 21.33) +$	(Post-stratum 2)
$5.40 + 12.60 + (\ 39.60 - \ 9.64) +$	
$2.70 + \ 6.30 + (\ 19.80 - \ 3.48) +$	
$1.35 + \ 3.15 + (\ \ 9.90 - \ 0.00)$	$= 410.26$

This agrees with the computed value of $\rho_1^{2\cdot}=0.41026$ found using Formula 3.A.2, representing the probability of recovering or sighting an animal released from pre-stratum 2 in year 1 during the entire experiment (410.26/1000=0.41026).

3.4.3 ESTIMATION

In this model there are al total emigration parameters ($M_i^{s\cdot}$), $a(b-1)l$ relative emigration parameters (m_i^{st}), abl sighting parameters (p_i^{st}), abl band-recovery parameters (f_i^{st}), $a(l-1)$ net survival over all post-strata parameters ($S_i^{s\cdot}$), and $ab(l-1)$ post-stratum specific survival rates (S_i^{st}), for a total of $a(4bl+l-b-1)$ parameters.

Using the methodology as outlined in Chapter 1, and the data representation shown in Appendix 3.A, the MSS can be identified. It has dimension $a(4bl+k-b-1)$, and one representation of the MSS is easily computed from the reduced-data array as:

$A_{\cdot j}^{st}$	$s=1...a$ $t=1...b$ $j=1...l$	The total number of animals released from pre-stratum s whose bands were recovered **AND** sighted in post-stratum t in year j.
$B_{\cdot j}^{st}$	$s=1...a$ $t=1...b$ $j=1...l$	The total number of animals released from pre-stratum s whose bands were recovered **BUT** not sighted in post-stratum t in year j.
$W_{\cdot j}^{st}$	$s=1...a$ $t=1...b$ $j=1...l$	The total number of animals released from pre-stratum s whose bands were sighted **WITHOUT** being recovered in post-stratum t in year j.

$W^{st\cdot}_{\cdot j\cdot}$	$s=1\ldots a$ $t=1\ldots b$ $j=1\ldots l-1$	The total number of animals out of $W^{st}_{\cdot j}$ that are subsequently recovered or sighted anywhere during the remainder of the experiment.
$Z^{s\cdot}_{i}$	$s=1\ldots a$ $i=1\ldots k-1$	The total number of animals released from pre-stratum s that were alive at time i and seen or recovered after time i.

The total number of unique animals from the N^{s}_{i} released that are recovered or sighted during the rest of the experiment can be derived from the MSS as:

$$A^{s\cdot}_{i\cdot}+B^{s\cdot}_{i\cdot}+W^{s\cdot}_{i\cdot}-W^{s\cdot\cdot}_{i\cdot\cdot} = Z^{s\cdot}_{i}+A^{s\cdot}_{\cdot i}+B^{s\cdot}_{\cdot i}+W^{s\cdot}_{\cdot i}-W^{s\cdot\cdot}_{\cdot i\cdot}-Z^{s\cdot}_{i-1}.$$

Since the dimension of the MSS is less than the number of parameters, some confounding still exists. However, it is restricted to parameters for years of recovery between the cessation of banding and the end of the experiment, i.e., in years $k+1\ldots l$.

A full rank set of identifiable parameters and their MLEs is presented in Table 3.4.3; variances and covariances may be found in Appendix 3.B. From the expressions in Appendix 3.B, it can be seen that the precision of the estimates depends greatly upon the sighting rate, with a high sighting rate giving good precision.

The estimates of the relative immigration rates and the relative harvest-derivation rates are found by simply replacing each parameter in the definition by its MLE, and using the independent estimates of the pre-stratum population sizes and the post-stratum band-reporting rates as required. Variances and covariances may be found using the

Table 3.4.3

MLEs for the partial-fidelity model with sightings in the post-strata

$$\hat{f}^{st}_{i} = \frac{A^{st}_{\cdot i}}{A^{st}_{\cdot i}+W^{st}_{\cdot i}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=1\dots l \end{array} \qquad = \frac{\text{number sighted and recovered}}{\text{number sighted}}$$

$$\hat{p}^{st}_{i} = \frac{A^{st}_{\cdot i}}{A^{st}_{\cdot i}+B^{st}_{\cdot i}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=1\dots l \end{array} \qquad = \frac{\text{number sighted and recovered}}{\text{number recovered}}$$

$$\hat{\rho}^{s\cdot}_{i} = \frac{A^{s\cdot}_{i\cdot}+B^{s\cdot}_{i\cdot}+W^{s\cdot}_{i\cdot}-W^{s\cdot\cdot}_{i\cdot\cdot}}{N^{s}_{i}} \qquad \begin{array}{l} s=1\dots a \\ i=1\dots k \end{array} \qquad = \frac{\text{total animals recovered or sighted from those released in pre-stratum s in year i}}{\text{total released in pre-stratum s in year i}}$$

$$S^{s\cdot}_{k}\dots \widehat{S^{s\cdot}_{i-1}\rho^{s\cdot}_{i}} = \frac{Z^{s\cdot}_{i-1}}{T^{s\cdot}_{k}}\,\hat{\rho}^{s\cdot}_{k} \qquad \begin{array}{l} s=1\dots a \\ i=k+1\dots l \end{array}$$

$$\widehat{M^{s\cdot}_{i} m^{st}_{i}} = \frac{(A^{st}_{\cdot i}+W^{st}_{\cdot i})(A^{st}_{\cdot i}+B^{st}_{\cdot i})}{A^{st}_{\cdot i}} \times \frac{\hat{\rho}^{s\cdot}_{i}}{T^{s\cdot}_{i}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=1\dots k \end{array}$$

$$\widehat{S^{s\cdot}_{k}\dots S^{s\cdot}_{i-1}M^{s\cdot}_{i} m^{st}_{i}} = \frac{(A^{st}_{\cdot i}+W^{st}_{\cdot i})(A^{st}_{\cdot i}+B^{st}_{\cdot i})}{A^{st}_{\cdot i}} \times \frac{\widehat{S^{s\cdot}_{k}\dots S^{s\cdot}_{i-1}\rho_{i}}}{T^{s\cdot}_{i}} \qquad \begin{array}{l} s=1\dots a \\ t=1\dots b \\ i=k+1\dots l \end{array}$$

Table 3.4.3 (continued)

$\hat{M}_i^{s\cdot} = \sum_{t=1}^{b} M_i^{s\cdot}\hat{m}_i^{st}$	s=1...a i=1...k	
$\widehat{S_k^{s\cdot}\cdots S_{i-1}^{s\cdot}M_i^{s\cdot}} = \sum_{t=1}^{b} \widehat{S_k^{s\cdot}\cdots S_{i-1}^{s\cdot}M_i^{s\cdot}}\, m_i^{st}$	s=1...a i=k+1...l	
$\hat{m}_i^{st} = M_i^{s\cdot}\hat{m}_i^{st}/\hat{M}_i^{s\cdot}$	s=1...a t=1...b i=1...k	
$\hat{m}_i^{st} = \widehat{S_k^{s\cdot}\cdots S_{i-1}^{s\cdot}M_i^{s\cdot}}\, m_i^{st}/\widehat{S_k^{s\cdot}\cdots S_{i-1}^{s\cdot}M_i^{s\cdot}}$	s=1...a t=1...b i=k+1...l	
$\hat{S}_i^{s\cdot} = \dfrac{\hat{\rho}_i^{s\cdot}}{\hat{\rho}_{i+1}^{s\cdot}}\,\dfrac{Z_i^{s\cdot}}{T_i^{s\cdot}}$	s=1...a i=1...k-1	This is obtained by treating the last sighting of an animal or its recovery as a "recovery" in Model 2a of Chapter 2.
$\widehat{S_i^{st}\rho_{i+1}^{s\cdot}} = \dfrac{W_{\cdot i\cdot}^{st\cdot}}{A_{\cdot i}^{st}+W_{\cdot i}^{st}}$	s=1...a t=1...b i=1...l-1	= $\dfrac{\text{number surviving and sighted or recovered after being sighted without being recovered in post-stratum t in year i}}{\text{number sighted in post-stratum t in year i}}$

delta method. Absolute or total immigration or harvest-derivation rates still cannot be estimated unless the pre-strata are exhaustive.

3.4.4 TESTING

3.4.4.1 A goodness-of-fit test

A general non-specific goodness-of-fit test to the Partial-Fidelity Model with sightings can, in theory, be constructed using the methods outlined in Chapter 1. However, as shown in Appendix 3.A, the full-data representation is complex, and the large-sample contingency table approximation will consist of many tables with small expected and observed counts which will require extensive pooling and will lack any appreciable power. (The same problems occurred in the general goodness-of-fit tests in capture-recapture models presented by Pollock, Hines, and Nichols, 1985).

Since the reduced-data array are the sufficient (but not minimally sufficient) statistics for the model, a goodness-of-fit test can be constructed using the methods of Chapter 1 with the reduced-data array, rather than the full-data array. The derivation is presented in Appendix 3.A, and a large sample contingency table that may be used to compute the approximate significance level of the test is presented in Table 3.4.4.1. This test is based upon the same intuitive ideas as the goodness-of-fit test in Chapter 2 by examining the recoveries or sightings of animals newly released and previously released. The contingency tables are slightly more complicated since an animal may be sighted more than once. As before, they are conditionally independent

Table 3.4.4.1
A large-sample contingency table used in the goodness-of-fit test for the Partial-Fidelity Model with sightings in the post-strata based upon the reduced-data array

A large-sample contingency table is constructed by considering the sightings or recoveries in year *j* conditional upon the animal being sighted or recovered in year *j* or later, for newly released and previously released animals from pre-stratum *s*. Note that there is a separate cell for each value of *t*=1...*b*, for a total of 4*b*+1 columns in the table.

Total unique animals released from pre-stratum s **in year i**, and sighted or recovered in year j or later.	Animals recovered **AND** sighted in year j in post-stratum t from those at left for t=1...b	Animals recovered **BUT** not sighted in year j in post-stratum t from those at left for t=1...b	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and not sighted or recovered after year j from those at left; t=1...b	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and sighted or recovered after year j from those at left; t=1...b	Animals recovered or sighted **only** after year j in any post-strata from those at left
Total unique animals released from pre-stratum s **before year i**, and sighted or recovered in year j or later.	Animals recovered **AND** sighted in year j in post-stratum t from those at left for t=1...b	Animals recovered **BUT** not sighted in year j in post-stratum t from those at left for t=1...b	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and not sighted or recovered after year j from those at left; t=1...b	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and sighted or recovered after year j from those at left; t=1...b	Animals recovered or sighted **only** after year j in any post-strata from those at left

Or:

$\sum_{m=j}^{l} A^{s\cdot}_{im}+B^{s\cdot}_{im}+W^{s\cdot}_{im}-W^{s\cdot\cdot}_{im\cdot}$	A^{st}_{ij} for t=1...b	B^{st}_{ij} for t=1...b	$W^{st}_{ij}-W^{st\cdot}_{ij\cdot}$ for t=1...b	$W^{st\cdot}_{ij\cdot}$ for t=1...b	$\sum_{m=j+1}^{l} (A^{s\cdot}_{im}+B^{s\cdot}_{im}+W^{s\cdot}_{im}-W^{s\cdot\cdot}_{im\cdot}) - W^{s\cdot\cdot}_{ij\cdot}$
$\sum_{v=1}^{i-1}\sum_{m=j}^{l} A^{s\cdot}_{vm}+B^{s\cdot}_{vm}+W^{s\cdot}_{vm}-W^{s\cdot\cdot}_{vm\cdot}$	$\sum_{v=1}^{i-1} A^{st}_{vj}$ for t=1...b	$\sum_{v=1}^{i-1} B^{st}_{vj}$ for t=1...b	$\sum_{v=1}^{i-1} W^{st}_{vj}-W^{st\cdot}_{vj\cdot}$ for t=1...b	$\sum_{v=1}^{i-1} W^{st\cdot}_{vj\cdot}$ for t=1...b	$\sum_{v=1}^{i-1}\sum_{m=j+1}^{l} (A^{s\cdot}_{vm}+B^{s\cdot}_{vm}+W^{s\cdot}_{vm}-W^{s\cdot\cdot}_{vm\cdot}) - W^{s\cdot\cdot}_{vj\cdot}$
$\sum_{v=1}^{i}\sum_{m=j}^{l} A^{s\cdot}_{vm}+B^{s\cdot}_{vm}+W^{s\cdot}_{vm}-W^{s\cdot\cdot}_{vm\cdot}$	$\sum_{v=1}^{i} A^{st}_{vj}$ for t=1...b	$\sum_{v=1}^{i} B^{st}_{vj}$ for t=1...b	$\sum_{v=1}^{i} W^{st}_{vj}-W^{st\cdot}_{vj\cdot}$ for t=1...b	$\sum_{v=1}^{i} W^{st\cdot}_{vj\cdot}$ for t=1...b	$\sum_{v=1}^{i}\sum_{m=j+1}^{l} (A^{s\cdot}_{vm}+B^{s\cdot}_{vm}+W^{s\cdot}_{vm}-W^{s\cdot\cdot}_{vm\cdot}) - W^{s\cdot\cdot}_{vj\cdot}$

Table 3.4.4.1 (continued)

There will be one such table for each combination of pre-stratum s=1...a, year of release i=2...k, and year of recovery j=i...l. Each table will have 4b degrees of freedom (except that when j=l, the table will have 3b-1 degrees of freedom).

There will be a total of $(k-1)(4bl-1)-b(2k^2-k-1)$ degrees of freedom for each pre-stratum s=1...a.

Intuitively, animals released from pre-statum s in year i should behave in the same way as previously released animals.

The test takes a slightly complicated form compared to the goodness-of-fit tests of Chapter 2 since the reduced-data array does not possess a simple multinomial structure due to possible multiple sightings of an animal in different years.

and the overall goodness-of-fit statistic is found by summing the individual test-statistics and degrees of freedom. Some of the contingency tables may have small observed and expected counts (particularly near the end of the experiment), and may either require pooling, or be omitted with a corresponding reduction in the degrees of freedom.

The goodness-of-fit test may indicate that the Partial-Fidelity Model is not appropriate if one or more of the sighting, recovery, survival, or migration rates in year j are not independent of the year of release. Typically, the experiment can be designed so that the sighting and recovery rates do not depend greatly upon the year of release, but it is more difficult (or impossible) to ensure that survival and migration rates do not depend upon the year of release. A common problem is that the stress of banding and release may adversely affect the survival rate in the first year after release. In this case, the survival rate of animals in year j would be smaller for those released in year j than for those in previous releases. As well, if survival was age dependent, and banding was done on young animals only, the survival rate of newly banded animals would likely be lower than previously banded animals. Both cases are reflected in smaller than expected values in the last column of the second row of the contingency table.

If the assumption of Markovian behaviour in selecting the post-strata in year j is not true, then there will be a gradual shift in the relative migration rates of a cohort of animals towards the post-strata with the higher survival rates. Consequently, if banding selects younger animals who have not yet established a migration pattern, their migration rates will differ from previous releases. This will be reflected in the differing relative counts between the two rows in the first $4b$ columns of the contingency tables.

3.4.4.2 Testing among models

When sightings of bands takes place in the post-strata, most of the problems outlined in Section 3.3.4 on testing hypotheses about the parameters no longer exist. However, many of the models with restrictions placed upon the parameters are less than full rank (i.e., the number of parameters is less than the dimension of the MSS), and many estimators of the parameters are not available in closed form; numerical methods must be used.

A computer program using the methods outlined in Appendix 3.F has been written to estimate the parameters under the full model and under various hypotheses restricting the parameters. It computes the value of the likelihood (up to constant terms) for each model so that likelihood ratio tests may be used to discriminate between models. A numerical example of the use of the computer program to analyze a set of data is presented in Section 3.7.

3.4.5 SUMMARY

By obtaining additional sightings of the banded animals in the post-strata, many of the problems caused by the confounding of the band-recovery and emigration rates can be resolved. The study must be designed carefully to ensure that the crucial assumption of independence between sightings and recoveries is not violated. Most parameters can now be estimated; confounding of parameters is restricted to years of recovery after banding has stopped. Tests of hypotheses about the biological parameters of interest can now be performed without any additional assumptions. Unfortunately, most restricted models are now less than full rank, and numerical methods (method of scoring, and likelihood ratio tests) should be used.

3.5 COMPLETE-FIDELITY MODEL USING ORDINARY BAND-RECOVERY DATA

Having dealt with the Partial-Fidelity Model, I will now examine inference in the Complete-Fidelity Model. The latter differs from the former in that an additional assumption is made that animals are faithful to both the pre-stratum of release and the post-stratum chosen in the first year of migration after release. Inference in this model follows closely that of the Partial-Fidelity Model.

In this section the assumptions and model parameters for the Complete-Fidelity Model are first discussed. Then the use of ordinary band-recovery data is examined and they are found to be inadequate except for inferences about the harvest-derivation rates. I then indicate what further assumptions are required for inferences about the other parameters of the model while remaining in an ordinary band-recovery context so that the feasibility of using existing data may be ascertained.

3.5.1 ASSUMPTIONS

The assumptions for the Complete-Fidelity Model are similar to those of the Partial-Fidelity Model given in Section 3.3.1 except for the assumption that:

- complete fidelity occurs to the post-stratum chosen in the first year of migration. Two common scenarios can be envisaged: (1) the banded-cohorts are young animals making their first migration, in which case animals will be faithful to the post-strata chosen in the first year after release; (2) animals choose the post-stratum prior to banding time (e.g., animals choose post-strata at age 1 but are not banded until age 3) and the banding-process is not post-stratum selective.

3.5.2 MODEL AND INTERPRETATION OF PARAMETERS

The number of recoveries in each post-stratum in each year from each year of release and each pre-stratum can be displayed in the same fashion as in the Partial-Fidelity Model (Figure 3.3.2a). Under the assumptions of Section 3.5.1, the recoveries from each year's releases from each pre-stratum can be modelled as independent multinomial distributions. The expected number of recoveries in the case of k=3 years of banding, l=4 years of recoveries, a=2 pre-strata where banding occurred, and b=2 post-strata where recoveries occur are shown in Figure 3.5.2a. A simple numerical example showing the expected number of recoveries assuming that the parameter values in Table 1.5a are the same for all releases and are constant over time is shown in Figure 3.5.2b and is discussed below. It is assumed that only animals from the first two pre-strata from Table 1.5a are banded, and that recoveries occur only in the first two post-strata corresponding to Case II in the table.

The parameter values of Table 1.5a can be used for both the Partial- and Complete-Fidelity Models since the parameters have similar interpretations in both models and since the timing of the migration process relative to banding and recovery times is the same in both models. The parameter f_i^{st} again represents the band-recovery rate for animals released from pre-stratum s and recovered in post-stratum t in year i. The parameter S_i^{st} again represents the post-stratum specific

Figure 3.5.2a

Expected number of recoveries in the Complete-Fidelity Model using ordinary band-recovery data in the case of k=3 years of releases, l=4 years of recovery, a=2 pre-strata where banding occurred, and b=2 post-strata where recoveried occurred

Expected Recoveries for pre-stratum 1

Year Banded	Number Banded	Post-stratum 1 recoveries by year: 1	2	3	4	Post-stratum 2 recoveries by year: 1	2	3	4
1	N^1_1	$N^1_1 M^{1\cdot}_1 m^{11}_1 f^{11}_1$	$N^1_1 M^{1\cdot}_1 m^{11}_1 S^{11}_1 f^{11}_2$	$N^1_1 M^{1\cdot}_1 m^{11}_1 S^{11}_1 S^{11}_2 f^{11}_3$	$N^1_1 M^{1\cdot}_1 m^{11}_1 S^{11}_1 S^{11}_2 S^{11}_3 f^{11}_4$	$N^1_1 M^{1\cdot}_1 m^{12}_1 f^{12}_1$	$N^1_1 M^{1\cdot}_1 m^{12}_1 S^{12}_1 f^{12}_2$	$N^1_1 M^{1\cdot}_1 m^{12}_1 S^{12}_1 S^{12}_2 f^{12}_3$	$N^1_1 M^{1\cdot}_1 m^{12}_1 S^{12}_1 S^{12}_2 S^{12}_3 f^{12}_4$
2	N^1_2		$N^1_2 M^{1\cdot}_2 m^{11}_2 f^{11}_2$	$N^1_2 M^{1\cdot}_2 m^{11}_2 S^{11}_2 f^{11}_3$	$N^1_2 M^{1\cdot}_2 m^{11}_2 S^{11}_2 S^{11}_3 f^{11}_4$		$N^1_2 M^{1\cdot}_2 m^{12}_2 f^{12}_2$	$N^1_2 M^{1\cdot}_2 m^{12}_2 S^{12}_2 f^{12}_3$	$N^1_2 M^{1\cdot}_2 m^{12}_2 S^{12}_2 S^{12}_3 f^{12}_4$
3	N^1_3			$N^1_3 M^{1\cdot}_3 m^{11}_3 f^{11}_3$	$N^1_3 M^{1\cdot}_3 m^{11}_3 S^{11}_3 f^{11}_4$			$N^1_3 M^{1\cdot}_3 m^{12}_3 f^{12}_3$	$N^1_3 M^{1\cdot}_3 m^{12}_3 S^{12}_3 f^{12}_4$

Expected Recoveries for pre-stratum 2

Year Banded	Number Banded	Post-stratum 1 recoveries by year: 1	2	3	4	Post-stratum 2 recoveries by year: 1	2	3	4
1	N^2_1	$N^2_1 M^{2\cdot}_1 m^{21}_1 f^{21}_1$	$N^2_1 M^{2\cdot}_1 m^{21}_1 S^{21}_1 f^{21}_2$	$N^2_1 M^{2\cdot}_1 m^{21}_1 S^{21}_1 S^{21}_2 f^{21}_3$	$N^2_1 M^{2\cdot}_1 m^{21}_1 S^{21}_1 S^{21}_2 S^{21}_3 f^{21}_4$	$N^2_1 M^{2\cdot}_1 m^{22}_1 f^{22}_1$	$N^2_1 M^{2\cdot}_1 m^{22}_1 S^{22}_1 f^{22}_2$	$N^2_1 M^{2\cdot}_1 m^{22}_1 S^{22}_1 S^{22}_2 f^{22}_3$	$N^2_1 M^{2\cdot}_1 m^{22}_1 S^{22}_1 S^{22}_2 S^{22}_3 f^{22}_4$
2	N^2_2		$N^2_2 M^{2\cdot}_2 m^{21}_2 f^{21}_2$	$N^2_2 M^{2\cdot}_2 m^{21}_2 S^{21}_2 f^{21}_3$	$N^2_2 M^{2\cdot}_2 m^{21}_2 S^{21}_2 S^{21}_3 f^{21}_4$		$N^2_2 M^{2\cdot}_2 m^{22}_2 f^{22}_2$	$N^2_2 M^{2\cdot}_2 m^{22}_2 S^{22}_2 f^{22}_3$	$N^2_2 M^{2\cdot}_2 m^{22}_2 S^{22}_2 S^{22}_3 f^{22}_4$
3	N^2_3			$N^2_3 M^{2\cdot}_3 m^{21}_3 f^{21}_3$	$N^2_3 M^{2\cdot}_3 m^{21}_3 S^{21}_3 f^{21}_4$			$N^2_3 M^{2\cdot}_3 m^{22}_3 f^{22}_3$	$N^2_3 M^{2\cdot}_3 m^{22}_3 S^{22}_3 f^{22}_4$

Figure 3.5.2b

Expected number of recoveries in the Complete-Fidelity Model using ordinary band-recovery data in the case of k=3 years of releases, l=4 years of recovery, a=2 pre-strata, and b=2 post-strata assuming that the parameters of Table 1.5a are constant over time.

Expected Recoveries for pre-stratum 1

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	1000	20.00	10.00	5.00	2.50	20.00	12.00	7.20	4.32
2	1000		20.00	10.00	5.00		20.00	12.00	7.20
3	1000			20.00	10.00			20.00	12.00

Expected Recoveries for pre-stratum 2

Year Banded	Number Banded	Post-stratum 1 recoveries by year 1	2	3	4	Post-stratum 2 recoveries by year 1	2	3	4
1	1000	32.00	16.00	8.00	4.00	36.00	21.60	12.96	7.78
2	1000		32.00	16.00	8.00		36.00	21.60	12.96
3	1000			32.00	16.00			36.00	21.60

The row-wise similarities are a result of assuming that the parameters of Table 1.6a are constant over time.

survival rate in post-stratum t between banding time in years i and i+1 for those animals released in pre-stratum s. The parameter $M_i^{s\cdot}$ still represents the total emigration rate of animals from pre-stratum s to any of the sampled post-strata but now is applicable only to animals released in year i. The parameter m_i^{st} still represents the relative emigration rate of animals from pre-stratum s to post-stratum t but again is only applicable to animals released in year i.

The Complete-Fidelity Model differs from the Partial-Fidelity Model in two important ways (compare Figures 3.5.2a and 3.3.2a):

- a post-stratum specific survival rate (as opposed to the net survival rate over all post-strata) enters into the model.
- only the emigration rates in the year of release enter into the model

Since complete fidelity to the post-strata is assumed to occur, all animals recovered in post-stratum t must have emigrated to post-stratum t in all years between banding and recovery and been subject to post-stratum t's survival rate. The migration rates in Table 1.5a apply only to the year of release, since migration in later years is completely determined from the initial migration rates and subsequent post-stratum specific survival rates.

The expected number of bands returned from animals released in year 1 in pre-stratum 2 and recovered in post-stratum 1 in year 1, $E(R_{11}^{21})$, is computed as:

$$E(R_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times f_1^{21} \qquad \text{or}$$

$$E(R_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.08 = 32.0.$$

Because the post-stratum specific survival rate in post-stratum 1 for animals released from pre-stratum 2 is 50% (Table 1.5a), only 200 of the 400 banded animals that emigrated to post-stratum 1 (1000×0.70×0.5714) will survive to return to pre-stratum 2. Under the complete-fidelity assumption, all 200 animals will emigrate in year 2 back to post-stratum 1. Hence the expected number of bands recovered in post-stratum 1 in year 2 from those released from pre-stratum 2 in year 1, $E(R_{12}^{21})$, is computed as:

$$E(R_{12}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times S_1^{21} \times f_2^{21} \quad \text{or}$$

$$E(R_{12}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.50 \times 0.08 = 16.00$$

3.5.3 ESTIMATION

In this model, there are *ak* total emigration parameters ($M_i^{s\cdot}$), *a(b-1)k* relative emigration parameters (m_i^{st}), *abl* band-recovery parameters (f_i^{st}), and *a(l-1)b* post-stratum specific survival parameters (S_i^{st}) for a total of *ab(2l+k-1)* parameters. The likelihood function is computed in a similar fashion as in the Partial-Fidelity Model; however, it is not immediately obvious if any confounding takes place.

Two questions are considered. First exactly what parameters may be estimated without further assumptions using ordinary band-recovery models? Second, what further assumptions are required in order to estimate any confounded parameters.

3.5.3.1 Estimation without further assumptions

The MSS has dimension $ab(l+k-1)$, and one representation of its components is:

$$R^{st}_{i\cdot} \quad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{array} \qquad\qquad R^{st}_{\cdot j} \quad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ j=1\ldots l-1 \end{array} .$$

One set of identifiable functions of the parameters (and their estimators) is found using the expected values of the MSS as:

$$M^{s\cdot}_{i}\hat{m}^{st}_{i}f^{st}_{i} = \frac{R^{st}_{i\cdot}R^{st}_{\cdot i}}{N^{s}_{i}\,T^{st}_{i}} \qquad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{array}$$

$$M^{s\cdot}_{k}\hat{m}^{st}_{k}S^{st}_{k}S^{st}_{k+1}\ldots f^{st}_{i} = \frac{R^{st}_{k\cdot}\,R^{st}_{\cdot i}}{N^{s}_{k}\,T^{st}_{k}} \qquad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=k+1\ldots l \end{array}$$

$$\frac{M^{s\cdot}_{i}\hat{m}^{st}_{i}}{M^{s\cdot}_{i+1}m^{st}_{i+1}}\,S^{st}_{i} = \frac{R^{st}_{i\cdot}\,Z^{st}_{i}\,N^{s}_{i+1}}{N^{s}_{i}\,T^{st}_{i}\,R^{st}_{i+1,\cdot}} \qquad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k-1 \end{array}$$

From this set of identifiable functions, it is seen that the Complete-Fidelity Model is a simple reparameterization of Model 3 of Chapter 2 for each pre-stratum as follows:

Parameters in Model 3 of Chapter 2	Function of parameters from current model
f^{t}_{i}	$M^{s\cdot}_{i}m^{st}_{i}f^{st}_{i}$
S^{t}_{i}	$\frac{M^{s\cdot}_{i}m^{st}_{i}}{M^{s\cdot}_{i+1}m^{st}_{i+1}}\,S^{st}_{i}$

(Note that the post-stratum is indicated here by a superscript t whereas it was indicated by a superscript s in Chapter 2.) As noted in Chapter 2, the gross "band-recovery rate" and "annual post-stratum specific survival rate" of Model 3 include hidden emigration components. As in the Partial-Fidelity Model, the band-recovery and emigration parameters of the Complete-Fidelity Model are confounded; only their product may be estimated. In contrast to the Partial-Fidelity Model, the emigration rates are also confounded with the annual survival rates. This is somewhat surprising since it might be hoped that the additional restrictions in the Complete-Fidelity Model would decrease the amount of confounding.

As before, the total and absolute immigration rates cannot be estimated if all pre-strata are not included in the banding program. As well, the confounding of the band-recovery and emigration rates implies that relative immigration rates cannot be estimated.

The only parameters of biological interest that can be estimated are the relative harvest-derivation rates obtained by weighting the gross recovery rates (product of total emigration, relative emigration and band-recovery rates, $M_i^{s\cdot} m_i^{st} f_i^{st}$) by the estimates of the absolute or relative population size (N_i^{s*}) and the inverse of the band-reporting rate (λ_i^{st}):

$$\hat{D}_i^{st} = \frac{\hat{N}_i^{s*} \cdot \hat{M}_i^{s\cdot} \hat{m}_i^{st} \hat{f}_i^{st} \;/\; \hat{\lambda}_i^{st}}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot \hat{M}_i^{s\cdot} \hat{m}_i^{st} \hat{f}_i^{st} \;/\; \hat{\lambda}_i^{st}} = \frac{\hat{N}_i^{s*} \cdot R_{i\cdot}^{st} R_{\cdot i}^{st} / (N_i^{s} T_i^{st} \cdot \hat{\lambda}_i^{st})}{\sum_{s=1}^{a} \hat{N}_i^{s*} \cdot R_{i\cdot}^{st} R_{\cdot i}^{st} / (N_i^{s} T_i^{st} \cdot \hat{\lambda}_i^{st})} \qquad \begin{array}{l} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{array}$$

Variances may be estimated using the delta-method. In some circumstances, it is reasonable to assume that the band-reporting rates within post-stratum *t* in year *i* are homogeneous among the pre-strata ($\lambda_i^{st} = \lambda_i^{\cdot t}$) with a corresponding simplification in the estimator.

3.5.3.2 Assumptions necessary to estimate the confounded parameters

Similar assumptions as outlined in the Partial-Fidelity Model (Section 3.3.3.2) are required in order to estimate the emigration or immigration rates. The results for the Complete-Fidelity Model are completely analogous upon replacing the estimators of $M_i^{s\cdot} m_i^{st} f_i^{st}$ in the Partial-Fidelity Model with those from the Complete-Fidelity Model and so will not be discussed further.

The post-stratum specific survival rates may be estimated if the absolute migration rates ($M_i^{s\cdot} m_i^{st}$) are assumed to be homogeneous over time. This could occur if newly banded animals were young animals who have not yet made their choice of post-stratum, and if their choice of post-stratum depended upon factors that did not change from year to year. In other circumstances, this assumption will likely not be biologically reasonable because of the close connection between the emigration rates and the post-stratum survival rates as outlined in Section 3.5.4.3. For this reason, estimation of the post-stratum specific survival rates is not discussed further.

3.5.3.3 Summary of the results on estimation

Even under the restriction of complete fidelity, most parameters of interest cannot be estimated using ordinary band-recovery data because of the confounding of the parameters. Use of this type of data implies that:

- total emigration rates and band-recovery rates cannot be estimated separately, but their product may be estimated;

· relative emigration rates may be estimated if the relative magnitudes of the band-recovery rates among post-strata are known or can be estimated from other studies, i.e., $f_i^{st}=\alpha_i^{\cdot t} f_i^{s1}$ and $\alpha_i^{\cdot t}$ are known or estimated;

· relative immigration rates may be estimated if it is assumed that the band-recovery rates are homogeneous among pre-strata within a post-stratum ($f_i^{st}=f_i^{\cdot t}$);

· relative harvest-derivation rates may be estimated if independent estimates of the absolute or relative pre-stratum population sizes and the band-reporting rates are available;

· net survival rates over all post-strata ($S_i^{s\cdot}$) cannot be estimated;

· post-stratum specific survival rates (S_i^{st}) may be estimated if the emigration rates are homogeneous over time.

The assumptions necessary for parameter estimation cannot be tested using the data from an ordinary band-recovery experiment, and must be assessed on biological grounds.

3.5.4 TESTING

As in the Partial-Fidelity Model, it is not too surprising that ordinary band-recovery data are not sufficient for testing hypotheses about the parameters of the Complete-Fidelity Model. Again, under certain assumptions, meaningful tests can be constructed. In this section, I discuss testing the complete-fidelity assumption; partially testing the goodness-of-fit to the model; and the assumptions necessary for testing the homogeneity of the parameters over strata or over time.

3.5.4.1 Testing for complete-fidelity to the post-strata

It is not possible to test if complete-fidelity to the post-strata has occurred because the band on each animal is seen only twice (at release and at recovery) and the intermediate migrations of an animals between release and recovery are unknown. If additional sightings of an animal between release and recovery reveal that an animal was spotted in two different post-strata in different years, then a definite rejection of this assumption would occur; failure to find any such animals does not, of course, imply that the fidelity assumption is true. This may be verified only if every animal is followed through every migration each year.

It should be noted that even though the Complete-Fidelity Model is a reparameterization of Model 3 of Chapter 2 and the Partial-Fidelity Model is a reparameterization of Model 2a, the test of Model 2a vs. Model 3 is not a test of the Partial- vs Complete-Fidelity Models. Rather, it can be shown that Model 2a is also a reparameterization of the Complete-Fidelity Model assuming that the post-stratum specific survival rates are the same in all post-strata. Hence, that test can be viewed only as a test of the homogeneity of the post-stratum specific survival rates within the Complete-Fidelity Model (i.e., a test if $S_i^{st}=S_i^{s\cdot}$).

3.5.4.2 A partial goodness-of-fit test

Since the Complete-Fidelity Model is a reparameterization of Model 3 of Chapter 2, a partial, non-specific goodness-of-fit test can be constructed using the results of that Chapter. As in the Partial-Fidelity Model, the goodness-of-fit test does not test all the aspects of the model, since not all parameters are identifiable. There are no interesting partitions of the test as were found for the Partial-Fidelity Model.

3.5.4.3 Tests of the emigration rates

As in the Partial-Fidelity Model, the confounding of the emigration and band-recovery rates implies that a test for homogeneity of these rates cannot be constructed using ordinary band-recovery data without further assumptions about the band-recovery rates. However, in contrast to the results for the Partial-Fidelity Model, the population emigration rates may be highly dependent upon the post-stratum specific survival rates. For example, suppose that in the first year of a banding study, a population of 100,000 animals emigrate to only two post-strata in the ratio 60,000:40,000 and that the post-stratum survival rates are 50% and 30% respectively. Then, the first year absolute emigration rates to the two post-strata are 0.60 and 0.40. Now, of the animals that emigrated, only 30,000 and 12,000 survive and return from their respective post-strata and again emigrate back to the post-strata in the next year. In the absence of new animals entering the population through birth or immigration from outside the experiment, the absolute emigration rates in the second year are now 0.714=30,000/(30,000+12,000) and 0.286=12,000/(30,000+12,000), changes due solely to the differing post-stratum survival rates. This does not occur in the Partial-Fidelity Model since the migration rates in a year are completely independent of the previous migration choices.

It is unlikely that the emigration rates will be homogeneous in time unless: (1) the post-stratum specific survival rates are equal; or (2) animals starting their first seasonal migration (who will then establish their migration patterns for life) choose post-strata in such a way to compensate for the differential survival rates. The latter could occur if animals starting their first seasonal migration choose their post-strata based upon environmental factors present at banding time that are unrelated to the post-stratum survival rates. For example, using the previous numerical illustration, if 40,000 animals enter the population in the second year and choose their post-strata in the ratio 19,200:20,800, then the overall migration rates in the second year will again be 0.40=(30,000+19,200)/(30,000+12,000+40000) and 0.40=(12,000+20,800)/(30,000+12,000+40,000). Since the exact mechanism that is operating in the population is unknown, a test of homogeneous emigration rates must be interpreted carefully since the test may reject the hypothesis of homogeneous migration caused by other mechanisms. A similar problem occurs when testing the homogeneity of migration rates among pre-strata.

Testing for homogeneous relative emigration rates at the time of release:

If it is assumed that the band-recovery rates are proportional from year to year among the post-strata ($f_i^{st}=\alpha_i^{s\cdot}f_1^{st}$), then it is possible to test if the parametric functions:

$$\frac{M_i^{s\cdot}m_i^{st}f_i^{st}}{\sum_{t=1}^{b} M_i^{s\cdot}m_i^{st}f_i^{st}} = \frac{m_i^{st}\alpha_i^{s\cdot}f_1^{st}}{\sum_{t=1}^{b} m_i^{st}\alpha_i^{s\cdot}f_1^{st}} = \frac{m_i^{st}f_1^{st}}{\sum_{t=1}^{b} m_i^{st}f_1^{st}} \quad \text{for } s=1...a,\ t=1...b$$

are homogeneous for all releases, which in turn is equivalent to testing for homogeneous emigration rates among all releases. Unfortunately, even under this restriction, the p-value of the exact test is difficult to compute (Appendix 3.C.1) and the test has no simple large-sample contingency table approximation.

Using the same arguments that lead to the simple test of Model 2b vs. Model 3 in Chapter 2, a simpler test using only the direct recoveries can be developed. This test is not expected to suffer much loss of power relative to the exact test, and a large-sample contingency table test can be developed (Table 3.5.4.3a). It may be used to test for:

(i) $m_i^{st} = m_{\cdot}^{st}$ assuming that $f_i^{st} = \alpha_i^{s\cdot} f_1^{st}$, or

(ii) $f_i^{st} = \alpha_i^{s\cdot} f_1^{st}$ assuming that $m_i^{st} = m_{\cdot}^{st}$.

(iii) gross band-recovery rates (product of emigration and band-recovery rates) proportional over time.

The last test may be of interest in the context of Chapter 2 since the Complete-Fidelity Model is a simple reparameterization of Model 3 of that Chapter.

Testing for homogeneous relative emigration rates among pre-strata: If it is assumed that the band-recovery rates among pre-strata are proportional ($f_i^{st} = \alpha_i^{s\cdot} f_i^{1t}$) then it is possible to test if the parametric functions:

$$\frac{M_i^{s\cdot} m_i^{st} f_i^{st}}{\sum_{t=1}^{b} M_i^{s\cdot} m_i^{st} f_i^{st}} = \frac{m_i^{st} \alpha_i^{s\cdot} f_i^{1t}}{\sum_{t=1}^{b} m_i^{st} \alpha_i^{s\cdot} f_i^{1t}} = \frac{m_i^{st} f_i^{1t}}{\sum_{t=1}^{b} m_i^{st} f_i^{1t}} \quad \text{for } s=1...a,\ t=1...b$$

Table 3.5.4.3a
A large-sample contingency table used in the test for homogeneous relative emigration rates among releases in the Complete-Fidelity Model using ordinary band-recovery data

H: $m_{j}^{st} = m_{\cdot}^{st}$ assuming $f_{j}^{st} = \alpha_{j}^{s\cdot} f_{1}^{st}$

A: relative emigration rates in the year of release differ among releases under the same assumption

	MSS	Dimension
H	Z_{j}^{st}	$a(bl+k-1)$
	$R_{\cdot\cdot}^{st}$	
	$R_{j\cdot}^{s\cdot}$	
A	$R_{j\cdot}^{st}$	$ab(l+k-1)$
	$R_{\cdot j}^{st}$	

Contingency Table for each pre-stratum[1]

R_{11}^{s1}	R_{11}^{s2}	...	R_{11}^{sb}	$R_{11}^{s\cdot}$
R_{22}^{s1}	R_{22}^{s2}	...	R_{22}^{sb}	$R_{22}^{s\cdot}$
	⋮			
R_{kk}^{s1}	R_{kk}^{s2}	...	R_{kk}^{sb}	$R_{kk}^{s\cdot}$

[1]The exact test has no simple contingency table equivalent and is presented in Appendix 3.C.1. Use of this contingency table is not expected to result in much loss in power since the direct recoveries are often the largest.

There will be one such table for each pre-stratum $s=1...a$. Each table has $(b-1)(k-1)$ degrees of freedom.

The direct recoveries are proportional to the product of the relative emigration rates and the band-recovery rates. Since the band-recovery rates are, by assumption, already proportional among rows, then the entries in each row will be proportional when the relative emigration rates in the year of release are homogeneous over releases.

are homogeneous among pre-strata, which in turn, is equivalent to a test for homogeneous relative emigration rates among pre-strata.

As before, the p-value of the exact test is difficult to compute (Appendix 3.C.2) and the test has no simple large-sample contingency table approximation. Again, a simpler test can be developed that uses only the direct recoveries, and a large sample contingency table test can be developed (Table 3.5.4.3b). It can be used to test either:

(i) $m_i^{st} = m_i^{\cdot t}$ assuming that $f_i^{st} = \alpha_i^{s\cdot} f_i^{1t}$, or

(ii) $f_i^{st} = \alpha_i^{s\cdot} f_i^{1t}$ assuming that $m_i^{st} = m_i^{\cdot t}$.

The latter interpretation could be of interest since it is a test of proportional band-recovery rates among pre-strata regardless of the survival rates when it is reasonable to assume that pre-strata have the same migration patterns.

3.5.4.4 Tests of the immigration rates

Results similar to those in Section 3.3.4.3 (Partial-Fidelity Model) also apply in the Complete-Fidelity Model:

· a test for homogeneous relative immigration rates among post-strata is equivalent to the test for homogeneous relative emigration rates among pre-strata;

· an *ad hoc* test for homogeneous relative immigration rates over time must be constructed since independent estimates of the pre-stratum population sizes at the different times are required in addition to the assumptions about the band-recovery rates. An example of the derivation of an *ad hoc* test when sightings are

Table 3.5.4.3b

A large-sample contingency table used in the test for homogeneous relative emigration rates among pre-strata in the Complete-Fidelity Model using ordinary band-recovery data

H: $m_j^{st} = m_j^{\cdot t}$ assuming $f_j^{st} = \alpha_j^{s\cdot} f_j^{1t}$

A: relative migration rates in the year of release are pre-stratum specific under the same assumption

	MSS	Dimension
H	z_j^{st}	$a(bl-b+k)+k(b-1)$
	$R_{\cdot j}^{s\cdot}$	
	$R_{j\cdot}^{\cdot t}$	
A	$R_{j\cdot}^{st}$	$ab(l+k-1)$
	$R_{\cdot j}^{st}$	

Contingency Table for each year-of-release[1]

R_{jj}^{11}	R_{jj}^{12}	...	R_{jj}^{1b}	$R_{jj}^{1\cdot}$
R_{jj}^{21}	R_{jj}^{22}	...	R_{jj}^{2b}	$R_{jj}^{2\cdot}$
⋮				
R_{jj}^{a1}	R_{jj}^{a2}	...	R_{jj}^{ab}	$R_{jj}^{a\cdot}$
$R_{jj}^{\cdot 1}$	$R_{jj}^{\cdot 2}$	...	$R_{jj}^{\cdot b}$	

[1] The exact test has no simple contingency table equivalent and is presented in Appendix 3.C.2. Use of this contingency table is not expected to result in much loss in power since the direct recoveries are often the largest.

There is one such table for each year of release $j=1\ldots k$. Each table has $(a-1)(b-1)$ degrees of freedom.

The direct recoveries are proportional to the product of the relative emigration rates and the band-recovery rates. Since the band-recovery rates are, by assumption, already proportional among rows, then the entries in each row will be proportional when the relative emigration rates are homogeneous among pre-strata.

present is given in Appendix 3.F and illustrated in the numerical example of Section 3.7.

3.5.4.5 Tests of the harvest-derivation rates

Results similar to those in Section 3.3.4.5 (Partial-Fidelity Model) apply to the Complete-Fidelity Model:

- a contingency table used to test for homogeneous relative harvest-derivation rates among post-strata when band-reporting rates are homogeneous is equivalent to the contingency table used to test for homogeneous relative emigration rates among pre-strata;
- an *ad hoc* test for homogeneous relative harvest-derivation rates over time must be constructed since independent estimates of the pre-stratum population sizes and the band-reporting rates at the different times are required. An example of the derivation of an *ad hoc* test when sightings are present is given in Appendix 3.F and illustrated in the numerical example of Section 3.7.

3.5.4.6 Tests of the post-stratum specific survival rates.

Since the post-stratum specific survival rates are confounded with the absolute emigration rates, it is not possible to develop tests of homogeneity over post-strata or over time, unless it is assumed that the emigration rates are homogeneous over time. Since it is difficult to distinguish changes in emigration apart from changes induced by differential survival, these tests are not pursued further.

3.5.4.7 Summary of the results on testing

As in the Partial-Fidelity Model, the confounding of the parameters causes numerous problems in hypothesis testing in this model. In summary:

· it is not possible to test the complete-fidelity assumption since animals are seen only twice - at release and at recovery;

· a partial goodness-of-fit test can be constructed using the results of Model 3 of Chapter 2;

· tests about the emigration and survival rates must be interpreted carefully since differences in survival may cause changes in the migration rates;

· a test for homogeneous relative emigration rates among pre-strata is possible if it is assumed that the post-stratum band-recovery rates are proportional among pre-strata ($f_i^{st}=\alpha_i^{s\cdot} f_1^{st}$). The p-value of this exact test is difficult to compute, but a simpler test using only the direct recoveries can be constructed;

· a test for homogeneous relative emigration rates among releases is possible if it is assumed that the band-recovery rates are proportional over time ($f_i^{st}=\alpha_i^{s\cdot} f_i^{1t}$). The p-value of this exact test is difficult to compute, but a simpler test using only the direct recoveries can be constructed;

· a test for homogeneous relative immigration rates among post-strata is equivalent to a test for homogeneous relative emigration rates among pre-strata;

· an *ad hoc* test for homogeneous relative immigration rates over time can be constructed when external estimates of the pre-stratum population sizes and their estimated precision are available and additional assumptions are made about the band-recovery rates;

· an *ad hoc* test for homogeneous relative harvest-derivation rates among post-strata can be constructed when external estimates of the band-reporting rates and their estimated precision are available. However, if the band-reporting rates are assumed to be independent of the pre-strata, the large-sample contingency table for this test is equivalent in form to the contingency table used in the test of homogeneous relative emigration rates over pre-strata;

· an *ad hoc* test for homogeneous relative harvest-derivation rates over time can be constructed when external estimates of the pre-stratum population sizes and band-reporting rates and their estimated precision are available;

3.5.5 SUMMARY OF THE COMPLETE-FIDELITY MODEL WITH ORDINARY BAND-RECOVERY DATA

The major problem in using ordinary band-recovery data with the Complete-Fidelity Model is again that the band-reporting rate is confounded with the emigration rate. This implies that estimation and tests of the emigration or immigration rates are not possible unless further assumptions about the band-recovery rates are made. These assumptions are not testable using the data at hand, and must be assessed on biological grounds.

Estimation and tests of the harvest-derivation may be possible if independent estimates of the pre-stratum population size and band-reporting rates are available.

Since the post-stratum survival rates and emigration rates may be highly dependent, tests about the emigration and survival rates should be interpreted carefully.

In short, there are numerous shortcomings in using ordinary band-recovery data with the Complete-Fidelity Model. Estimation and hypothesis testing is possible under various restrictions, but these restrictions must be assessed on biological grounds only.

3.6 A MODIFICATION TO THE EXPERIMENTAL DESIGN IN THE COMPLETE-FIDELITY MODEL

The problem in using ordinary band-recovery data in the Complete-Fidelity Model is the confounding of the parameters. As in the Partial-Fidelity Model, this can be resolved if additional sightings are available in the post-strata. Live recaptures may also be used as outlined in the Partial-Fidelity Model.

Sightings of the animals in the pre-strata may or may not be informative. Three scenarios can be envisaged:

- An animal is sighted in the pre-stratum of release before its recovery or last sighting in a post-stratum. Since the animal is assumed to be faithful to its post-stratum of recovery in all years between release and recovery, these sightings in the pre-strata are uninformative since all they indicate is that the animal survived the seasonal migration to that specific post-stratum which can already be inferred from the recovery information alone.
- An animal is sighted in the pre-stratum of release after its 'last' sighting in a post-stratum and is never recovered. These are informative about the post-stratum survival rates since the fidelity assumption implies that the animal must have returned to the post-stratum of sighting and the sighting in the pre-stratum implies that the animal has survived for additional years after its last sighting in the post-stratum.
- An animal is sighted in the pre-stratum of release only and is never sighted in a post-stratum nor is its band recovered. These sightings are uninformative about the post-stratum survival rates since it is unknown to which post-stratum the animal has migrated.

They can be used to obtain information about the survival rates over all post-strata.

In all cases, the sightings in the pre-strata are uninformative about the migration rates since they contain no new information about the post-stratum chosen by the animals over that provided by the recoveries or sightings. The modifications to the procedures in this Section to incorporate sightings in the pre-strata are straightforward, but tedious; however, since these are uninformative about the migration rates, this generalization will not be pursued further.

3.6.1 ASSUMPTIONS

The additional assumptions over those made in the Complete-Fidelity Model with ordinary band-recovery data are similar to those additional assumptions made in the Partial-Fidelity Model with sightings with the following revisions:

- if an animal is sighted in a post-stratum, it implies that the animal has chosen to migrate to this post-stratum in every year.

As in the Partial-Fidelity Model, the assumption of independence between sightings and recoveries is crucial and easily violated unless the study is carefully designed.

3.6.2 MODEL AND INTERPRETATION OF THE PARAMETERS

As shown in Appendix 3.D, the set of sighting and recovery histories from a release can be modelled using multinomial distributions. The data representation is not as complex as in the partial-fidelity model; however, for consistency, a similar reduced-data array can be used.

A symbolic representation of the revised reduced-data array in the case of k=3 years of releases, and l=4 years of recoveries is shown in Figure 3.6.2a. This reduced-data array will be identical to that of the Partial-Fidelity Model except that now $W_{ij\cdot}^{stt}$ is the number of animals from W_{ij}^{st} that are subsequently recovered in post-stratum t (rather than any post-stratum). According to the assumptions of the Complete-Fidelity Model, animals must be completely faithful to their post-strata so sightings or recoveries in other post-strata should not be possible.

As in the Partial-Fidelity Model, an animal may contribute to several elements of the reduced-data array. For example, an animal with a history of:

- released from pre-stratum 1 in year 1;
- sighted **WITHOUT** being recovered in post-stratum 2 in year 2;
- neither sighted nor recovered in year 3;
- recovered **AND** sighted in post-stratum 2 in year 4;

will contribute to the terms:

$$W_{12}^{12},\quad W_{12\cdot}^{122},\ \text{and}\ A_{14}^{12}.$$

The general expression for the expected number of animals observed for each element of the reduced-data array is shown in Figure 3.6.2b in the case of k=3 years of releases, and l=4 years of recoveries. The major differences between the expected values of the reduced-data array between the Complete- and Partial-Fidelity Models are the presence of the post-stratum specific survival rates, and the continued presence of

Figure 3.6.2a

Symbolic representation of the reduced-data array in the Complete-Fidelity Model with sightings in the post-strata in the case of k=3 years of release and l=4 years of recoveries

Year Released	Number Banded	Year of recovery or sighting of animals in post-stratum t[a] 1	2	3	4
1	N_1^s	A_{11}^{st}	A_{12}^{st}	A_{13}^{st}	A_{14}^{st}
		B_{11}^{st}	B_{12}^{st}	B_{13}^{st}	B_{14}^{st}
		W_{11}^{st}	W_{12}^{st}	W_{13}^{st}	W_{14}^{st}
		$W_{11\cdot}^{stt}$	$W_{12\cdot}^{stt}$	$W_{13\cdot}^{stt}$	b
2	N_2^s		A_{22}^{st}	A_{23}^{st}	A_{24}^{st}
			B_{22}^{st}	B_{23}^{st}	B_{24}^{st}
			W_{22}^{st}	W_{23}^{st}	W_{24}^{st}
			$W_{22\cdot}^{stt}$	$W_{23\cdot}^{stt}$	b
3	N_3^s			A_{33}^{st}	A_{34}^{st}
				B_{33}^{st}	B_{34}^{st}
				W_{33}^{st}	W_{34}^{st}
				$W_{33\cdot}^{stt}$	b

Statistics

A_{ij}^{st} = number of animals released from pre-stratum s in year i that are recovered **AND** sighted in post-stratum t in year j

B_{ij}^{st} = number of animals released from pre-stratum s in year i that are recovered **BUT** not sighted in post-stratum t in year j

W_{ij}^{st} = number of animals released from pre-stratum s in year i that are sighted **WITHOUT** being recovered in post-stratum t in year j.

$W_{ij\cdot}^{stt}$ = number of animals released in pre-stratum s in year i that are sighted without being recovered in post-stratum t in year j and are subsequently sighted or recovered in post-stratum t

[a] There will one such array for every combination of pre- and post-stratum as laid out in Figure 3.4.2a

[b] Must be 0 since experiment is terminated in year 4.

Figure 3.6.2b

Expected values of the reduced-data array in the Complete-Fidelity Model with sightings in the post-strata in the case of k=3 year of releases and l=4 years of recoveries.

Year	Number Banded	Expected number of animals recovered or sighted in post-stratum t[a] by year 1	2	3	4
1	N_1^s	$N_1^s M_1^{s\cdot} m_1^{st} \times p_1^{st} f_1^{st}$	$N_1^s M_1^{s\cdot} m_1^{st} S_1^{st} \times p_2^{st} f_2^{st}$	$N_1^s M_1^{s\cdot} m_1^{st} S_1^{st} S_2^{st} \times p_3^{st} f_3^{st}$	$N_1^s M_1^{s\cdot} m_1^{st} S_1^{st} S_2^{st} S_3^{st} \times p_4^{st} f_4^{st}$
		" $\times (1-p_1^{st}) f_1^{st}$	" $\times (1-p_2^{st}) f_2^{st}$	" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
		" $\times p_1^{st}(1-f_1^{st})$	" $\times p_2^{st}(1-f_2^{st})$	" $\times p_3^{st}(1-f_3^{st})$	" $\times p_4^{st}(1-f_4^{st})$
		" $\times p_1^{st} S_1^{st} \rho_2^{st} (M_2^{s\cdot} m_2^{st})^{-1}$	" $\times p_2^{st} S_2^{st} \rho_3^{st} (M_3^{s\cdot} m_3^{st})^{-1}$	" $\times p_3^{st} S_3^{st} \rho_4^{st} (M_4^{s\cdot} m_4^{st})^{-1}$	b
2	N_2^s		$N_2^s M_2^{s\cdot} m_2^{st} \times p_2^{st} f_2^{st}$	$N_2^s M_2^{s\cdot} m_2^{st} S_2^{st} \times p_3^{st} f_3^{st}$	$N_2^s M_2^{s\cdot} m_2^{st} S_2^{st} S_3^{st} \times p_4^{st} f_4^{st}$
			" $\times (1-p_2^{st}) f_2^{st}$	" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
			" $\times p_2^{st}(1-f_2^{st})$	" $\times p_3^{st}(1-f_3^{st})$	" $\times p_4^{st}(1-f_4^{st})$
			" $\times p_2^{st} S_2^{st} \rho_3^{st} (M_3^{s\cdot} m_3^{st})^{-1}$	" $\times p_3^{st} S_3^{st} \rho_4^{st} (M_4^{s\cdot} m_4^{st})^{-1}$	b
3	N_3^s			$N_3^s M_3^{s\cdot} m_3^{st} \times p_3^{st} f_3^{st}$	$N_3^s M_3^{s\cdot} m_3^{st} S_3^{st} \times p_4^{st} f_4^{st}$
				" $\times (1-p_3^{st}) f_3^{st}$	" $\times (1-p_4^{st}) f_4^{st}$
				" $\times p_3^{st}(1-f_3^{st})$	" $\times p_4^{st}(1-f_4^{st})$
				" $\times p_3^{st} S_3^{st} \rho_4^{st} (M_4^{s\cdot} m_4^{st})^{-1}$	b

[a] There will one such array for every combination of pre- and post-strata laid out as in Figure 3.6.2a. Refer to Figure 3.6.2a for the correspondence between these formulae and the reduced-data array components.

[b] Must be 0 since experiment is terminated in year 4.

the emigration rates in the first year after release in all subsequent years. Figure 3.6.2b should be compared with Figure 3.6.2a to see the correspondence between the reduced-data array elements and the general formulae. A numerical example using the parameters of Table 1.5a, assuming they are constant over time, and assuming a uniform sighting rate of 30% among all pre-strata within each post-stratum for all years, is shown in Figure 3.6.2c and discussed below. Note that the migration rates in Table 1.5a apply only to the first year after release since animals are faithful to their chosen post-strata in subsequent years as explained in Section 3.5.2.

The parameters $M_i^{s\cdot}$, m_i^{st}, and f_i^{st} were discussed in Section 3.5.2 and retain their interpretations. The parameter p_i^{st} was discussed in Section 3.4.2 and retains its interpretation.

Then, for example, in Figure 3.6.2c the expected number of animals released from pre-stratum 2 in year 1, and whose band is recovered **AND** sighted in post-stratum 1 in year 1, $E(A_{11}^{21})$, is computed as:

$$E(A_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times p_1^{21} \times f_1^{21} \qquad \text{(or)}$$

$$E(A_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.30 \times 0.08 = 9.60.$$

In a similar way, the expected number of animals released from pre-stratum 2 in year 1 and whose band is recovered **BUT** not sighted, in post-stratum 1 in year 1, $(E(B_{11}^{21})$, Figure 3.6.2c), is computed as:

Figure 3.6.2c

Expected reduced-data array in the Complete-Fidelity Model with sightings in the post-strata using the parameters of Table 1.5a and assuming a constant sighting rate of 0.30 for all pre-strata within each post-stratum for all years.

Releases from pre-stratum 1

Year	Number Banded	Expected sightings or recoveries in post-stratum 1 by year: 1	2	3	4	Expected sightings or recoveries in post-stratum 2 by year: 1	2	3	4
1	1000	6.00	3.00	1.50	0.75	6.00	3.60	2.16	1.30
		14.00	7.00	3.50	1.75	14.00	8.40	5.04	3.02
		114.00	57.00	28.50	14.25	114.00	68.40	41.04	24.62
		29.60	13.57	5.03		38.51	20.55	8.68	
2	1000		6.00	3.00	1.50		6.00	3.60	2.16
			14.00	7.00	3.50		14.00	8.40	5.04
			114.00	57.00	28.50		114.00	68.40	41.04
			27.14	10.05			34.25	14.47	
3	1000			6.00	3.00			6.00	3.60
				14.00	7.00			14.00	8.40
				114.00	57.00			114.00	68.40
				20.10				24.12	

Figure 3.6.2c (continued)

Releases from pre-stratum 2

Year	Number Banded	Expected sightings or recoveries in post-stratum 1 by year				Expected sightings or recoveries in post-stratum 2 by year			
		1	2	3	4	1	2	3	4
1	1000	9.60	4.80	2.40	1.20	10.80	6.48	3.89	2.33
		22.40	11.20	5.60	2.80	25.20	15.12	9.07	5.44
		110.40	55.20	27.60	13.80	79.20	23.76	14.26	8.55
		31.45	14.42	5.34		33.10	17.67	7.46	
2	1000		9.60	4.80	2.40		10.80	6.48	3.89
			22.40	11.20	5.60		25.20	15.12	9.07
			110.40	55.20	27.60		79.20	23.76	14.26
			28.84	10.68			29.45	12.44	
3	1000			9.60	4.80			10.80	6.48
				22.40	11.20			25.20	15.12
				110.40	55.20			79.20	23.76
				21.36				20.74	

The row-wise similarities in each table are a result of assuming that the parameters of Table 1.6a are constant over time, and assuming that the sighting rate is 30% for all pre-strata in all post-strata in all years.

$$E(B_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times (1-p_1^{21}) \times f_1^{21} \qquad \text{(or)}$$

$$E(B_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times (1.00-0.30) \times 0.08 = 22.40.$$

Note that the expected number of animals released from pre-stratum 2 in year 1 and whose band is recovered in post-stratum 1 in year 1 (regardless if sighted or not), $E(R_{11}^{21})$, is again computed as the sum of these two components, and equals that shown in Figure 3.6.2b:

$$E(R_{11}^{21}) = 32.00 = E(A_{11}^{21}) + E(B_{11}^{21}) = 9.60 + 22.40 \quad .$$

The expected number of animals released from pre-stratum 2 in year 1, and whose band is sighted **WITHOUT** being recovered in post-stratum 1 in year 1, ($E(W_{11}^{21})$, Figure 3.6.2c), is computed as:

$$E(W_{11}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times p_1^{21} \times (1-f_1^{21}) \qquad \text{(or)}$$

$$E(W_{11}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.30 \times (1.00-0.08) = 110.40.$$

Since the animals are completely faithful to their post-strata, the parameter S_i^{st} represents the post-stratum specific survival rate in post-stratum *t* from the time of banding in year *i* to the time of banding in year *i*+1 for those animals released from pre-stratum *s*. Hence, in Figure 3.6.2c, the expected number of animals released from pre-stratum 2 in year 1 and whose bands are either: recovered **AND** sighted; recovered **BUT** not sighted; or sighted **WITHOUT** being recovered in post-stratum 1 in year 2 are computed as:

$$E(A_{12}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times S_1^{21} \times p_2^{21} \times f_2^{21} \quad \text{(or)}$$

$$E(A_{12}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.50 \times 0.30 \times 0.08 = 4.80 \quad ,$$

$$E(B_{12}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times S_1^{21} \times (1-p_2^{21}) \times f_2^{21} \quad \text{(or)}$$

$$E(B_{12}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.50 \times (1.00-0.30) \times 0.08 = 11.20,$$

and

$$E(W_{12}^{21}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times S_1^{21} \times p_2^{21} \times (1-f_2^{21}) \quad \text{(or)}$$

$$E(W_{12}^{21}) = 1000 \times 0.70 \times 0.5714 \times 0.50 \times 0.30 \times (1.00-0.08) = 55.20$$

respectively.

The remaining entry in the reduced-data array is the number of animals released from pre-stratum s in year i, and whose bands are sighted without being recovered in post-stratum t in year j and are subsequently recovered or sighted in later years in post-stratum t ($W_{ij\cdot}^{stt}$). In order for a band to be sighted or recovered subsequent to being sighted without being recovered in post-stratum t in year j, the animal must survive in post-stratum t in year j and then it will be subject to similar forces of recovery or sightings as new releases in year j+1. For example, in Figure 3.6.2c, the expected number of animals released from pre-stratum 2 in year 1 whose bands were sighted without being recovered in post-stratum 1 in year 2, and whose bands are subsequently recovered or sighted during the remainder of the experiment, is computed as:

$$E(W_{12\cdot}^{211}) = N_1^2 \times M_1^{2\cdot} \times m_1^{21} \times S_1^{21} \times p_2^{21} \times S_2^{21} \times \rho_3^{21} (M_3^{2\cdot} m_3^{21})^{-1}$$

where ρ_3^{21} is the probability than an animal will be recovered or sighted in post-stratum 1 when released in pre-stratum 2 in year 3. The term $(M_3^{2\cdot} m_3^{21})^{-1}$ adjusts ρ_3^{21} for the emigration component of the next year's releases. Or,

$$E(W_{12\cdot}^{211}) = 1000 \times 0.70 \times 0.5714 \times 0.50 \times 0.30 \times 0.50 \times \rho_3^{21}(0.70\mathrm{x}0.5714)^{-1}$$

$$= 30.00 \times \rho_3^{21}(0.40)^{-1}.$$

(Note that the band-recovery rate does not enter into the computation since, by definition, the post-stratum specific survival rate includes, as a hidden component, the probability of not being recovered).

Now ρ_3^{21} is tedious to compute but using Formula 3.D.2 presented in Appendix 3.D, $\rho_3^{21} = 0.19224$, and so

$$E(W_{12\cdot}^{211}) = 30.00 \times 0.19224 \times (0.40)^{-1} = 14.42.$$

Hence, of the 1000 animals banded and released in pre-stratum 2 in year 1, 55.20 animals are expected to be sighted without being recovered in post-stratum 1 in year 2 (W_{12}^{21}), and of these, 14.42 animals are expected to be subsequently sighted or recovered in post-stratum 1 during the remainder of the experiment $(W_{12\cdot}^{211})$. As well,

$$E(W_{12}^{21}) - E(W_{12\cdot}^{211}) = 55.20 - 14.42 = 40.78$$

is the expected number of animals released from pre-stratum 2 in year 1 whose bands were sighted for the last time in post-stratum 1 in year 2.

The expected total number of animals banded and released in pre-stratum 2 in year 1 that are sighted or recovered in post-stratum 1 during the entire experiment, ignoring duplicate sightings, is computed as:

$$E\left(\sum_{j=1}^{4}\left(A_{1j}^{21}+B_{1j}^{21}+\left(W_{1j}^{21}-W_{1j\cdot}^{211}\right)\right)\right)$$

or, from Figure 3.6.2c,

$$\begin{array}{l} 9.60 + 22.40 + (110.40 - 31.45) + \\ 4.80 + 11.20 + (\ 55.20 - 14.42) + \\ 2.40 + \ 5.60 + (\ 27.60 - \ 5.34) + \\ 1.20 + \ 2.80 + (\ 13.80 - \ 0.00) = 215.79 \end{array}$$

This agrees with the computed value of ρ_1^{21}=0.21579 found using Formula 3.D.2, representing the probability of recovering or sighting an animal released from pre-stratum 2 in year 1 in post-stratum 1 during the entire experiment (215.79/1000=0.21579).

3.6.3 ESTIMATION

In this model there are *ak* total emigration parameters ($M_i^{s\cdot}$), *a(b-1)k* relative emigration parameters (m_i^{st}), *abl* sighting parameters (p_i^{st}), *abl* band-recovery parameters (f_i^{st}), and *ab(l-1)* post-stratum specific survival rates (S_i^{st}), for a total of *ab(3l+k*-1) parameters.

Using the methodology outlined in Chapter 1, and the data representation shown in Appendix 3.D, the MSS can be identified. It has dimension *ab(3l+k*-1), and one representation of the MSS is easily computed from the reduced-data array as:

$A_{\cdot j}^{st}+W_{\cdot j}^{st}$	s=1...a t=1...b j=1...l	The total number of animals released from pre-stratum s whose bands were sighted in post-stratum t in year j.
$A_{\cdot j}^{st}+B_{\cdot j}^{st}$	s=1...a t=1...b j=1...l	The total number of animals released from pre-stratum s whose bands were recovered in post-stratum t in year j.

$W^{st}_{\cdot j}-W^{stt}_{\cdot j \cdot}$	$s=1\ldots a$ $t=1\ldots b$ $j=1\ldots l$	The total number of animals released from pre-stratum s whose bands were sighted without being recovered in post-stratum t in year j and were not sighted or recovered in later years.
Z^{st}_{i}	$s=1\ldots a$ $t=1\ldots b$ $i=1\ldots k-1$	The total number of animals released from pre-stratum s that were alive at time i and seen or recovered after time i in post-stratum t.

Since the dimension of the MSS equals the number of parameters, all parameters are identifiable and their MLEs are presented in Table 3.6.3; variances and covariances may be found in Appendix 3.E. Unfortunately, in this model, the estimators often do not have a simple intuitive form. From the expressions in Appendix 3.E, it can be seen that the precision of the estimates depends mainly upon terms involving sightings, and so a high sighting rate will give good precision.

The estimates of the relative immigration rates and the relative harvest-derivation rates are found by simply replacing each parameter in the definition by its MLE, and by using the independent estimates of the pre-stratum population sizes and the post-stratum band-reporting rates as required. Variances may be obtained using the delta-method. Absolute or total immigration or derivation rates still cannot be estimated unless the pre-strata are exhaustive.

3.6.4 TESTING

3.6.4.1 A goodness-of-fit test

A general non-specific goodness-of-fit test to the Complete-Fidelity Model with sightings can, in theory, be constructed using the methods outlined in Chapter 1. However, as in the Partial-Fidelity Model, the large-sample contingency tables will consist of many tables with small

Table 3.6.3

MLEs for the Complete-Fidelity Model with sightings in the post-strata

$$\hat{f}_i^{st} = \frac{(A^{st}_{\cdot i}+B^{st}_{\cdot i})(A^{st}_{\cdot i}+W^{stt}_{\cdot i\cdot})}{(A^{st}_{\cdot i}+W^{st}_{\cdot i})(A^{st}_{\cdot i}+B^{st}_{\cdot i}+Z^{st}_{i})} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots l \end{matrix}$$

$$\hat{p}_i^{st} = \frac{A^{st}_{\cdot i}+W^{stt}_{\cdot i\cdot}}{A^{st}_{\cdot i}+B^{st}_{\cdot i}+Z^{st}_{i}} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots l \end{matrix}$$

$$\hat{\rho}_i^{st} = \frac{A^{st}_{i\cdot}+B^{st}_{i\cdot}+W^{st}_{i\cdot}-W^{stt}_{i\cdot\cdot}}{N^{s}_{i}} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{matrix} \quad = \frac{\text{total animals recovered or sighted from those released in pre-stratum s in year i}}{\text{total released in pre-stratum s in year i}}$$

$$M^{s\cdot}_{i}\hat{m}^{st}_{i} = \frac{(A^{st}_{\cdot i}+W^{st}_{\cdot i})(A^{st}_{\cdot i}+B^{st}_{\cdot i}+Z^{st}_{i})}{A^{st}_{\cdot i}+W^{stt}_{\cdot i\cdot}} \times \frac{\hat{\rho}^{st}_{i}}{T^{st}_{i}} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{matrix}$$

$$\hat{M}^{s\cdot}_{i} = \sum_{t=1}^{b} M^{s\cdot}_{i}\hat{m}^{st}_{i} \qquad \begin{matrix} s=1\ldots a \\ i=1\ldots k \end{matrix}$$

$$\hat{m}^{st}_{i} = M^{s\cdot}_{i}\hat{m}^{st}_{i}/\hat{M}^{s\cdot}_{i} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots k \end{matrix}$$

$$\hat{S}^{st}_{i} = \frac{Z^{st}_{i}}{T^{st}_{i+1}} \; \frac{(A^{st}_{\cdot i}+W^{stt}_{\cdot i\cdot})\,(A^{st}_{\cdot i+1}+W^{st}_{\cdot i+1})\,(A^{st}_{\cdot i+1}+B^{st}_{\cdot i+1}+Z^{st}_{i+1})}{(A^{st}_{\cdot i+1}+W^{stt}_{\cdot i+1\cdot})\,(A^{st}_{\cdot i}+W^{st}_{\cdot i})\,(A^{st}_{\cdot i}+B^{st}_{\cdot i}+Z^{st}_{i})} \qquad \begin{matrix} s=1\ldots a \\ t=1\ldots b \\ i=1\ldots l-1 \end{matrix}$$

expected counts which will require extensive pooling and will lack any appreciable power.

Since the reduced-data array are the sufficient (but not minimally sufficient) statistics for the model, a goodness-of-fit test can be constructed using the methods of Chapter 1 with the reduced-data array, rather than the full-data array. The derivation is presented in Appendix 3.D.

This goodness-of-fit test has two components. Large sample contingency tables that can be used in the test of each component are shown in Tables 3.6.4.1a and 3.6.4.1b. Some of the contingency tables may have small expected counts (particularly near the end of the experiment), and may either require pooling or may be omitted with a corresponding reduction in the degrees of freedom.

The first component is very similar to the goodness-of-fit test of the Partial-Fidelity Model (Table 3.3.4.1) the difference being that one such table is now constructed for each post-stratum rather than all post-strata being combined into one table. As such, violations of the Complete-Fidelity Model assumptions will be detected in similar ways as outlined in Section 3.3.4.1.

The second component examines if the sighting rate of recovered animals differs from the sighting rate of non-recovered animals alive and present in the post-stratum. This component could not be extracted in the Partial-Fidelity Model since information obtained from

Table 3.6.4.1a

A large-sample contingency table that can be used in a component of the goodness-of-fit test for the Complete-Fidelity Model with sightings in the post-strata based upon the reduced-data array

A large-sample contingency table is constructed by considering the sightings or recoveries in year *j* conditional upon the animal being sighted or recovered in year *j* or later, for newly released and previously released animals from pre-stratum *s*.

Total unique animals released from pre-stratum s **in year i,** and sighted or recovered in year j or later in post-stratum t	Animals recovered **AND** sighted in year j in post-stratum t from those at left	Animals recovered **BUT** not sighted in year j in post-stratum t from those at left	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and not sighted or recovered after year j from those at left	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and sighted or recovered after year j from those at left	Animals recovered or sighted **only** after year j in post-stratum t from those at left
Total unique animals released from pre-stratum s **before year i,** and sighted or recovered in year j or later in post-stratum t	Animals recovered **AND** sighted in year j in post-stratum t from those at left	Animals recovered **BUT** not sighted in year j in post-stratum t from those at left	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and not sighted or recovered after year j from those at left	Animals sighted **WITHOUT** being recovered in year j in post-stratum t and sighted or recovered after year j from those at left	Animals recovered or sighted **only** after year j in post-stratum t from those at left

Or:

$\sum_{m=j}^{l} A^{st}_{im}+B^{st}_{im}+W^{st}_{im}-W^{stt}_{im\cdot}$	A^{st}_{ij}	B^{st}_{ij}	$W^{st}_{ij}-W^{stt}_{ij\cdot}$	$W^{stt}_{ij\cdot}$	$\sum_{m=j+1}^{l} (A^{st}_{im}+B^{st}_{im}+W^{st}_{im}-W^{stt}_{im\cdot}) - W^{stt}_{ij\cdot}$
$\sum_{v=1}^{i-1} \sum_{m=j}^{l} A^{st}_{vm}+B^{st}_{vm}+W^{st}_{vm}-W^{stt}_{vm\cdot}$	$\sum_{v=1}^{i-1} A^{st}_{vj}$	$\sum_{v=1}^{i-1} B^{st}_{vj}$	$\sum_{v=1}^{i-1} W^{st}_{vj}-W^{stt}_{vj\cdot}$	$\sum_{v=1}^{i-1} W^{stt}_{vj\cdot}$	$\sum_{v=1}^{i-1} \sum_{m=j+1}^{l} (A^{st}_{vm}+B^{st}_{vm}+W^{st}_{vm}-W^{stt}_{vm\cdot}) - W^{stt}_{vj\cdot}$
$\sum_{v=1}^{i} \sum_{m=j}^{l} A^{st}_{vm}+B^{st}_{vm}+W^{st}_{vm}-W^{stt}_{vm\cdot}$	$\sum_{v=1}^{i} A^{st}_{vj}$	$\sum_{v=1}^{i} B^{st}_{vj}$	$\sum_{v=1}^{i} W^{st}_{vj}-W^{stt}_{vj\cdot}$	$\sum_{v=1}^{i} W^{stt}_{vj\cdot}$	$\sum_{v=1}^{i} \sum_{m=j+1}^{l} (A^{st}_{vm}+B^{st}_{vm}+W^{st}_{vm}-W^{stt}_{vm\cdot}) - W^{stt}_{vj\cdot}$

Table 3.6.4.1a (continued)

There will be one such table for each combination of pre-stratum $s=1...a$, post-stratum $t=1...b$, year of release $i=2...k$, and year of recovery $j=i...l$. Each table will have 4 degrees of freedom (except that when $j=l$, the last two columns do not exist and the table will have 2 degrees of freedom).

There will be a total of $2(k-1)(2l-k-1)$ degrees of freedom for each combination of pre-stratum s=1...a and post-stratum t=1...b.

Intuitively, animals released from pre-statum s in year i and recovered in post-stratum t should behave in the same way as previously released animals.

This contingency table is similar to those of the Partial-Fidelity Model except that only one post-stratum is considered at a time.

Table 3.6.4.1b

A large-sample contingency table that can be used in a component of the goodness-of-fit test for the Complete-Fidelity Model with sightings in the post-strata based upon the reduced-data array

A large-sample contingency table is constructed by considering animals sighted and recovered in year j in post-stratum t from all releases conditional upon the total animals recovered in year j in post-stratum t and the animals from all releases that are first sighted without being recovered in year j in post-stratum t and are subsequently sighted or recovered conditional upon those seen only after year j.

Total unique animals released from pre-stratum s in all years recovered in year j in post-stratum t	Animals recovered **AND** sighted in post-stratum t from those at left	Animals recovered **BUT** not sighted in post-stratum t from those at left
Total unique animals released from pre-stratum s in all years and sighted or recovered after year j in post-stratum t	Animals also sighted in year j in post-stratum t from those at left	Animals not sighted in year j in post-stratum t from those at left

Or:

$A^{st}_{\cdot j}+B^{st}_{\cdot j}$	$A^{st}_{\cdot j}$	$B^{st}_{\cdot j}$
Z^{st}_{j}	$W^{stt}_{\cdot j \cdot}$	$Z^{st}_{j}-W^{stt}_{\cdot j \cdot}$
$A^{st}_{\cdot j}+B^{st}_{\cdot j}+Z^{st}_{j}$	$A^{st}_{\cdot j}+W^{stt}_{\cdot j \cdot}$	$B^{st}_{\cdot j}+Z^{st}_{j}-W^{stt}_{\cdot j \cdot}$

Table 3.6.4.1b (continued)

There will be one such table for each combination of pre-stratum s=1...a, post-stratum t=1...b, year of recovery j=1...(l-1). Each table will have 1 degree of freedom.

There will be a total of (l-1) degrees of freedom for each combination of pre-stratum s=1...a and post-stratum t=1...b.

Intuitively, the sighting rate of recovered animals should be the same as the sighting rates of non-recovered animals alive and present in the post-stratum.

recoveries or sightings in future years contains no information about the animals location in the current year. The assumption of post-stratum fidelity implies that recoveries or sightings in later years are informative about the location of the animal in the current year.

3.6.4.2 Testing among models

When sighting of bands takes place in the post-strata, all parameters can be estimated, and hypotheses about the parameters may be tested without any further restrictions. However, many of the models with restrictions placed upon the parameters are less than full rank and many estimators of the parameters are not available in closed form; numerical methods must be used.

A computer program using the methods outlined in Appendix 3.F has been written to estimate the parameters under the full model and under various hypotheses involving restrictions on the parameters. It computes the value of the likelihood (up to constant terms) for each model so that likelihood ratio tests may be performed. A numerical example of the use of the computer program to analyze a set of data is presented in Section 3.7.

3.6.5 SUMMARY

By obtaining additional sightings of the banded animals in the post-strata, all of the problems caused by the confounding of the band-recovery and emigration rates are resolved. However, the study my be carefully designed to ensure that the crucial assumption of independence between sightings and recoveries is not violated. All parameters in the full Complete-Fidelity Model can now be estimated. Tests of hypotheses about the biological parameters of interest can now be performed without any additional assumptions. However, many of the restricted models are still less than full rank and numerical methods must again be used.

3.7 **A NUMERICAL EXAMPLE**

3.7.1 INTRODUCTION

In this section, an example of the analysis of simulated data using the computer program described in Appendix 3.F is presented. The purpose of these examples is not to present a definitive analysis, but rather to illustrate some of the possible steps that would be taken in building a model to describe migration patterns. The advantage of using simulated data is that the true model structure and values of the parameters are known, and the results of the analysis can be assessed against the known properties.

The parameter values given in Table 1.5a (with a uniform sighting rate of 30%) were used to generate the simulated data for both the Partial- and Complete-Fidelity models assuming that the parameter values were constant over time. The interpretation of the band-recovery and sighting rates does not depend upon the fidelity assumption, but the interpretation of the remaining parameters is different in the two models, even though they have the same numerical values. In particular:

- the post-stratum specific survival rates only apply to animals that migrate to this post-stratum in a particular year. In the Complete-Fidelity Model, the animals always return to this post-stratum in later years, while in the Partial-Fidelity Model, they may migrate to other post-strata. However, in both models, the subsequent survival probabilities are assumed to be independent of all previous survival rates;

· the net survival rate over all post-strata is not required in the Complete-Fidelity Model; in the Partial-Fidelity Model, it is derived from the migration and post-stratum survival rates as shown in Section 3.4;

· the migration rates in year j in the Partial-Fidelity Model apply to all animals alive in year j regardless of when released, while those for the Complete-Fidelity Model apply only to newly released animals. Subsequent migration patterns in the Complete-Fidelity Model are completely determined after the first migration of the animal after banding.

The reduced-data arrays, consisting of the number of animals recovered and/or sighted in each year after release in each post-stratum given a fixed, known number of releases, were generated by using the distributions of the reduced-data array elements given in Appendices 3.A and 3.D, and involve the generation of multinomial variates in the order required by the conditioning of the distribution of the MSS. The appropriate subroutines from IMSL (1984) were used.

Since estimation of the immigration and harvest-derivation rates also requires estimates of the pre-stratum population sizes and band-reporting rates, typical values for the estimates (and their standard errors) of these parameters were included with simulated data. This information is usually obtained from other studies, ~~e.g.,~~ (Henny, Anderson, and Pospahla, (1972), or Henny and Burnham, (1976). Hence the complete set of data consists of the generated reduced-data arrays and the external estimates (with estimated standard errors) of the pre-stratum population sizes and band-reporting rates, and represents the type of data that would be available from a real banding experiment.

In Section 3.7.2, an example of the analysis of data from the Partial-Fidelity Model is presented. This section concentrates on estimation and testing of the fundamental parameters rather than the derived harvest-derivation and immigration rates. In Section 3.7.3, an example of the analysis of data from the Complete-Fidelity Model is presented and concentrates on the derived parameters. The computer program described in Appendix 3.F can produce both types of analysis for either model.

3.7.2 PARTIAL-FIDELITY MODEL WITH SIGHTINGS IN THE POST-STRATA. Simulated data using the parameter values shown in Table 1.5a were generated assuming that animals behaved according to the assumptions of the Partial-Fidelity Model. There were 3 years of releases, 4 years of recoveries, 2 pre-strata where banding occurred, and 2 post-strata where recoveries occurred. The parameter values in Table 1.5a were assumed to be constant over time and a uniform sighting rate of 30% was used. The simulated reduced-data array along with the summary statistics are presented in Figure 3.7.2a following the layout of Table 3.4.2 and the log-likelihood (up to constant terms) used in assessing the goodness-of-fit to models in the Partial-Fidelity family is -10959.6; such an 'unstructured' model would require 132 parameters.

As a first step, the full Partial-Fidelity Model without any restrictions on the parameters is fit to the data (Figure 3.7.2b). The

Figure 3.7.2 a
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES

NUMBER OF PRE-STRATA : 2
NUMBER OF POST-STRATA : 2
NUMBER OF YEARS OF RELEASES : 3
NUMBER OF YEARS OF RECOVERIES : 4

ESTIMATED POPULATION SIZES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	PRE STRATUM	POPULATION ESTIMATE	S.E.
1	1	100000.	20000.
1	2	200000.	50000.
2	1	150000.	30000.
2	2	300000.	75000.
3	1	75000.	15000.
3	2	150000.	20000.

ESTIMATED BAND-REPORTING RATES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	PRE	ESTIMATES AND (S.E.)	
	STRATUM	POST-STRATUM 1	POST-STRATUM 2
1	1	0.5000 (0.10)	0.2500 (0.05)
1	2	0.4000 (0.08)	0.4000 (0.08)
2	1	0.5000 (0.10)	0.2500 (0.05)
2	2	0.4000 (0.08)	0.4000 (0.08)
3	1	0.5000 (0.10)	0.2500 (0.05)
3	2	0.4000 (0.08)	0.4000 (0.08)

Figure 3.7.2 a (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES

==================== RELEASES FROM PRE-STRATUM 1 ====================

***** RECOVERIES IN POST-STRATUM 1

YEAR	NUMBER RELEASED	1	2	3	4	TOTALS
1	1000.	4.00	4.00	2.00	4.00	14.00
		17.00	5.00	6.00	4.00	32.00
		115.00	80.00	40.00	19.00	254.00
		37.00	18.00	5.00	0.00	60.00
2	1000.	0.00	5.00	2.00	2.00	9.00
		0.00	17.00	11.00	4.00	32.00
		0.00	127.00	71.00	45.00	243.00
		0.00	23.00	8.00	0.00	31.00
3	1000.	0.00	0.00	3.00	6.00	9.00
		0.00	0.00	17.00	7.00	24.00
		0.00	0.00	108.00	83.00	191.00
		0.00	0.00	14.00	0.00	14.00
COLUMN TOTALS		4.00	9.00	7.00	12.00	
		17.00	22.00	34.00	15.00	
		115.00	207.00	219.00	147.00	
		37.00	41.00	27.00	0.00	
T(I,S,T)		240.00	394.00	407.00	174.00	
Z(I,S,T)		141.00	197.00	174.00	0.00	

***** RECOVERIES IN POST-STRATUM 2

YEAR	NUMBER RELEASED	1	2	3	4	TOTALS
1	1000.	10.00	1.00	2.00	4.00	17.00
		9.00	10.00	7.00	3.00	29.00
		113.00	88.00	32.00	29.00	262.00
		24.00	16.00	7.00	0.00	47.00
2	1000.	0.00	5.00	2.00	1.00	8.00
		0.00	10.00	9.00	3.00	22.00
		0.00	102.00	70.00	44.00	216.00
		0.00	23.00	16.00	0.00	39.00
3	1000.	0.00	0.00	6.00	2.00	8.00
		0.00	0.00	10.00	6.00	16.00
		0.00	0.00	107.00	54.00	161.00
		0.00	0.00	13.00	0.00	13.00
COLUMN TOTALS		10.00	6.00	10.00	7.00	
		9.00	20.00	26.00	12.00	
		113.00	190.00	209.00	127.00	
		24.00	39.00	36.00	0.00	
T(I,S,T)		261.00	360.00	355.00	146.00	
Z(I,S,T)		153.00	183.00	146.00	0.00	

Figure 3.7.2 a (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES

==================== RELEASES FROM PRE-STRATUM 2 ====================

YEAR	NUMBER RELEASED	***** RECOVERIES IN POST-STRATUM 1: 1	2	3	4	TOTALS	***** RECOVERIES IN POST-STRATUM 2: 1	2	3	4	TOTALS
1	1000.	12.00	5.00	3.00	0.00	20.00	12.00	6.00	2.00	4.00	24.00
		23.00	11.00	3.00	2.00	39.00	26.00	10.00	6.00	2.00	44.00
		106.00	33.00	23.00	9.00	171.00	79.00	44.00	23.00	7.00	153.00
		18.00	3.00	1.00	0.00	22.00	17.00	13.00	4.00	0.00	34.00
2	1000.	0.00	12.00	4.00	1.00	17.00	0.00	12.00	2.00	8.00	22.00
		0.00	24.00	8.00	4.00	36.00	0.00	19.00	13.00	8.00	40.00
		0.00	109.00	55.00	24.00	188.00	0.00	86.00	45.00	24.00	155.00
		0.00	23.00	10.00	0.00	33.00	0.00	29.00	6.00	0.00	35.00
3	1000.	0.00	0.00	9.00	6.00	15.00	0.00	0.00	11.00	10.00	21.00
		0.00	0.00	23.00	13.00	36.00	0.00	0.00	31.00	8.00	39.00
		0.00	0.00	116.00	48.00	164.00	0.00	0.00	104.00	35.00	139.00
		0.00	0.00	13.00	0.00	13.00	0.00	0.00	15.00	0.00	15.00
COLUMN TOTALS		12.00	17.00	16.00	7.00		12.00	18.00	15.00	22.00	
		23.00	35.00	34.00	19.00		26.00	29.00	50.00	18.00	
		106.00	142.00	194.00	81.00		79.00	130.00	172.00	66.00	
		18.00	26.00	24.00	0.00		17.00	42.00	25.00	0.00	
T(I,S,T)		208.00	293.00	327.00	107.00		187.00	269.00	318.00	106.00	
Z(I,S,T)		85.00	125.00	107.00	0.00		87.00	134.00	106.00	0.00	

LOG-LIKELIHOOD FOR MODEL WITH NO STRUCTURE = -10959.6 WITH 132 PARMS

Figure 3.7.2 b
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RHO	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.85845	0.63913	0.50100				
1	1	1				0.72777	0.03361	0.19048	0.67592
1	1	2				0.27223	0.08130	0.52632	0.42418
1	2		0.97206	0.60689	0.46000				
1	2	1				0.46695	0.04167	0.29032	0.49690
1	2	2				0.53305	0.03061	0.23077	0.52089
1	3		1.05883		0.38200				
1	3	1				0.62672	0.03097	0.17073	0.11947
1	3	2				0.37328	0.04566	0.27778	0.16438
1	4		0.36168		0.16042				
1	4	1				0.49587	0.07547	0.44444	
1	4	2				0.50413	0.05224	0.36842	
2	1		0.63233	0.44103	0.39500				
2	1	1				0.54428	0.10169	0.34286	0.39113
2	1	2				0.45572	0.13187	0.31579	0.47901
2	2		0.60568	0.46563	0.39000				
2	2	1				0.55723	0.10692	0.32692	0.42363
2	2	2				0.44277	0.12162	0.38298	0.73519
2	3		0.87768		0.38600				
2	3	1				0.44747	0.07619	0.32000	0.11429
2	3	2				0.55253	0.08021	0.23077	0.13369
2	4		0.29136		0.12747				
2	4	1				0.67136	0.07955	0.26923	
2	4	2				0.32864	0.25000	0.55000	

FINAL LOG-LIKELIHOOD= -10990.6 WITH 64 PARMS

Figure 3.7.2 b (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.28078	0.03822				
1	1	1			0.09806	0.01652	0.08569	0.09510
1	1	2			0.09806	0.02464	0.11455	0.07903
1	2		0.22223	0.03885				
1	2	1			0.11197	0.01360	0.08152	0.07265
1	2	2			0.11197	0.01230	0.08263	0.07754
1	3		0.24938					
1	3	1			0.10082	0.01152	0.05876	0.02157
1	3	2			0.10082	0.01411	0.07465	0.02504
1	4		0.06664					
1	4	1			0.09146	0.02095	0.09563	
1	4	2			0.09146	0.01922	0.11066	
2	1		0.10085	0.03522				
2	1	1			0.08040	0.02782	0.08023	0.08627
2	1	2			0.08040	0.03547	0.07541	0.10646
2	2		0.08084	0.03369				
2	2	1			0.06533	0.02451	0.06505	0.07784
2	2	2			0.06533	0.02687	0.07091	0.10038
2	3		0.13306					
2	3	1			0.07384	0.01831	0.06597	0.02195
2	3	2			0.07384	0.01986	0.05226	0.02489
2	4		0.06321					
2	4	1			0.07667	0.02884	0.08699	
2	4	2			0.07667	0.04616	0.07866	

Figure 3.7.2 b (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST SE	BAND-REPORTING EST SE	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	100000 (20000)	0.500 (0.100)	4200 (1495)	0.194 (0.079)	62475 (30362)	0.476 (0.148)
1	1	2	200000 (50000)	0.400 (0.080)	17500 (6311)	0.806 (0.079)	68833 (23200)	0.524 (0.148)
1	2	1	100000 (20000)	0.250 (0.050)	7600 (2757)	0.286 (0.104)	23370 (6885)	0.289 (0.092)
1	2	2	200000 (50000)	0.400 (0.080)	19000 (6793)	0.714 (0.104)	57633 (19499)	0.711 (0.092)
2	1	1	150000 (30000)	0.500 (0.100)	5674 (1900)	0.173 (0.069)	68085 (23265)	0.402 (0.112)
2	1	2	300000 (75000)	0.400 (0.080)	27064 (9434)	0.827 (0.069)	101251 (31971)	0.598 (0.112)
2	2	1	150000 (30000)	0.250 (0.050)	9517 (3274)	0.280 (0.099)	77724 (31601)	0.491 (0.128)
2	2	2	300000 (75000)	0.400 (0.080)	24462 (8599)	0.720 (0.099)	80452 (24795)	0.509 (0.128)
3	1	1	75000 (15000)	0.500 (0.100)	3083 (998)	0.216 (0.072)	49770 (19648)	0.458 (0.115)
3	1	2	150000 (20000)	0.400 (0.080)	11221 (3130)	0.784 (0.072)	58910 (14261)	0.542 (0.115)
3	2	1	75000 (15000)	0.250 (0.050)	5414 (1780)	0.271 (0.084)	29643 (9854)	0.290 (0.086)
3	2	2	150000 (20000)	0.400 (0.080)	14587 (3947)	0.729 (0.084)	72742 (18719)	0.710 (0.086)

MLEs and their estimated standard errors equal the value obtained from the closed form expressions in Table 3.4.3 and Appendix 3.B. Note that some care must be taken when examining estimates involving confounded parameters; e.g., the estimated total migration in year 4, is the MLE for $S_3^{s\cdot} M_4^{s\cdot}$. From these results, it can be seen that the estimates of the net survival rates over all post-strata are quite precise (estimated coefficients of variation of about 5%), while the other estimates have estimated coefficients of variation of around 20%-35%. One estimate of the total migration rate is out of range (1.05863 in year 3 in pre-stratum 1) but has an estimated standard error of 0.25. From these estimates, it appears that the overall survival rates differ between the two pre-strata, but not among years which agrees with the true parameter values. There appear to be differences in the band-recovery rates between the pre-strata but no differences in the sighting rates between pre-strata; again, consistent with the true model. Because of the large variability in the estimated migration rates, there is not much evidence of different migration patterns in either the absolute or relative rates, contrary to the true model. Also, the large standard errors of the estimates of the post-stratum survival rates would seem to permit the conclusion that the survival rates are homogeneous among pre-strata, but in light of the differences in net survival rates over all post-strata, this is unlikely. The estimates of harvest-derivation and immigration are close to their true values derived from Tables 1.5b and 1.5c. As in real life experiments, the estimates of the immigration and harvest-derivation rates have two sources of variability: sampling variation in the estimates of the migration and band-recovery parameter from the banding experiment and sampling variation in the estimates of the pre-stratum population sizes and band-reporting rates from the external studies.

The log-likelihood (up to constants) of the full model is -10990.6 and the model requires 64 parameters. When this is compared to the log-likelihood of the 'unstructured' model, the chi-square test-statistic for the goodness-of-fit of the full model against a general alternative is found to be 62.0=2(-10959.6-(-10990.6)) with 68=132-64 degrees of freedom which has a p-value of 0.68. There is no evidence that the full Partial-Fidelity Model does not apply.

As noted earlier, it does not appear that the sighting rates are different among the pre-strata. Biologically, this is often a reasonable assumption. A reduced model, assuming that the sighting rates are common among pre-strata ($p_i^{st}=p_i^{\cdot t}$) was then fitted. The iterative procedure converged in four iterations, and the MLEs and their estimated standard errors are presented in Figure 3.7.2c. All estimates are now in range, and the precision of most estimates has improved. The log-likelihood of this reduced model (up to constant terms) has a value of -10996.8 and the model requires 56 parameters. When this reduced model is compared to the full model, the chi-square likelihood ratio test statistic has a value of 12.4=2(-10990.6-(-10996.8)) with 8=64-56 degrees of freedom, corresponding to a p-value of 0.13. Hence there is little evidence that this restricted model is not acceptable, which is consistent with the true model. A goodness-of-fit test for this restricted model is performed by comparing its log-likelihood with that of the 'unstructured' model. The chi-square

Figure 3.7.2 c
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RHO	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.73527	0.63913	0.50100				
1	1	1				0.57598	0.04959	0.28571	0.66475
1	1	2				0.42402	0.06094	0.38596	0.43358
1	2		0.79049	0.60689	0.46000				
1	2	1				0.53392	0.04481	0.31325	0.49527
1	2	2				0.46608	0.04305	0.32877	0.51420
1	3		0.89627		0.38200				
1	3	1				0.50758	0.04518	0.25275	0.11772
1	3	2				0.49242	0.04089	0.24752	0.16521
1	4		0.35815		0.16042				
1	4	1				0.61175	0.06178	0.35849	
1	4	2				0.38825	0.06850	0.49153	
2	1		0.64868	0.44103	0.39500				
2	1	1				0.62588	0.08621	0.28571	0.39788
2	1	2				0.37412	0.15658	0.38596	0.46537
2	2		0.65767	0.46563	0.39000				
2	2	1				0.53318	0.10291	0.31325	0.42553
2	2	2				0.46682	0.10623	0.32877	0.74807
2	3		0.94402		0.38600				
2	3	1				0.51828	0.06116	0.25275	0.11615
2	3	2				0.48172	0.08554	0.24752	0.13292
2	4		0.25507		0.12747				
2	4	1				0.59112	0.10320	0.35849	
2	4	2				0.40888	0.22952	0.49153	

FINAL LOG-LIKELIHOOD= -10996.8 WITH 56 PARMS

Figure 3.7.2 c (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.10626	0.03822				
1	1	1			0.06947	0.01497	0.06037	0.09343
1	1	2			0.06947	0.01711	0.06448	0.08033
1	2		0.09558	0.03885				
1	2	1			0.06048	0.01079	0.05091	0.07229
1	2	2			0.06048	0.01103	0.05498	0.07649
1	3		0.11622					
1	3	1			0.06420	0.01069	0.04556	0.02125
1	3	2			0.06420	0.00982	0.04294	0.02511
1	4		0.04681					
1	4	1			0.05727	0.01615	0.06587	
1	4	2			0.05727	0.01782	0.06509	
2	1		0.09378	0.03522				
2	1	1			0.06407	0.02265	0.06037	0.08744
2	1	2			0.06407	0.03415	0.06448	0.10340
2	2		0.07714	0.03369				
2	2	1			0.05882	0.02119	0.05091	0.07796
2	2	2			0.05882	0.02266	0.05498	0.10134
2	3		0.11929					
2	3	1			0.06286	0.01379	0.04556	0.02226
2	3	2			0.06286	0.01772	0.04294	0.02471
2	4		0.03287					
2	4	1			0.05832	0.02691	0.06587	
2	4	2			0.05832	0.04247	0.06509	

Figure 3.7.2 c (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST SE	BAND-REPORTING EST SE	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	100000 (20000)	0.500 (0.100)	4200 (1495)	0.194 (0.079)	42350 (12513)	0.343 (0.077)
1	1	2	200000 (50000)	0.400 (0.080)	17500 (6311)	0.806 (0.079)	81200 (26545)	0.657 (0.077)
1	2	1	100000 (20000)	0.250 (0.050)	7600 (2757)	0.286 (0.104)	31177 (8343)	0.391 (0.082)
1	2	2	200000 (50000)	0.400 (0.080)	19000 (6793)	0.714 (0.104)	48536 (14642)	0.609 (0.082)
2	1	1	150000 (30000)	0.500 (0.100)	5674 (1900)	0.173 (0.069)	63309 (16560)	0.376 (0.079)
2	1	2	300000 (75000)	0.400 (0.080)	27064 (9434)	0.827 (0.069)	105198 (31456)	0.624 (0.079)
2	2	1	150000 (30000)	0.250 (0.050)	9517 (3274)	0.280 (0.099)	55266 (14658)	0.375 (0.079)
2	2	2	300000 (75000)	0.400 (0.080)	24462 (8599)	0.720 (0.099)	92105 (27786)	0.625 (0.079)
3	1	1	75000 (15000)	0.500 (0.100)	3083 (998)	0.216 (0.072)	34120 (9290)	0.317 (0.056)
3	1	2	150000 (20000)	0.400 (0.080)	11221 (3130)	0.784 (0.072)	73391 (16586)	0.683 (0.056)
3	2	1	75000 (15000)	0.250 (0.050)	5414 (1780)	0.271 (0.084)	33100 (8909)	0.327 (0.057)
3	2	2	150000 (20000)	0.400 (0.080)	14587 (3947)	0.729 (0.084)	68212 (14939)	0.673 (0.057)

test-statistic has a value of 74.4=2(-10959.6-(-10996.8)) with 76=132-56 degrees of freedom, and a p-value of 0.53. There is no evidence that this restricted model does not provide an adequate fit to the data.

If the sighting rates are homogeneous among pre-strata, then it is often of interest to examine if the band-recovery rates are also homogeneous among pre-strata. A model where both the band-recovery and the sighting rates are homogeneous among pre-strata, i.e., where $f_i^{st}=f_i^{\cdot t}$ and $p_i^{st}=p_i^{\cdot t}$, was fit to the data. The starting values for the iterative procedure were computed using the average band-recovery rate from the previous model. The iterative procedure converged in three iterations, and the MLEs and estimated standard errors are shown in Figure 3.7.2d. The log-likelihood under this new restricted model (up to constant terms) is -11036.8 and this model requires 48 parameters. When this is compared to the model where only the sighting rates are homogeneous over pre-strata, the likelihood ratio chi-square test-statistic has the value of 80.0 = 2(-10996.8-(-11036.8)) with 8=56-48 degrees of freedom, and a p-value <0.0001. There is good evidence that the recovery rates are not homogeneous among pre-strata, which is again consistent with the true parameter values.

One final model was fit to the data, assuming that the sighting rates in years 1...4 and absolute migration rates ($M_i^{s\cdot}m_i^{st}$) in year 1...3 are homogeneous among pre-strata. Note that the absolute migration rates in year 4 are confounded with the overall survival rates, and it is not biologically reasonable to assume that these

Figure 3.7.2 d
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: F AND P ARE THE SAME OVER PRE-STRATA (MODEL 10)

ESTIMATES OF PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RHO	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.70119	0.62941	0.50100				
1	1	1				0.58082	0.06751	0.28571	0.65221
1	1	2				0.41918	0.10280	0.38596	0.41425
1	2		0.75321	0.59760	0.46000				
1	2	1				0.53420	0.06933	0.31325	0.48255
1	2	2				0.46580	0.06977	0.32877	0.49985
1	3		0.86408		0.38200				
1	3	1				0.51629	0.05275	0.25275	0.11678
1	3	2				0.48371	0.06158	0.24752	0.16164
1	4		0.34142		0.15873				
1	4	1				0.61983	0.07692	0.35849	
1	4	2				0.38017	0.13063	0.49153	
2	1		0.68276	0.45004	0.39500				
2	1	1				0.61842	0.06751	0.28571	0.40602
2	1	2				0.38158	0.10280	0.38596	0.49504
2	2		0.70009	0.47868	0.39000				
2	2	1				0.53288	0.06933	0.31325	0.44146
2	2	2				0.46712	0.06977	0.32877	0.77859
2	3		0.98244		0.38600				
2	3	1				0.50872	0.05275	0.25275	0.11719
2	3	2				0.49128	0.06158	0.24752	0.13640
2	4		0.27447		0.12924				
2	4	1				0.58000	0.07692	0.35849	
2	4	2				0.42000	0.13063	0.49153	

FINAL LOG-LIKELIHOOD= -11036.8 WITH 48 PARMS

Figure 3.7.2 d (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: F AND P ARE THE SAME OVER PRE-STRATA (MODEL 10)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.09930	0.03762				
1	1	1			0.06755	0.01630	0.06037	0.09180
1	1	2			0.06755	0.02076	0.06448	0.07697
1	2		0.08894	0.03826				
1	2	1			0.05907	0.01312	0.05091	0.07055
1	2	2			0.05907	0.01374	0.05498	0.07450
1	3		0.11059					
1	3	1			0.06322	0.01071	0.04556	0.02109
1	3	2			0.06322	0.01193	0.04294	0.02460
1	4		0.04401					
1	4	1			0.05533	0.01696	0.06587	
1	4	2			0.05533	0.02262	0.06509	
2	1		0.09960	0.03582				
2	1	1			0.06577	0.01630	0.06037	0.08895
2	1	2			0.06577	0.02076	0.06448	0.10876
2	2		0.08393	0.03447				
2	2	1			0.06012	0.01312	0.05091	0.08045
2	2	2			0.06012	0.01374	0.05498	0.10424
2	3		0.12498					
2	3	1			0.06346	0.01071	0.04556	0.02243
2	3	2			0.06346	0.01193	0.04294	0.02528
2	4		0.03577					
2	4	1			0.06033	0.01696	0.06587	
2	4	2			0.06033	0.02262	0.06509	

Figure 3.7.2 d (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: F AND P ARE THE SAME OVER PRE-STRATA (MODEL 10)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST	SE	BAND-REPORTING EST	SE	HARVEST DERIVATION	(SE)	RELATIVE DERIVATION	(SE)	IMMIGRATION	(SE)	RELATIVE IMMIGRATION	(SE)
1	1	1	100000	(20000)	0.500	(0.100)	5499	(1744)	0.278	(0.089)	40726	(11914)	0.325	(0.074)
1	1	2	200000	(50000)	0.400	(0.080)	14253	(4995)	0.722	(0.089)	84447	(27729)	0.675	(0.074)
1	2	1	100000	(20000)	0.250	(0.050)	12087	(3824)	0.474	(0.111)	29393	(7743)	0.361	(0.079)
1	2	2	200000	(50000)	0.400	(0.080)	13392	(4708)	0.526	(0.111)	52105	(15879)	0.639	(0.079)
2	1	1	150000	(30000)	0.500	(0.100)	8369	(2563)	0.301	(0.092)	60354	(15640)	0.350	(0.076)
2	1	2	300000	(75000)	0.400	(0.080)	19399	(6640)	0.699	(0.092)	111919	(33677)	0.650	(0.076)
2	2	1	150000	(30000)	0.250	(0.050)	14687	(4542)	0.462	(0.109)	52627	(13814)	0.349	(0.076)
2	2	2	300000	(75000)	0.400	(0.080)	17112	(5905)	0.538	(0.109)	98107	(29816)	0.651	(0.076)
3	1	1	75000	(15000)	0.500	(0.100)	3530	(1077)	0.263	(0.074)	33459	(9072)	0.309	(0.055)
3	1	2	150000	(20000)	0.400	(0.080)	9887	(2633)	0.737	(0.074)	74968	(16978)	0.691	(0.055)
3	2	1	75000	(15000)	0.250	(0.050)	7721	(2345)	0.409	(0.093)	31347	(8363)	0.302	(0.054)
3	2	2	150000	(20000)	0.400	(0.080)	11145	(2946)	0.591	(0.093)	72398	(15996)	0.698	(0.054)

confounded parameters are homogeneous among pre-strata. The starting values for the iterative procedure were computed using the average of the parameter values from an earlier model. Convergence occurred in three iterations. The MLEs and their estimated standard errors are presented in Figure 3.7.2e. The log-likelihood (up to constant terms) for this new model has a value of -11002.7 and this model requires 50 parameters. When this model is compared to the model where only the sighting rates were homogeneous among pre-strata, the chi-square likelihood ratio test-statistic has the value of 11.8 = 2(-10996.8-(-11002.7)) with 6=56-50 degrees of freedom, and a p-value of 0.067. There is some evidence that the absolute migration rates are not homogeneous among pre-strata, which is again consistent with the true parameter values. A goodness-of-fit can be computed as illustrated earlier, and the chi-square test-statistic has a value of 86.2 = 2(-10959.6-(-11002.7)) with 82=132-50 degrees of freedom, and a p-value of 0.35. Hence, even though the previous test indicated some evidence that the absolute migration rates are not homogeneous among pre-strata, the goodness-of-fit test fails to find evidence that this restricted model would be inadequate - probably caused by the low power against a wide variety of alternatives.

This procedure of fitting reduced models can be continued in a similar fashion until a biologically reasonable model that provides an adequate fit to the data is determined. A summary of the models considered above is shown in Figure 3.7.2f. In our simulated example, none of the tests incorrectly rejected the null hypothesis when it is was true, or, with one exception, accepted the null hypothesis when it

Figure 3.7.2 e
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P AND ABS. MIG. ARE SAME OVER PRE-STRATA (MODEL 50)

ESTIMATES OF PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RHO	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.67909	0.67263	0.48979				
1	1	1				0.60601	0.05149	0.28794	0.69448
1	1	2				0.39399	0.06827	0.39991	0.45033
1	2		0.70867	0.58815	0.43943				
1	2	1				0.53398	0.04867	0.32102	0.48505
1	2	2				0.46602	0.04672	0.33742	0.50370
1	3		0.92324		0.38847				
1	3	1				0.51283	0.04391	0.25155	0.11787
1	3	2				0.48717	0.04037	0.24658	0.16529
1	4		0.36078		0.16160				
1	4	1				0.61175	0.06178	0.35849	
1	4	2				0.38825	0.06850	0.49153	
2	1		0.67909	0.41813	0.40801				
2	1	1				0.60601	0.08429	0.28794	0.37780
2	1	2				0.39399	0.14797	0.39991	0.44546
2	2		0.70867	0.48420	0.41159				
2	2	1				0.53398	0.09790	0.32102	0.43531
2	2	2				0.46602	0.10152	0.33742	0.76503
2	3		0.92324		0.37944				
2	3	1				0.51283	0.06254	0.25155	0.11597
2	3	2				0.48717	0.08612	0.24658	0.13283
2	4		0.25339		0.12663				
2	4	1				0.59112	0.10320	0.35849	
2	4	2				0.40888	0.22952	0.49153	

FINAL LOG-LIKELIHOOD= -11002.7 WITH 50 PARMS

Figure 3.7.2 e (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P AND ABS. MIG. ARE SAME OVER PRE-STRATA (MODEL 50)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRATION	OVERALL SURVIVAL	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.09382	0.03852				
1	1	1			0.06225	0.01511	0.06081	0.09706
1	1	2			0.06225	0.01864	0.06453	0.08324
1	2		0.07939	0.03488				
1	2	1			0.05601	0.01137	0.05134	0.06991
1	2	2			0.05601	0.01163	0.05542	0.07403
1	3		0.11366					
1	3	1			0.06127	0.01029	0.04543	0.02128
1	3	2			0.06127	0.00954	0.04265	0.02512
1	4		0.04700					
1	4	1			0.05727	0.01615	0.06587	
1	4	2			0.05727	0.01782	0.06509	
2	1		0.09382	0.03238				
2	1	1			0.06225	0.02216	0.06081	0.08253
2	1	2			0.06225	0.03160	0.06453	0.09817
2	2		0.07939	0.03320				
2	2	1			0.05601	0.02002	0.05134	0.07908
2	2	2			0.05601	0.02150	0.05542	0.10202
2	3		0.11366					
2	3	1			0.06127	0.01397	0.04543	0.02223
2	3	2			0.06127	0.01767	0.04265	0.02469
2	4		0.03255					
2	4	1			0.05832	0.02691	0.06587	
2	4	2			0.05832	0.04247	0.06509	

Figure 3.7.2 e (continued)
PARTIAL-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P AND ABS. MIG. ARE SAME OVER PRE-STRATA (MODEL 50)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST	SE	BAND-REPORTING EST	SE	HARVEST DERIVATION	(SE)	RELATIVE DERIVATION	(SE)	IMMIGRATION	(SE)	RELATIVE IMMIGRATION	(SE)
1	1	1	100000	(20000)	0.500	(0.100)	4238	(1498)	0.196	(0.080)	41154	(11805)	0.333	(0.071)
1	1	2	200000	(50000)	0.400	(0.080)	17344	(6278)	0.804	(0.080)	82308	(26643)	0.667	(0.071)
1	2	1	100000	(20000)	0.250	(0.050)	7307	(2655)	0.270	(0.100)	26756	(6800)	0.333	(0.071)
1	2	2	200000	(50000)	0.400	(0.080)	19795	(7053)	0.730	(0.100)	53511	(15792)	0.667	(0.071)
2	1	1	150000	(30000)	0.500	(0.100)	5525	(1844)	0.166	(0.067)	56762	(14416)	0.333	(0.071)
2	1	2	300000	(75000)	0.400	(0.080)	27785	(9691)	0.834	(0.067)	113524	(33485)	0.667	(0.071)
2	2	1	150000	(30000)	0.250	(0.050)	9258	(3173)	0.269	(0.096)	49539	(12718)	0.333	(0.071)
2	2	2	300000	(75000)	0.400	(0.080)	25145	(8842)	0.731	(0.096)	99077	(29459)	0.667	(0.071)
3	1	1	75000	(15000)	0.500	(0.100)	3118	(1008)	0.219	(0.073)	35510	(9499)	0.333	(0.053)
3	1	2	150000	(20000)	0.400	(0.080)	11105	(3092)	0.781	(0.073)	71019	(15774)	0.667	(0.053)
3	2	1	75000	(15000)	0.250	(0.050)	5447	(1791)	0.273	(0.084)	33733	(8844)	0.333	(0.053)
3	2	2	150000	(20000)	0.400	(0.080)	14525	(3920)	0.727	(0.084)	67466	(14551)	0.667	(0.053)

was false. The single exception was the goodness-of-fit test to the model where sighting and absolute migration rates were assumed to be homogeneous among pre-strata. The cause of this Type II error is that the goodness-of-fit tests have low power.

Since the true values of the parameters are known in this situation, estimates of the power of the tests performed earlier can be determined by repeating the analyses using the expected numbers of recoveries as 'data'. This can also be done when investigating the power of a proposed banding study before it is undertaken, and 'guesses' are used for the likely parameter values. The value of the chi-square test-statistic using these expected values is (in large samples) the non-centrality parameter of a non-central chi-square distribution that can be used to estimate the power function. The sequence of model tests described earlier was repeated using the expected values generated using the parameter values of Table 1.5a, and a summary is presented in Figure 3.7.2f. The same computer program was used to analyze the 'expected' data.

Since data were generated using the full model, it is not surprising that the non-centrality parameter of the goodness-of-fit test has the value of 0.0=2(-11017.3-(-11017.3)) and so the goodness-of-fit test will be subject to a Type I error only.

Similarly, the true parameter values show that the sighting rates are homogeneous among pre-strata, and so the non-centrality parameter for the test of homogeneous sighting rates is also zero.

Figure 3.7.2f

Summary of the log-likelihood values of fitted models using the simulated data and expected values generated using the parameter values in Table 1.6a in the Partial-Fidelity Model with sightings

Simulated Data

Model with no structure
-10959.6 with 132 parms

Full Model
-10990.6 with 64 parms

Homogeneous sighting rates
-10996.8 with 56 parm

Homogeneous sighting and recovery rates
-11036.8 with 48 parms

Homogeneous sighting and absolute migration rates
-11002.7 with 50 parms

Expected Data

Model with no structure
-11017.3 with 132 parms

Full Model
-11017.3 with 64 parms

Homogeneous sighting rates
-11017.3 with 56 parm

Homogeneous sighting and recovery rates
-11050.0 with 48 parms

Homogeneous sighting and absolute migration rates
-11027.5 with 50 parms

When the model where both the recovery and sighting rates are homogeneous among pre-strata is compared to the model where only the sighting rates are homogeneous, the non-centrality parameter is found to be 65.7 = 2(-11017.3-(-11050.0) with 8=56-48 degrees of freedom. The power of the likelihood ratio test to detect the actual degree of heterogeneity that was present between the band-recovery rates found in Table 1.5a is estimated to be over 99% when testing at the 5% or 10% levels.

Similarly, when testing if the absolute migration rates in years 1...3 are homogeneous among pre-strata (assuming that the sighting rates are homogeneous among pre-strata), the estimated non-centrality parameter is found to be 20.4=2(-11017.3-(-11027.5)) with 6=56-50 degrees of freedom. The power of the likelihood ratio test to detect the actual degree of heterogeneity in the absolute migration rates that was present in Table 1.5a is estimated to be 94% when testing at the 5% level, and 97% when testing at the 10% level.

Any sequence of tests can be investigated in a similar fashion, and the number of releases can be varied until a design with sufficient power to detect the heterogeneity of interest is obtained. It is somewhat surprising that a study of this size yields such high power for most of the tests. A larger study examined in Chapter 2 has much lower power to detect differences among survival and recovery rates. The reason for the high powers of the tests considered in this example is the additional information from the sightings in the post-strata.

Since the cost of performing sightings in the post-strata is often small relative to the cost of banding additional animals, it provides a cost-effective way to increase the utility of a banding study.

3.7.3 COMPLETE-FIDELITY MODEL WITH SIGHTINGS IN THE POST-STRATA.

Simulated data using the parameter values shown in Table 1.5a were generated assuming that animals behaved according to the assumptions of the Complete-Fidelity Model. There were again 3 years of releases, 4 years of recoveries, 2 pre-strata where banding occurred, and 2 post-strata where recoveries occurred. The parameter values in Table 1.5a were assumed to be constant over time and a uniform sighting rate of 30% was used. The simulated reduced-data array and the summary statistics are presented in Figure 3.7.3a along with typical values for the external estimates (and their standard errors) for the pre-stratum population sizes and band-reporting rates. The log-likelihood (up to constant terms) used in assessing the goodness-of-fit to models in the Complete-Fidelity family is -10422.2 and such an 'unstructured' model would require 132 parameters.

The full Complete-Fidelity Model without any restrictions on the parameters is first fit to the data (Figure 3.7.3a). The MLE and their estimated standard errors (Figure 3.7.3b) equal those determined using the closed form expressions presented in Table 3.6.3 and Appendix 3.E. It can be seen that the estimates of the migration and sighting rates are quite precise (estimated coefficients of variation of 5-10%), while the other estimates have estimated coefficients of variation of around 15%-25%. Most estimates are close to their true values. However, one estimate of the post-stratum specific survival rate is out of range (1.25 in post-stratum 1 for animals released in year 3 in pre-stratum 1) but has an estimated standard error of 0.68. As one might expect, the precision of the estimates is generally higher in the Complete-

Figure 3.7.3 a
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES

NUMBER OF PRE-STRATA : 2
NUMBER OF POST-STRATA : 2
NUMBER OF YEARS OF RELEASES : 3
NUMBER OF YEARS OF RECOVERIES: 4

ESTIMATED POPULATION SIZES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	PRE STRATUM	POPULATION ESTIMATE	S.E.
1	1	100000.	20000.
1	2	200000.	50000.
2	1	150000.	30000.
2	2	300000.	75000.
3	1	75000.	15000.
3	2	150000.	20000.

ESTIMATED BAND-REPORTING RATES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	PRE STRATUM	ESTIMATES AND (S.E.) POST-STRATUM 1	POST-STRATUM 2
1	1	0.5000 (0.10)	0.2500 (0.05)
1	2	0.4000 (0.08)	0.4000 (0.08)
2	1	0.5000 (0.10)	0.2500 (0.05)
2	2	0.4000 (0.08)	0.4000 (0.08)
3	1	0.5000 (0.10)	0.2500 (0.05)
3	2	0.4000 (0.08)	0.4000 (0.08)

Figure 3.7.3a (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES

==================== RELEASES FROM PRE-STRATUM 1 ====================

***** RECOVERIES IN POST-STRATUM 1

YEAR	NUMBER RELEASED	1	2	3	4	TOTALS
1	1000.	6.00	2.00	1.00	0.00	9.00
		11.00	6.00	2.00	0.00	19.00
		115.00	66.00	35.00	16.00	232.00
		35.00	17.00	6.00	0.00	58.00
2	1000.	0.00	5.00	5.00	2.00	12.00
		0.00	15.00	9.00	7.00	31.00
		0.00	120.00	57.00	17.00	194.00
		0.00	24.00	11.00	0.00	35.00
3	1000.	0.00	0.00	7.00	1.00	8.00
		0.00	0.00	8.00	16.00	24.00
		0.00	0.00	111.00	47.00	158.00
		0.00	0.00	22.00	0.00	22.00
COLUMN TOTALS		6.00	7.00	13.00	3.00	
		11.00	21.00	19.00	23.00	
		115.00	186.00	203.00	80.00	
		35.00	41.00	39.00	0.00	
T(I,S,T)		202.00	307.00	302.00	106.00	
Z(I,S,T)		105.00	134.00	106.00	0.00	

***** RECOVERIES IN POST-STRATUM 2

YEAR	NUMBER RELEASED	1	2	3	4	TOTALS
1	1000.	6.00	1.00	4.00	0.00	11.00
		13.00	6.00	5.00	1.00	25.00
		121.00	68.00	37.00	24.00	250.00
		45.00	23.00	7.00	0.00	75.00
2	1000.	0.00	4.00	4.00	6.00	14.00
		0.00	16.00	6.00	5.00	27.00
		0.00	123.00	71.00	44.00	238.00
		0.00	37.00	16.00	0.00	53.00
3	1000.	0.00	0.00	9.00	4.00	13.00
		0.00	0.00	10.00	11.00	21.00
		0.00	0.00	124.00	69.00	193.00
		0.00	0.00	28.00	0.00	28.00
COLUMN TOTALS		6.00	5.00	17.00	10.00	
		13.00	22.00	21.00	17.00	
		121.00	191.00	232.00	137.00	
		45.00	60.00	51.00	0.00	
T(I,S,T)		211.00	342.00	383.00	164.00	
Z(I,S,T)		116.00	184.00	164.00	0.00	

Figure 3.7.3a (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

==================== RELEASES FROM PRE-STRATUM 2 ====================

YEAR	NUMBER RELEASED	***** RECOVERIES IN POST-STRATUM 1: 1	2	3	4	TOTALS	***** RECOVERIES IN POST-STRATUM 2: 1	2	3	4	TOTALS
1	1000.	8.00	4.00	4.00	1.00	17.00	13.00	5.00	4.00	3.00	25.00
		31.00	15.00	1.00	2.00	49.00	27.00	21.00	7.00	4.00	59.00
		101.00	65.00	29.00	13.00	208.00	66.00	51.00	25.00	19.00	161.00
		31.00	16.00	5.00	0.00	52.00	25.00	20.00	10.00	0.00	55.00
2	1000.	0.00	8.00	9.00	0.00	17.00	0.00	7.00	2.00	1.00	10.00
		0.00	19.00	12.00	7.00	38.00	0.00	24.00	17.00	7.00	48.00
		0.00	97.00	45.00	27.00	169.00	0.00	65.00	38.00	34.00	137.00
		0.00	31.00	6.00	0.00	37.00	0.00	22.00	14.00	0.00	36.00
3	1000.	0.00	0.00	12.00	6.00	18.00	0.00	0.00	8.00	9.00	17.00
		0.00	0.00	23.00	12.00	35.00	0.00	0.00	26.00	11.00	37.00
		0.00	0.00	102.00	58.00	160.00	0.00	0.00	80.00	49.00	129.00
		0.00	0.00	21.00	0.00	21.00	0.00	0.00	18.00	0.00	18.00
COLUMN TOTALS		8.00	12.00	25.00	7.00		13.00	12.00	14.00	13.00	
		31.00	34.00	36.00	21.00		27.00	45.00	50.00	22.00	
		101.00	162.00	176.00	98.00		66.00	116.00	143.00	102.00	
		31.00	47.00	32.00	0.00		25.00	42.00	42.00	0.00	
T(I,S,T)		222.00	300.00	331.00	126.00		190.00	268.00	302.00	137.00	
Z(I,S,T)		113.00	139.00	126.00	0.00		109.00	137.00	137.00	0.00	

LOG-LIKELIHOOD FOR MODEL WITH NO STRUCTURE = -10422.2 WITH 132 PARAMETERS

Figure 3.7.3 b
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF THE PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL	RHO
1	1		0.69623					0.41300
1	1	1		0.51714	0.04722	0.33607	0.61876	0.20200
1	1	2		0.48286	0.05652	0.37778	0.64193	0.21100
1	2		0.84904					0.42800
1	2	1		0.50480	0.04299	0.29630	0.39048	0.20200
1	2	2		0.49520	0.04244	0.30806	0.55852	0.22600
1	3		0.70321					0.36700
1	3	1		0.45347	0.05582	0.37681	1.25488	0.16800
1	3	2		0.54653	0.05137	0.33663	0.53659	0.19900
1	4							
1	4	1			0.03614	0.11538		
1	4	2			0.06803	0.37037		
2	1		0.73458					0.41200
2	1	1		0.57831	0.09180	0.25658	0.48375	0.22200
2	1	2		0.42169	0.12913	0.25503	0.60378	0.19000
2	2		0.61291					0.34600
2	2	1		0.55487	0.08431	0.31892	0.50755	0.18700
2	2	2		0.44513	0.12395	0.27835	0.55591	0.15900
2	3		0.69039					0.35700
2	3	1		0.55404	0.09251	0.30481	0.63692	0.19200
2	3	2		0.44596	0.11357	0.27861	0.54943	0.16500
2	4							
2	4	1			0.06667	0.25000		
2	4	2			0.11304	0.37143		

FINAL LOG-LIKELIHOOD= -10462.8 WITH 56 PARMS

Figure 3.7.3 b (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.04893				
1	1	1		0.03986	0.01220	0.04277	0.10119
1	1	2		0.03986	0.01349	0.04173	0.08781
1	2		0.06068				
1	2	1		0.03945	0.00914	0.03588	0.06109
1	2	2		0.03945	0.00876	0.03178	0.07241
1	3		0.05015				
1	3	1		0.03538	0.01097	0.04125	0.67921
1	3	2		0.03538	0.00920	0.03325	0.13883
1	4						
1	4	1			0.02049	0.06266	
1	4	2			0.02077	0.09293	
2	1		0.05690				
2	1	1		0.04838	0.01730	0.03542	0.07628
2	1	2		0.04838	0.02308	0.03571	0.09014
2	2		0.04327				
2	2	1		0.04292	0.01399	0.03427	0.07218
2	2	2		0.04292	0.01884	0.03218	0.07783
2	3		0.05032				
2	3	1		0.04402	0.01422	0.03366	0.21086
2	3	2		0.04402	0.01690	0.03162	0.12604
2	4						
2	4	1			0.02434	0.08183	
2	4	2			0.02953	0.08167	

Figure 3.7.3 b (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: FULL MODEL

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST	SE	BAND-REPORTING EST	SE	HARVEST DERIVATION	(SE)	RELATIVE DERIVATION	(SE)	IMMIGRATION	(SE)	RELATIVE IMMIGRATION	(SE)
1	1	1	100000	(20000)	0.500	(0.100)	3400	(1262)	0.148	(0.065)	36005	(8248)	0.298	(0.075)
1	1	2	200000	(50000)	0.400	(0.080)	19500	(6953)	0.852	(0.065)	84964	(23438)	0.702	(0.075)
1	2	1	100000	(20000)	0.250	(0.050)	7600	(2760)	0.275	(0.102)	33618	(7520)	0.352	(0.082)
1	2	2	200000	(50000)	0.400	(0.080)	20000	(7174)	0.725	(0.102)	61953	(17615)	0.648	(0.082)
2	1	1	150000	(30000)	0.500	(0.100)	5527	(1886)	0.204	(0.080)	64289	(14834)	0.387	(0.084)
2	1	2	300000	(75000)	0.400	(0.080)	21505	(7611)	0.796	(0.080)	102026	(27561)	0.613	(0.084)
2	2	1	150000	(30000)	0.250	(0.050)	10705	(3671)	0.297	(0.102)	63067	(14015)	0.435	(0.088)
2	2	2	300000	(75000)	0.400	(0.080)	25363	(8900)	0.703	(0.102)	81847	(22770)	0.565	(0.088)
3	1	1	75000	(15000)	0.500	(0.100)	2670	(897)	0.168	(0.061)	23916	(5479)	0.294	(0.059)
3	1	2	150000	(20000)	0.400	(0.080)	13269	(3643)	0.832	(0.061)	57376	(9808)	0.706	(0.059)
3	2	1	75000	(15000)	0.250	(0.050)	5923	(1940)	0.311	(0.092)	28824	(6327)	0.384	(0.067)
3	2	2	150000	(20000)	0.400	(0.080)	13113	(3630)	0.689	(0.092)	46182	(8398)	0.616	(0.067)

Fidelity Model than in the Partial-Fidelity Model. There appear to be differences in the band-recovery rates among the pre-strata but no large differences among the sighting rates, consistent with the true parameter values. The differences in the migration rates are about the same size as their standard errors; it is difficult to detect any differences among them. There appear to be large differences in the relative harvest-derivation rates among post-strata; pre-stratum 2 contributing much more heavily to the harvest in post-stratum 1 than in post-stratum 2. The differences among the estimates of the immigration rates among post-strata are smaller, but show a consistent pattern where the contribution from pre-stratum 1 is about six percentage points smaller in post-stratum 1 than in post-stratum 2.

The log-likelihood (up to constants) of the full model is -10462.8 and the model requires 56 parameters. When this is compared to the log-likelihood of the 'unstructured' model, the chi-square test-statistic for the goodness-of-fit of the full model against a general alternative is found to be 81.2=2(-10422.2-(-10462.8)) with 76=132-56 degrees of freedom which has a p-value of 0.32. There is no evidence that the full Complete-Fidelity Model does not apply.

As noted earlier, it does not appear that the sighting rates are different among the pre-strata. A reduced model, assuming that the sighting rates are common among pre-strata, i.e., that $p_i^{st}=p_i^{\cdot t}$ was fit to the data. The iterative procedure converged in six iterations, and the MLEs and their estimated standard errors are presented in Figure 3.7.3c. The log-likelihood of this reduced model (up to

Figure 3.7.3 c
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF THE PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL	RHO
1	1		0.77352					0.41300
1	1	1		0.51195	0.04293	0.29197	0.54605	0.20200
1	1	2		0.48805	0.05033	0.31338	0.59014	0.21100
1	2		0.85005					0.42800
1	2	1		0.48938	0.04429	0.30836	0.44003	0.20200
1	2	2		0.51062	0.04111	0.29383	0.57799	0.22600
1	3		0.75939					0.36700
1	3	1		0.45930	0.05104	0.33538	0.73047	0.16800
1	3	2		0.54070	0.04809	0.30769	0.50149	0.19900
1	4							
1	4	1			0.05677	0.18519		
1	4	2			0.06813	0.37097		
2	1		0.67159					0.41200
2	1	1		0.58332	0.09955	0.29197	0.53646	0.22200
2	1	2		0.41668	0.14294	0.31338	0.64801	0.19000
2	2		0.61231					0.34600
2	2	1		0.56799	0.08245	0.30836	0.46391	0.18700
2	2	2		0.43201	0.12785	0.29383	0.53850	0.15900
2	3		0.64669					0.35700
2	3	1		0.55286	0.09897	0.33538	0.90402	0.19200
2	3	2		0.44714	0.12093	0.30769	0.58565	0.16500
2	4							
2	4	1			0.05025	0.18519		
2	4	2			0.11292	0.37097		

FINAL LOG-LIKELIHOOD= -10469.2 WITH 48 PARMS

Figure 3.7.3 c (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.04977				
1	1	1		0.03670	0.01093	0.02747	0.07725
1	1	2		0.03670	0.01200	0.02753	0.07626
1	2		0.04980				
1	2	1		0.03258	0.00890	0.02479	0.05661
1	2	2		0.03258	0.00830	0.02263	0.06590
1	3		0.04697				
1	3	1		0.03191	0.00966	0.02619	0.21708
1	3	2		0.03191	0.00837	0.02299	0.09275
1	4						
1	4	1			0.01949	0.05286	
1	4	2			0.01700	0.06135	
2	1		0.04054				
2	1	1		0.03975	0.01730	0.02747	0.07083
2	1	2		0.03975	0.02339	0.02753	0.07776
2	2		0.03765				
2	2	1		0.03928	0.01317	0.02479	0.05639
2	2	2		0.03928	0.01819	0.02263	0.06224
2	3		0.03884				
2	3	1		0.03753	0.01399	0.02619	0.26568
2	3	2		0.03753	0.01646	0.02299	0.10557
2	4						
2	4	1			0.01703	0.05286	
2	4	2			0.02568	0.06135	

Figure 3.7.3 c (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: P ARE THE SAME OVER PRE-STRATA (MODEL 05)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST SE	BAND-REPORTING EST SE	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	100000 (20000)	0.500 (0.100)	3400 (1262)	0.148 (0.065)	39600 (8855)	0.336 (0.075)
1	1	2	200000 (50000)	0.400 (0.080)	19500 (6953)	0.852 (0.065)	78350 (20900)	0.664 (0.075)
1	2	1	100000 (20000)	0.250 (0.050)	7600 (2759)	0.275 (0.102)	37752 (8360)	0.403 (0.083)
1	2	2	200000 (50000)	0.400 (0.080)	20000 (7174)	0.725 (0.102)	55968 (15300)	0.597 (0.083)
2	1	1	150000 (30000)	0.500 (0.100)	5527 (1886)	0.204 (0.080)	62400 (13741)	0.374 (0.079)
2	1	2	300000 (75000)	0.400 (0.080)	21505 (7611)	0.796 (0.080)	104336 (27778)	0.626 (0.079)
2	2	1	150000 (30000)	0.250 (0.050)	10705 (3668)	0.297 (0.102)	65108 (14101)	0.451 (0.085)
2	2	2	300000 (75000)	0.400 (0.080)	25364 (8917)	0.703 (0.102)	79357 (21701)	0.549 (0.085)
3	1	1	75000 (15000)	0.500 (0.100)	2670 (897)	0.168 (0.061)	26159 (5815)	0.328 (0.058)
3	1	2	150000 (20000)	0.400 (0.080)	13269 (3643)	0.832 (0.061)	53629 (8612)	0.672 (0.058)
3	2	1	75000 (15000)	0.250 (0.050)	5923 (1940)	0.311 (0.092)	30795 (6652)	0.415 (0.064)
3	2	2	150000 (20000)	0.400 (0.080)	13113 (3627)	0.689 (0.092)	43374 (7346)	0.585 (0.064)

constant terms) has a value of -10469.2 and the model requires 48 parameters. When this reduced model is compared to the full model, the chi-square likelihood ratio test statistic has a value of 12.8=2(-10462.8-(-10469.2)) with 8=56-48 degrees of freedom, corresponding to a p-value of 0.12. Hence there is little evidence that this restricted model is not acceptable, consistent with the true parameter values. The goodness-of-fit chi-square test-statistic has a value of 94.0=2(-10422.2-(-10469.2)) with 84=132-48 degrees of freedom, and a p-value of 0.21. There is no evidence that this restricted model does not provide an adequate fit to the data.

A model with homogeneous sighting rates among pre-strata and homogeneous relative harvest-derivation rates among post-strata, i.e., where $D_i^{st}=D_i^{s\cdot}$ and $p_i^{st}=p_i^{\cdot t}$, was fit to the data. The fitting procedure requires the use of the *ad hoc* procedure described in Appendix 3.F since the precision of the estimates of the pre-stratum population sizes and the post-stratum band-reporting rates will partly determine if this reduced model is acceptable. The iterative procedure converged in eight iterations, and the MLEs and estimated standard errors are shown in Figure 3.7.3d. Note that the *ad hoc* procedure has modified the external estimates when finding the new maximum of the total likelihood function. The log-likelihood under this new restricted model (up to constant terms) is -10471.8 and this model requires 45 parameters. (Note that restricting the relative derivation rates to be homogeneous among post-strata makes it difficult to write down an explicit set of parameters). When this new model is compared to the model where only the sighting rates are homogeneous among pre-strata,

Figure 3.7.3 d
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. HARV. DERIVATION AMONG POST-STRATA (MODEL 60)

ESTIMATES OF THE PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL	RHO
1	1		0.77330					0.41300
1	1	1		0.51472	0.04868	0.29254	0.54127	0.20444
1	1	2		0.48528	0.04430	0.31300	0.59544	0.20856
1	2		0.85003					0.42800
1	2	1		0.49166	0.04697	0.30874	0.43618	0.20372
1	2	2		0.50834	0.03852	0.29355	0.58239	0.22428
1	3		0.75923					0.36700
1	3	1		0.46382	0.05570	0.33613	0.72859	0.17081
1	3	2		0.53618	0.04436	0.30712	0.50249	0.19619
1	4							
1	4	1			0.05677	0.18519		
1	4	2			0.06813	0.37097		
2	1		0.67108					0.41200
2	1	1		0.57791	0.09434	0.29254	0.54214	0.21919
2	1	2		0.42209	0.14982	0.31300	0.64013	0.19281
2	2		0.61202					0.34600
2	2	1		0.56308	0.07968	0.30874	0.46720	0.18500
2	2	2		0.43692	0.13108	0.29355	0.53424	0.16100
2	3		0.64637					0.35700
2	3	1		0.54492	0.09475	0.33613	0.91048	0.18869
2	3	2		0.45508	0.12566	0.30712	0.58121	0.16831
2	4							
2	4	1			0.05025	0.18519		
2	4	2			0.11292	0.37097		

FINAL LOG-LIKELIHOOD= -10471.8 WITH 45 PARMS

Figure 3.7.3 d (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. HARV. DERIVATION AMONG POST-STRATA (MODEL 60)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.04973				
1	1	1		0.03683	0.01095	0.02748	0.07650
1	1	2		0.03683	0.01030	0.02752	0.07687
1	2		0.04978				
1	2	1		0.03263	0.00874	0.02480	0.05601
1	2	2		0.03263	0.00751	0.02263	0.06644
1	3		0.04690				
1	3	1		0.03208	0.00973	0.02620	0.21654
1	3	2		0.03208	0.00763	0.02298	0.09294
1	4						
1	4	1			0.01949	0.05286	
1	4	2			0.01700	0.06135	
2	1		0.04047				
2	1	1		0.03908	0.01632	0.02748	0.07133
2	1	2		0.03908	0.02346	0.02752	0.07687
2	2		0.03760				
2	2	1		0.03845	0.01257	0.02480	0.05668
2	2	2		0.03845	0.01813	0.02263	0.06174
2	3		0.03879				
2	3	1		0.03654	0.01336	0.02620	0.26744
2	3	2		0.03654	0.01657	0.02298	0.10483
2	4						
2	4	1			0.01703	0.05286	
2	4	2			0.02568	0.06135	

Figure 3.7.3 d (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. HARV. DERIVATION AMONG POST-STRATA (MODEL 60)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST	SE	BAND-REPORTING EST	SE	HARVEST DERIVATION	(SE)	RELATIVE DERIVATION	(SE)	IMMIGRATION	(SE)	RELATIVE IMMIGRATION	(SE)
1	1	1	100000	(20000)	0.447	(0.100)	4335	(1437)	0.205	(0.070)	39803	(8889)	0.339	(0.076)
1	1	2	200000	(50000)	0.435	(0.080)	16825	(5608)	0.795	(0.070)	77565	(20692)	0.661	(0.076)
1	2	1	100000	(20000)	0.272	(0.050)	6116	(1994)	0.205	(0.070)	37527	(8327)	0.398	(0.082)
1	2	2	200000	(50000)	0.358	(0.080)	23739	(8219)	0.795	(0.070)	56650	(15419)	0.602	(0.082)
2	1	1	150000	(30000)	0.462	(0.100)	6370	(1992)	0.248	(0.077)	62688	(13791)	0.377	(0.079)
2	1	2	300000	(75000)	0.426	(0.080)	19328	(6369)	0.752	(0.077)	103384	(27518)	0.623	(0.079)
2	2	1	150000	(30000)	0.266	(0.050)	9373	(2888)	0.248	(0.077)	64816	(14052)	0.447	(0.084)
2	2	2	300000	(75000)	0.370	(0.080)	28438	(9569)	0.752	(0.077)	80220	(21842)	0.553	(0.084)
3	1	1	75000	(15000)	0.430	(0.100)	3422	(1071)	0.233	(0.063)	26411	(5860)	0.333	(0.058)
3	1	2	150000	(20000)	0.443	(0.080)	11288	(2734)	0.767	(0.063)	52833	(8485)	0.667	(0.058)
3	2	1	75000	(15000)	0.277	(0.050)	4886	(1446)	0.233	(0.063)	30531	(6608)	0.409	(0.064)
3	2	2	150000	(20000)	0.344	(0.080)	16121	(4265)	0.767	(0.063)	44122	(7373)	0.591	(0.064)

the likelihood ratio chi-square test-statistic has the value of 5.2 = 2(-10469.2-(-10471.8)) with 3=48-45 degrees of freedom, and a p-value of 0.158. There is no evidence that the relative derivation rates are not homogeneous among post-strata. This is an incorrect decision since, in fact, the relative harvest-derivation rates are not homogeneous among the post-strata. However, the estimated standard errors are large enough that it is difficult to detect any heterogeneity in the rates.

One final model was fit to the data, where it was assumed that the relative immigration rates (as opposed to the harvest-derivation rates) are homogeneous among the post-strata along with the previous assumption about the sighting rates. The relative immigration rates may be homogeneous while the relative derivation rates are not since the harvest and reporting rates may not be homogeneous among post-strata. Note that requiring both the relative harvest-derivation and relative immigration rates to be homogeneous among post-strata is equivalent to requiring that the band-recovery rates be proportional among the pre-strata for every post-strata. For this reason, only the restriction on the relative immigration rates was examined. This does not require the *ad hoc* procedure used previously since computation of the relative immigration rates only requires the external estimates of the pre-stratum population sizes, and these are, by definition, the same for all post-strata in a given year. Hence, the precision of the estimate is not important in determining if the rates are homogeneous. Convergence occurred in ten iterations. The MLEs and their estimated standard errors, and the derived parameters and their standard errors are presented in Figure 3.7.3e. The log-likelihood (up to constant terms) for this new model has a value of -10475.6 and this model requires 45 parameters. When this model is compared to the model where only the sighting rates were homogeneous among pre-strata, the chi-square likelihood ratio test-statistic has the value of 12.8 = 2(-10469.2-(-10475.6)) with 3=48-45 degrees of freedom, and a p-value of 0.005. Hence there is good evidence that the relative immigration rates are not homogeneous among post-strata which is consistent with the true parameter values. The goodness-of-fit chi-square test-statistic has a value of 106.8 = 2(-10422.2-(-10475.6)) with 87=132-45 degrees of freedom, and a p-value of 0.074 which is further evidence against this restricted model.

As before, this procedure of fitting reduced models can be continued until a biologically reasonable model that provides an adequate fit to the data is determined. A summary of the models considered above is shown in Figure 3.7.3f. All but one of the tests indicated the correct decision to make with respect to the null and alternate hypotheses. A Type II error occurred when the hypothesis of homogeneous harvest-derivation rates was accepted.

Since the true values of the parameters are known in this situation, estimates of the power of the tests can be determined as before. The sequence of model tests described earlier was repeated using the expected values generated using the parameter values of Table 1.5a, and a summary is presented in Figure 3.7.3f.

Figure 3.7.3 e
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. IMMIGRATION AMONG POST-STRATA (MODEL 70)

ESTIMATES OF THE PARAMETERS

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL	RHO
1	1		0.77557					0.41302
1	1	1		0.54321	0.04130	0.29277	0.52902	0.21164
1	1	2		0.45679	0.05221	0.31387	0.60638	0.20138
1	2		0.85071					0.42800
1	2	1		0.51902	0.04318	0.30969	0.43224	0.21289
1	2	2		0.48098	0.04214	0.29284	0.58728	0.21511
1	3		0.75895					0.36700
1	3	1		0.49948	0.04953	0.33636	0.70886	0.18124
1	3	2		0.50052	0.04939	0.30708	0.51509	0.18576
1	4							
1	4	1			0.05677	0.18519		
1	4	2			0.06813	0.37097		
2	1		0.66641					0.41200
2	1	1		0.54322	0.10429	0.29277	0.55175	0.21005
2	1	2		0.45678	0.13678	0.31387	0.63450	0.20196
2	2		0.61045					0.34600
2	2	1		0.51900	0.08572	0.30969	0.47490	0.17351
2	2	2		0.48100	0.12240	0.29284	0.52621	0.17249
2	3		0.64646					0.35700
2	3	1		0.49943	0.10276	0.33636	0.93865	0.17610
2	3	2		0.50057	0.11579	0.30708	0.56076	0.18091
2	4							
2	4	1			0.05025	0.18519		
2	4	2			0.11292	0.37097		

FINAL LOG-LIKELIHOOD= -10475.6 WITH 45 PARMS

Figure 3.7.3 e (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. IMMIGRATION AMONG POST-STRATA (MODEL 70)

ESTIMATES OF S.E. OF PARAMETER ESTIMATES

PRE-STRATUM	YEAR	POST-STRATUM	TOTAL MIGRAT	RELATIVE MIGRATION	BAND RECOVERY	SIGHTING RATE	POST-STR SURVIVAL
1	1		0.04984				
1	1	1		0.03387	0.01059	0.02748	0.07464
1	1	2		0.03387	0.01227	0.02754	0.07634
1	2		0.04975				
1	2	1		0.03085	0.00873	0.02481	0.05566
1	2	2		0.03085	0.00842	0.02261	0.06606
1	3		0.04681				
1	3	1		0.03014	0.00945	0.02621	0.21074
1	3	2		0.03014	0.00850	0.02298	0.09487
1	4						
1	4	1			0.01949	0.05286	
1	4	2			0.01700	0.06135	
2	1		0.04013				
2	1	1		0.02732	0.01764	0.02748	0.06986
2	1	2		0.02732	0.02248	0.02754	0.07589
2	2		0.03744				
2	2	1		0.02490	0.01342	0.02481	0.05603
2	2	2		0.02490	0.01746	0.02261	0.06066
2	3		0.03875				
2	3	1		0.02507	0.01424	0.02621	0.27496
2	3	2		0.02507	0.01584	0.02298	0.10107
2	4						
2	4	1			0.01703	0.05286	
2	4	2			0.02568	0.06135	

Figure 3.7.3 e (continued)
COMPLETE-FIDELITY MODEL
SIMULATED DATA USING TABLE 1.5a PARAMETER VALUES
MODEL: EQUAL P AND REL. IMMIGRATION AMONG POST-STRATA (MODEL 70)

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	POST- & PRE- STRATUM		POPULATION EST (SE)	BAND-REPORTING EST (SE)	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	100000 (20000)	0.500 (0.100)	3480 (1296)	0.156 (0.068)	42129 (9297)	0.368 (0.076)
1	1	2	200000 (50000)	0.400 (0.080)	18877 (6712)	0.844 (0.068)	72402 (19041)	0.632 (0.076)
1	2	1	100000 (20000)	0.250 (0.050)	7399 (2679)	0.262 (0.098)	35427 (7828)	0.368 (0.076)
1	2	2	200000 (50000)	0.400 (0.080)	20818 (7407)	0.738 (0.098)	60881 (16003)	0.632 (0.076)
2	1	1	150000 (30000)	0.500 (0.100)	5720 (1953)	0.219 (0.084)	66230 (14419)	0.411 (0.079)
2	1	2	300000 (75000)	0.400 (0.080)	20368 (7184)	0.781 (0.084)	95047 (24937)	0.589 (0.079)
2	2	1	150000 (30000)	0.250 (0.050)	10346 (3540)	0.277 (0.097)	61376 (13314)	0.411 (0.079)
2	2	2	300000 (75000)	0.400 (0.080)	26954 (9367)	0.723 (0.097)	88089 (23080)	0.589 (0.079)
3	1	1	75000 (15000)	0.500 (0.100)	2816 (946)	0.185 (0.065)	28431 (6218)	0.370 (0.058)
3	1	2	150000 (20000)	0.400 (0.080)	12441 (3399)	0.815 (0.065)	48429 (7523)	0.630 (0.058)
3	2	1	75000 (15000)	0.250 (0.050)	5629 (1842)	0.286 (0.087)	28490 (6179)	0.370 (0.058)
3	2	2	150000 (20000)	0.400 (0.080)	14050 (3828)	0.714 (0.087)	48539 (7463)	0.630 (0.058)

Figure 3.7.3f

Summary of the log-likelihood values of fitted models using the simulated data and expected values generated using the parameter values in Table 1.6a in the Complete-Fidelity Model with sightings

<u>Simulated Data</u>

Model with no structure
-10422.2 with 132 parms

Full Model
-10462.8 with 56 parms

Homogeneous sighting rates
-10469.2 with 48 parms

Homogeneous sighting and relative derivation rates
-10471.8 with 45 parms

Homogeneous sighting and relative immigration rates
-10475.6 with 45 parms

<u>Expected Data</u>

Model with no structure
-10607.4 with 132 parms

Full Model
-10607.4 with 56 parms

Homogeneous sighting rates
-10607.4 with 56 parm

Homogeneous sighting and relative derivation rates
-10609.1 with 45 parms

Homogeneous sighting and relative immigration rates
-10612.4 with 45 parms

Since data were generated using the full Complete-Fidelity Model, it is not surprising that the non-centrality parameter of the goodness-of-fit test again has the value of 0.0=2(-10607.4-(-10607.4)). Similarly, the sighting rates are homogeneous among pre-strata, and so the non-centrality parameter for the test of homogeneous sighting rates is also zero.

When the model where the sighting rates are homogeneous among pre-strata and the relative harvest-derivation is homogeneous among post-strata is compared to the model where only the sighting rates are homogeneous, the non-centrality parameter is found to be 3.4 = 2(-10607.4-(-10609.1)) with 3=48-45 degrees of freedom. The power of the likelihood ratio test to detect the degree of heterogeneity among the relative harvest-derivation rates using the parameters of Table 1.5a is estimated to be only 31% when testing at the 5% level, and 39% when testing at the 10% level.

Similarly, when testing if the relative immigration rates are homogeneous among post-strata (assuming that the sighting rates are homogeneous among pre-strata), the estimated non-centrality parameter is found to be 10.0=2(-10607.4-(-10612.4)) with 3=48-45 degrees of freedom. The power of the likelihood ratio test to detect the degree of heterogeneity in the relative immigration rates using the parameters of Table 1.5a is estimated to be 76% when testing at the 5% level, and 85% when testing at the 10% level.

3.8 SUMMARY

In both models of this Chapter, ordinary band-recovery data were shown to be inadequate for estimating the fundamental parameters unless further assumptions are made. These assumptions cannot be tested using the data from the experiment and must be assessed on biological grounds. An understanding of exactly what assumptions must be made in order to obtain migration estimates from ordinary band-recovery data is an important exercise since past ordinary banding experiments can be assessed to determine if they will be of value in studying migration. A simple modification to the experimental design using live resightings in the post-strata allows the fundamental parameters to be estimated and the migration and derivation rates to be determined.

The Partial- and Complete-Fidelity Models of this Chapter, and the Non-Fidelity Model of the next Chapter represent three models of seasonal migration that are biologically plausible for many species of animals. The choice among these models must be made on biological grounds since an objective test to distinguish among the models has not been constructed. As well, no real population of animals is completely faithful to a breeding or a wintering site, and the presence of a single animal not showing fidelity is technically sufficient to reject a model that assumes fidelity. Even though the fidelity assumption may not be completely true, the bias in the estimates will likely be small in magnitude and small relative to standard errors of the estimates if the degree of non-fidelity is small. In any case, the effect of any assumed model on the procedures of this chapter can be easily investigated using the computer programs illustrated in Section 3.7.

A logical extension to these models is a 'super' model where the degree of fidelity could be estimated. However, as will be seen in the next Chapter, this model will be extremely complex and will require data normally unavailable. Indeed, it would require resightings in **both** the pre- and post-strata, and the resighting rate will have to be high to obtain estimates with good precision. It will likely be more advantageous to employ radio-telemetry devices on fewer animals and expend more effort in ensuring that the animals are monitored for extended periods of time.

Appendix 3.A

Full-data representation for the Partial-Fidelity Model with sightings in the post-strata

The complete sighting and recovery history of an animal may be written as a $2x(l+1)$ matrix as follows:

- the last column $(l+1)$ indicates the pre-stratum and year of release in rows 1 and 2 respectively;
- columns $1 \ldots l$ indicate the post-stratum and type of sighting or recovery of the band (either: not seen; recovered **AND** sighted; recovered **BUT** not sighted; or sighted **WITHOUT** being recovered), in rows 1 and 2 respectively.

An example of a four year history matrix is:

$$\begin{bmatrix} 0 & t & 0 & u & s \\ 0 & \begin{array}{c}\text{sighted} \\ \textbf{WITHOUT}\text{ being} \\ \text{recovered}\end{array} & 0 & \begin{array}{c}\text{recovered} \\ \textbf{BUT}\text{ not} \\ \text{sighted}\end{array} & 1 \end{bmatrix} \tag{A.1}$$

It indicates that the animal was released in pre-stratum s in year 1, was neither sighted nor recovered in year 1, was sighted **WITHOUT** being recovered in post-stratum t in year 2, was neither sighted nor recovered in year 3, and was recovered **BUT** not sighted in post-stratum u in year 4. Clearly all columns corresponding to years after a band-recovery until the end of the experiment will be zero, as will all columns corresponding to years before the year of release.

The total number of distinct histories for animals released from pre-stratum s in year i can be computed as follows:

- there is one history for animals never seen or recovered after being released

· if an animal is last seen or recovered in year j ($i \le j \le l$), then the animal can either be: not seen; or sighted WITHOUT being recovered in one of the b post-strata in years $i \ldots j-1$. This is followed by one of: recovered AND sighted; recovered BUT not sighted; or sighted WITHOUT being recovered in one of the b post-strata, for a total of $(b+1)^{j-i}3b$ possible histories for $j=i \ldots l$.

Hence there are a total of

$$1 + \sum_{j=i}^{l} 3b(b+1)^{j-i} = 3(b+1)^{l-i+1}-2$$

possible histories for animals released from pre-stratum s in year i.

As can be appreciated, the number of possible histories can be large in small experiments, the data representation is complex, and the actual set of observed histories may be small in comparison. This is the reason for introducing the reduced-data array of Section 3.4.

Since animals are assumed to act independently, and the histories are exclusive and exhaustive, the numbers of animals in each history follow a multinomial distribution under the assumptions of the partial-fidelity model. Each pre-stratum and each year's releases are independent, and so the likelihood of the data from the complete experiment can be written as:

$$L = \prod_{s=1}^{a} \prod_{i=1}^{k} \frac{N_i^s!}{\prod_{\omega \in \Omega_i^s} n_{i(\omega)}^s!} \prod_{\omega \in \Omega_i^s} (\pi_\omega)^{n_{i(\omega)}^s}$$

where

ω is a history

Ω_i^s is the complete set of all possible histories for animals released from pre-stratum s in year i

$n_{i(\omega)}^s$ is the number of animals released from pre-stratum s in year i with history ω.

π_ω is the probability of the history ω.

The probability of a history is easily computed in a similar manner to that of the reduced-data array in Section 3.4. For example, the probability of the history specified by the history matrix (A.1) is computed as the product of:

- $(S_1^{s\cdot} - \sum_{v=1}^{b} M_1^{s\cdot} m_1^{sv} p_1^{sv} S_1^{sv})$ since the animal is known to have survived year 1 without being sighted in any post-stratum in year 1;

- $M_2^{s\cdot} m_2^{st} p_2^{st} (1-f_2^{st})$ since the animal is known to have migrated from pre-stratum s to post-stratum t in year 2, was sighted without being recovered;

- $S_2^{st}/(1-f_2^{st})$ since the animal is known to have survived post-stratum t in year 2 conditional upon not being recovered;

- $(S_3^{s\cdot} - \sum_{v=1}^{b} M_3^{s\cdot} m_3^{sv} p_3^{sv} S_3^{sv})$ since the animal is known to have survived year 3 without being sighted in any post-strata;

- $M_4^{s\cdot} m_4^{su} (1-p_4^{su}) f_4^{su}$ since the animal is known to have migrated from pre-stratum s to post-stratum u in year 4, and was recovered but not sighted.

Or:

$$\pi_\omega = (S_1^{s\cdot} - \sum_{v=1}^{b} M_1^{s\cdot} m_1^{sv} p_1^{sv} S_1^{sv})\ M_2^{s\cdot} m_2^{st} p_2^{st} S_2^{st} (S_3^{s\cdot} - \sum_{v=1}^{b} M_3^{s\cdot} m_3^{sv} p_3^{sv} S_3^{sv}) \times$$
$$M_4^{s\cdot} m_4^{su} (1-p_4^{su}) f_4^{s}$$

The probability of the history corresponding to animals never seen or recovered after being released or being sighted is obtained by subtraction.

After simplification, the likelihood reduces to:

$$L = \prod_{s=1}^{a} \prod_{j=1}^{k} \frac{N_{j}^{s}!}{\prod_{\omega\in\Omega_{j}^{s}} n_{j(\omega)}^{s}!}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \left(M_{j}^{s\cdot}\right)^{A_{\cdot j}^{s\cdot} + B_{\cdot j}^{s\cdot} + W_{\cdot j}^{s\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(m_{j}^{st}\right)^{A_{\cdot j}^{st} + B_{\cdot j}^{st} + W_{\cdot j}^{st}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(p_{j}^{st}\right)^{A_{\cdot j}^{st} + W_{\cdot j}^{st}} \left(1-p_{j}^{st}\right)^{B_{\cdot j}^{st}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(f_{j}^{st}\right)^{A_{\cdot j}^{st} + B_{\cdot j}^{st}} \left(1-f_{j}^{st}\right)^{W_{\cdot j}^{st} - W_{\cdot j\cdot}^{st\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l-1} \prod_{t=1}^{b} \left(S_{j}^{st}\right)^{W_{\cdot j\cdot}^{st\cdot}} \prod_{s=1}^{a} \prod_{j=1}^{l-1} \prod_{t=1}^{b} \left(1-S_{j}^{st}\rho_{j+1}^{s\cdot}(1-f_{j}^{st}\ )^{-1}\right)^{W_{\cdot j}^{st}-W_{\cdot j\cdot}^{st\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k} \left(1-\rho_{j}^{s\cdot}\right)^{N_{j}^{s} - A_{j\cdot}^{s\cdot} - B_{j\cdot}^{s\cdot} - W_{j\cdot}^{s\cdot} + W_{j\cdot\cdot}^{s\cdot\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l-1} \left(S_{j}^{s\cdot} - \sum_{v=1}^{b} M_{j}^{s\cdot} m_{j}^{sv} p_{j}^{sv} S_{j}^{sv}\ \right)^{Z_{j}^{s\cdot} - W_{\cdot j\cdot}^{s\cdot\cdot}} \quad .$$

where $\rho_{j}^{s\cdot}$ is the probability that an animal will be sighted or recovered after being released in pre-stratum *s* in year *j* and is computed as:

$$\rho_{l}^{s\cdot} = \sum_{t=1}^{b} M_{l}^{s\cdot} m_{l}^{st} (f_{l}^{st} + p_{l}^{st} - f_{l}^{st} p_{l}^{st}) \tag{A.2}$$

$$\rho_{j}^{s\cdot} = \sum_{t=1}^{b} M_{j}^{s\cdot} m_{j}^{st} (f_{j}^{st} + p_{j}^{st} - f_{j}^{st} p_{j}^{st}) + (S_{j}^{s\cdot} - \sum_{t=1}^{b} M_{j}^{s\cdot} m_{j}^{st} p_{j}^{st} S_{j}^{st})\rho_{j+1}^{st} \quad j=1...l-1$$

The MSS are easily derived and are presented in Section 3.4.3. Not all parameters are identifiable; the likelihood can be rewritten in terms of the identifiable parameters of Table 3.4.3 as:

$$L = \prod_{s=1}^{a} \prod_{j=1}^{k} \frac{N_j^s!}{\prod_{\omega\in\Omega_j^s} n_{j(\omega)}^s!}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k} \left(M_j^{s\cdot}\right)^{A^{s\cdot}_{\cdot j}+B^{s\cdot}_{\cdot j}+W^{s\cdot}_{\cdot j}} \quad \prod_{s=1}^{a} \prod_{j=k+1}^{l} \left(S_k^{s\cdot}\cdots S_{j-1}^{s\cdot}M_j^{s\cdot}\right)^{A^{s\cdot}_{\cdot j}+B^{s\cdot}_{\cdot j}+W^{s\cdot}_{\cdot j}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(m_j^{st}\right)^{A^{st}_{\cdot j}+B^{st}_{\cdot j}+W^{st}_{\cdot j}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(p_j^{st}\right)^{A^{st}_{\cdot j}+W^{st}_{\cdot j}} \left(1-p_j^{st}\right)^{B^{st}_{\cdot j}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(f_j^{st}\right)^{A^{st}_{\cdot j}+B^{st}_{\cdot j}} \left(1-f_j^{st}\right)^{W^{st}_{\cdot j}-W^{st\cdot}_{\cdot j\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k-1} \prod_{t=1}^{b} \left(S_j^{st}\right)^{W^{st\cdot}_{\cdot j\cdot}} \quad \prod_{s=1}^{a} \prod_{j=k}^{l-1} \prod_{t=1}^{b} \left(S_j^{st}\rho_{j+1}^{s\cdot}\right)^{W^{st\cdot}_{\cdot j\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l-1} \prod_{t=1}^{b} \left(1-S_j^{st}\rho_{j+1}^{s\cdot}(1-f_j^{st})^{-1}\right)^{W^{st}_{\cdot j}-W^{st\cdot}_{\cdot j\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k} \left(1-\rho_j^{s\cdot}\right)^{N_j^s-A^{s\cdot}_{j\cdot}-B^{s\cdot}_{j\cdot}-W^{s\cdot}_{j\cdot}+W^{s\cdot\cdot}_{j\cdot\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k-1} \left(S_j^{s\cdot}-\sum_{v=1}^{b} M_j^{s\cdot} m_j^{sv} p_j^{sv} S_j^{sv}\right)^{Z_j^{s\cdot}-W^{s\cdot\cdot}_{\cdot j\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=k}^{l-1} \left(S_k^{s\cdot}\cdots S_j^{s\cdot}\rho_{j+1}^{s\cdot} - \sum_{v=1}^{b} S_k^{s\cdot}\cdots S_{j-1}^{s\cdot}M_j^{s\cdot} m_j^{sv} p_j^{sv} S_j^{sv}\rho_{j+1}^{s\cdot}\right)^{Z_j^{s\cdot}-W^{s\cdot\cdot}_{\cdot j\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=k}^{l-1} \left(S_k^{s\cdot}\cdots S_j^{s\cdot}\rho_{j+1}^{s\cdot}\right)^{-Z_j^{s\cdot}}.$$

Using techniques similar to those presented in Chapter 2, the distribution of the MSS is found to be a product of the following conditionally independent multinomial or binomial distributions:

- the distribution of the number of animals released from pre-stratum *s* and sighted or recovered in year *j* conditional upon the number of animals from pre-stratum *s* sighted or recovered in year *j* or later which is a:

Multinomial($T_l^{s\cdot}$ animals sighted or recovered in year *l*;

$A_{\cdot l}^{st}$ with probability $S_k^{s\cdot}\ldots S_{l-1}^{s\cdot} M_l^{s\cdot} m_l^{st} p_l^{st} f_l^{st} / (S_k^{s\cdot}\ldots S_{l-1}^{s\cdot}\rho_l^{s\cdot})$ t=1...b;

$B_{\cdot l}^{st}$ with probability $S_k^{s\cdot}\ldots S_{l-1}^{s\cdot} M_l^{s\cdot} m_l^{st} (1-p_l^{st}) f_l^{st} / (S_k^{s\cdot}\ldots S_{l-1}^{s\cdot}\rho_l^{s\cdot})$ t=1...b;

$W_{\cdot l}^{st}$ with probability $S_k^{s\cdot}\ldots S_{l-1}^{s\cdot} M_l^{s\cdot} m_l^{st} p_l^{st} (1-f_l^{st}) / (S_k^{s\cdot}\ldots S_{l-1}^{s\cdot}\rho_l^{s\cdot})$ t=1...b)

for s=1...a.

Multinomial($T_j^{s\cdot}$ animals sighted or recovered in year j or later;

$A_{\cdot j}^{st}$ with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot} M_j^{s\cdot} m_j^{st} p_j^{st} f_j^{st} / (S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

$B_{\cdot j}^{st}$ with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot} M_j^{s\cdot} m_j^{st} (1-p_j^{st}) f_j^{st} / (S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

$W_{\cdot j}^{st}$ with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot} M_j^{s\cdot} m_j^{st} p_j^{st} (1-f_j^{st}) / (S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

$Z_j^{s\cdot} - W_{\cdot j\cdot}^{s\cdot\cdot}$ with probability $(S_k^{s\cdot}\ldots S_j^{s\cdot}\rho_{j+1}^{s\cdot} - \sum_{v=1}^{b} S_k^{s\cdot}\ldots S_{j-1}^{s\cdot} M_j^{s\cdot} m_j^{sv} p_j^{sv} S_j^{sv} \rho_{j+1}^{s\cdot})/(S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot}))$

for s=1...a, j=k...l-1.

Multinomial($T_j^{s\cdot}$ animals sighted or recovered in year j or later;

$A_{\cdot j}^{st}$ with probability $M_j^{s\cdot} m_j^{st} p_j^{st} f_j^{st} / \rho_j^{s\cdot}$ t=1...b;

$B_{\cdot j}^{st}$ with probability $M_j^{s\cdot} m_j^{st} (1-p_j^{st}) f_j^{st} / \rho_j^{s\cdot}$ t=1...b;

$W_{\cdot j}^{st}$ with probability $M_j^{s\cdot} m_j^{st} p_j^{st} (1-f_j^{st}) / \rho_j^{s\cdot}$ t=1...b;

$Z_j^{s\cdot} - W_{\cdot j\cdot}^{s\cdot\cdot}$ with probability $(S_j^{s\cdot} - \sum_{v=1}^{b} M_j^{s\cdot} m_j^{sv} p_j^{sv} S_j^{sv})\rho_{j+1}^{s\cdot}/\rho_j^{s\cdot})$.

for s=1...a, j=1...k-1.

· the distribution of the total unique animals released from pre-stratum s in year i and sighted or recovered during the rest of the experiment

Binomial(N_i^s total animals released ;

$A_{i\cdot}^{s\cdot} + B_{i\cdot}^{s\cdot} + W_{i\cdot}^{s\cdot} - W_{i\cdot\cdot}^{s\cdot\cdot}$ with probability $\rho_i^{s\cdot}$;

$N_i^s - A_{i\cdot}^{s\cdot} + B_{i\cdot}^{s\cdot} + W_{i\cdot}^{s\cdot} - W_{i\cdot\cdot}^{s\cdot\cdot}$ with probability $1-\rho_i^{s\cdot}$).

for s=1...a, i=1...k.

· the distribution of animals released from pre-stratum s and sighted without being recovered in post-stratum t in year j and subsequently sighted or recovered during the rest of the experiment:

Binomial($W_{\cdot j}^{st}$ animals sighted without being recovered;

$W_{\cdot j\cdot}^{st\cdot}$ with probability $S_j^{st}\rho_{j+1}^{s\cdot}/(1-f_j^{st})$;

$W_{\cdot j}^{st} - W_{\cdot j\cdot}^{st\cdot}$ with probability $1-S_j^{st}\rho_{j+1}^{s\cdot}/(1-f_j^{st})$).

for s=1...a, j=1...l-1, and t=1...b.

The MLEs can be derived from the distribution of the MSS, or using the method of moments as outlined in Chapter 1, and were presented in Table 3.4.3; variances and covariances are shown in Appendix 3.B.

The distribution of the data conditional upon the MSS can be used as a general non-specific goodness-of-fit test in a similar fashion as in Pollock, Hines and Nichols (1985). Unfortunately, as in Pollock *et al.* (1985), the large number of capture histories implies that most of the components of the test will involve small counts, require extensive pooling in the large sample contingency table approximations, and will likely have poor power. They could, in theory, be used to test if the previous sighting history has an effect on subsequent recovery or sightings.

More useful, is a goodness-of-fit test based upon the reduced-data array elements which are sufficient (but not minimal) statistics for the full likelihood. The distribution of the reduced-data array elements is required, and it too can be found using techniques presented in Chapter 2. It is found to be the product of the following conditionally independent binomial or multinomial distributions:

- the distribution of the total unique animals released from pre-stratum s in year i and sighted or recovered during the rest of the experiment:

Binomial(N_i^s total animals released;

$A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}$ with probability $\rho_i^{s\cdot}$;

$N_i^s-A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}$ with probability $1-\rho_i^{s\cdot}$)

for s=1...a, and i=1...k.

- the distribution of the animals released from pre-stratum s in year i and sighted or recovered in year j conditional upon the animal being sighted or recovered in year j or later:

Multinomial($\sum_{m=j}^{l} A_{im}^{s\cdot}+B_{im}^{s\cdot}+W_{im}^{s\cdot}-W_{im\cdot}^{s\cdot\cdot}$ animals sighted or recovered in year j or later

A_{ij}^{st} with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}M_j^{s\cdot}m_j^{st}p_j^{st}f_j^{st}/(S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

B_{ij}^{st} with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}M_j^{s\cdot}m_j^{st}(1-p_j^{st})f_j^{st}/(S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

W_{ij}^{st} with probability $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}M_j^{s\cdot}m_j^{st}p_j^{st}(1-f_j^{st})/(S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}\rho_j^{s\cdot})$ t=1...b;

$\sum_{m=j+1}^{l}(A_{im}^{s\cdot}+B_{im}^{s\cdot}+W_{im}^{s\cdot}-W_{im\cdot}^{s\cdot\cdot})-W_{ij\cdot}^{s\cdot\cdot}$ with probability

$$(S_k^{s\cdot}\ldots S_j^{s\cdot}\rho_{j+1}^{s\cdot}-\sum_{v=1}^{b}S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}M_j^{s\cdot}m_j^{sv}p_j^{sv}S_j^{sv}\rho_{j+1}^{s\cdot})/\rho_j^{s\cdot}).$$

for s=1...a, i=1...k, j=k...l.

$$\text{Multinomial}\Big(\sum_{m=j}^{l} A_{im}^{s\cdot} + B_{im}^{s\cdot} + W_{im}^{s\cdot} - W_{im\cdot}^{s\cdot\cdot} \text{ animals sighted or recovered in year } j \text{ or later}$$

$$A_{\cdot j}^{st} \quad \text{with probability} \quad M_j^{s\cdot} m_j^{st} p_j^{st} f_j^{st} / \rho_j^{s\cdot} \qquad t=1\ldots b;$$

$$B_{\cdot j}^{st} \quad \text{with probability} \quad M_j^{s\cdot} m_j^{st} (1-p_j^{st}) f_j^{st} / \rho_j^{s\cdot} \qquad t=1\ldots b;$$

$$W_{\cdot j}^{st} \quad \text{with probability} \quad M_j^{s\cdot} m_j^{st} p_j^{st} (1-f_j^{st}) / \rho_j^{s\cdot} \qquad t=1\ldots b;$$

$$\sum_{m=j+1}^{l} (A_{im}^{s\cdot} + B_{im}^{s\cdot} + W_{im}^{s\cdot} - W_{im\cdot}^{s\cdot\cdot}) - W_{ij\cdot}^{s\cdot\cdot} \quad \text{with probability}$$

$$(S_j^{s\cdot} \rho_{j+1}^{s\cdot} - \sum_{v=1}^{b} M_j^{s\cdot} m_j^{sv} p_j^{sv} S_j^{sv} \rho_{j+1}^{s\cdot}) / \rho_j^{s\cdot}).$$

for s=1...a, i=1...k, j=i...k-1.

· the distribution of animals released from pre-stratum s in year i, that were sighted without being recovered in post-stratum t in year j, and are subsequently sighted or recovered during the remainder of the experiment:

$$\text{Binomial}\Big(W_{ij}^{st} \quad \begin{array}{l}\text{animals released in year } i \text{ and sighted without being recovered} \\ \text{in year } j \text{ in post-stratum } t;\end{array}$$

$$W_{ij\cdot}^{st\cdot} \qquad \text{with probability } S_j^{st} \rho_{j+1}^{s\cdot} / (1-f_j^{st}) \quad ;$$

$$W_{ij}^{st} - W_{ij\cdot}^{st\cdot} \quad \text{with probability } 1- S_j^{st} \rho_{j+1}^{s\cdot} / (1-f_j^{st})).$$

for s=1...a, i=1...k, t=1...b, j=i...l-1.

The goodness-of-fit test based upon the reduced array is constructed as outlined in Chapter 1 and, after simplification, is based upon the conditional distribution:

$$\prod_{s=1}^{a} \frac{\displaystyle\prod_{i=1}^{k} \prod_{j=i}^{l} \left(\begin{array}{c} \displaystyle\sum_{m=j}^{l} (A_{im}^{s\cdot} + B_{im}^{s\cdot} + W_{im}^{s\cdot} - W_{im\cdot}^{s\cdot\cdot}) \\ \{A_{ij}^{st},\ B_{ij}^{st},\ W_{ij}^{st} - W_{ij\cdot}^{st\cdot},\ W_{ij\cdot}^{st\cdot}\ t=1\ldots b\},\ \displaystyle\sum_{m=j+1}^{l} (A_{im}^{s\cdot} + B_{im}^{s\cdot} + W_{im}^{s\cdot} - W_{im\cdot}^{s\cdot\cdot}) - W_{ij\cdot}^{s\cdot\cdot} \end{array} \right)}{\displaystyle\prod_{j=1}^{l} \left(\begin{array}{c} T_j^{s\cdot} \\ \{A_{\cdot j}^{st},\ B_{\cdot j}^{st},\ W_{\cdot j}^{st} - W_{\cdot j\cdot}^{st\cdot},\ W_{\cdot j\cdot}^{st\cdot}\ t=1\ldots b\},\ Z_j^{s\cdot} - W_{\cdot j\cdot}^{s\cdot\cdot} \end{array} \right)}$$

which is equivalent to:

$$\prod_{s=1}^{a} \frac{\displaystyle\prod_{i=1}^{k}\prod_{j=i}^{l} \left\{ \begin{array}{c} \text{Total animals released from pre-stratum } s \\ \textbf{in year i} \text{ and sighted or recovered at or after year } j \\ \begin{array}{lllll} \begin{array}{l} \text{Recovered} \\ \textbf{AND} \text{ sighted} \\ \text{in year } j \\ \text{in post-} \\ \text{stratum } t \\ \\ \\ t=1...b \end{array}, & \begin{array}{l} \text{Recovered} \\ \textbf{BUT} \text{ not} \\ \text{sighted} \\ \text{in year } j \\ \text{in post-} \\ \text{stratum } t \\ \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted } \textbf{WITHOUT} \\ \text{being recovered} \\ \text{in year } j \text{ in} \\ \text{post-stratum } t \\ \text{and not sighted} \\ \text{or recovered} \\ \text{after year } j \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted } \textbf{WITHOUT} \\ \text{being recovered} \\ \text{in year } j \text{ in} \\ \text{post-stratum } t \\ \text{and sighted or} \\ \text{recovered after} \\ \text{year } j \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted or} \\ \text{recovered} \\ \text{in any post-} \\ \text{strata } \textbf{only} \\ \text{after year } j \\ \\ \\ \\ \end{array} \end{array} \end{array} \right\}}{\displaystyle\prod_{j=1}^{l} \left\{ \begin{array}{c} \text{Total animals released from pre-stratum } s \\ \textbf{in all years} \text{ and sighted or recovered at or after year } j \\ \begin{array}{lllll} \begin{array}{l} \text{Recovered} \\ \textbf{AND} \text{ sighted} \\ \text{in year } j \\ \text{in post-} \\ \text{stratum } t \\ \\ \\ t=1...b \end{array}, & \begin{array}{l} \text{Recovered} \\ \textbf{BUT} \text{ not} \\ \text{sighted} \\ \text{in year } j \\ \text{in post-} \\ \text{stratum } t \\ \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted } \textbf{WITHOUT} \\ \text{being recovered} \\ \text{in year } j \text{ in} \\ \text{post-stratum } t \\ \text{and not sighted} \\ \text{or recovered} \\ \text{after year } j \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted } \textbf{WITHOUT} \\ \text{being recovered} \\ \text{in year } j \text{ in} \\ \text{post-stratum } t \\ \text{and sighted or} \\ \text{recovered after} \\ \text{year } j \\ t=1...b \end{array}, & \begin{array}{l} \text{Sighted or} \\ \text{recovered} \\ \text{in any post-} \\ \text{strata } \textbf{only} \\ \text{after year } j \\ \\ \\ \\ \end{array} \end{array} \end{array} \right\}}$$

This distribution is similar to the distribution used in the goodness-of-fit test for Model 3 of Chapter 2; a large sample contingency table for the test is presented in Table 3.4.4.1. This contingency table is used to examine if the reduced-data array may be combined over releases to obtain the MSS. The overall goodness-of-fit test is broken into a series of tables, one for each year of recovery (unlike the case in Chapter 2 where there was one table covering all years of recoveries) since animals may be seen more than once. Other than this difference, the two goodness-of-fit tests are completely analogous.

Appendix 3.B
Estimators of selected non-zero covariances in the Partial-Fidelity Model with sightings in the post-strata

The non-zero covariances involving confounded parameters (i.e. involving $S_i^{s\cdot}\rho_i^{s\cdot}$ or $S_k^{s\cdot}\ldots S_{j-1}^{s\cdot}M_j^{s\cdot}$) are not shown since they are not of biological interest. The variance-covariance matrix involving all identifiable parameters is available from the computer program described in Appendix 3.F. The estimators of the parameters are presented in Table 3.4.3.

$$\widehat{\text{cov}}(\hat S_i^{s\cdot}, \hat S_j^{u\cdot}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = \hat S_i^{s\cdot}\hat S_i^{s\cdot}\left[\frac{1}{A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_i^s} + \frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^s} + \frac{1}{Z_i^{s\cdot}} - \frac{1}{T_i^{s\cdot}}\right]$$

$$\text{when } \begin{matrix} u=s \\ j=i+1 \end{matrix} = -\hat S_i^{s\cdot}\hat S_{i+1}^{s\cdot}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^s}\right]$$

$$\widehat{\text{cov}}(\hat S_i^{s\cdot}, \hat S_j^{uv}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = \hat S_i^{s\cdot}\hat S_i^{sv}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^s} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{st}-W_{\cdot i\cdot}^{st\cdot}}{Z_i^{s\cdot}(A_{\cdot i}^{st}+W_{\cdot i}^{st})}\right]$$

$$\text{when } \begin{matrix} u=s \\ j=i-1 \end{matrix} = -\hat S_i^{s\cdot}\hat S_{i-1}^{sv}\left[\frac{1}{A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_i^s}\right]$$

$$\widehat{\text{cov}}(\hat S_i^{s\cdot}, \hat M_j^{u\cdot}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = \sum_{v=1}^{b}\hat S_i^{s\cdot}\hat M_i^{s\cdot}\hat m_i^{sv}\left[\frac{1}{A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_i^s} + \frac{W_{\cdot i\cdot}^{sv\cdot}}{Z_i^{s\cdot}(A_{\cdot i}^{sv}+W_{\cdot i}^{sv})} - \frac{1}{T_i^{s\cdot}}\right]$$

$$\text{when } \begin{matrix} u=s \\ j=i+1 \end{matrix} = -\hat S_i^{s\cdot}\hat M_{i+1}^{s\cdot}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^s}\right]$$

$$\hat{\text{cov}}(\hat{S}_i^{s\cdot}, \hat{m}_j^{uv}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = \hat{S}_i^{s\cdot}\hat{m}_i^{sv}\left[\frac{W_{\cdot i\cdot}^{sv\cdot}}{Z_i^{s\cdot}(A_{\cdot i}^{sv}+W_{\cdot i}^{sv})} - \sum_{w=1}^{b}\hat{m}_i^{sw}\frac{W_{\cdot i\cdot}^{sw\cdot}}{Z_i^{s\cdot}(A_{\cdot i}^{sw}+W_{\cdot i}^{sw})}\right]$$

$$\hat{\text{cov}}(\hat{S}_i^{s\cdot}, \hat{f}_j^{uv}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = -\hat{S}_i^{s\cdot}\hat{f}_i^{sv}\left[\frac{W_{\cdot i\cdot}^{sv\cdot}}{Z_i^{s\cdot}(A_{\cdot i}^{sv}+W_{\cdot i}^{sv})}\right]$$

$$\hat{\text{cov}}(\hat{S}_i^{st}, \hat{S}_j^{uv}) \text{ when } \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} = \hat{S}_i^{st}\hat{S}_i^{st}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^{s}} + \frac{1}{W_{\cdot i\cdot}^{st\cdot}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}}\right]$$

$$\text{when } \begin{matrix} u=s \\ v\neq t \\ j=i \end{matrix} = \hat{S}_i^{st}\hat{S}_i^{sv}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^{s}}\right]$$

$$\hat{\text{cov}}(\hat{S}_i^{st}, \hat{M}_j^{u\cdot}) \text{ when } \begin{matrix} u=s \\ j=i \end{matrix} = \hat{S}_i^{st}\hat{M}_i^{s\cdot}\hat{m}_i^{st}\left[\frac{B_{\cdot i}^{st}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st})}\right]$$

$$\text{when } \begin{matrix} u=s \\ j=i+1 \end{matrix} = -\hat{S}_i^{st}\hat{M}_{i+1}^{s\cdot}\left[\frac{1}{A_{i+1,\cdot}^{s\cdot}+B_{i+1,\cdot}^{s\cdot}+W_{i+1,\cdot}^{s\cdot}-W_{i+1,\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_{i+1}^{s}}\right]$$

Appendix 3.B (continued)

$$\widehat{\text{cov}}(\hat{S}_i^{st}, \hat{m}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \\ v=t \end{matrix} \quad = \hat{S}_i^{st}\hat{m}_i^{st}(1-\hat{m}_i^{st}) \left[\frac{B_{\cdot i}^{st}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\text{when} \quad \begin{matrix} u=s \\ j=i \\ v\neq t \end{matrix} \quad = -\hat{S}_i^{st}\hat{m}_i^{st}\hat{m}_i^{sv} \left[\frac{B_{\cdot i}^{st}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\widehat{\text{cov}}(\hat{S}_i^{st}, \hat{f}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \\ v=t \end{matrix} \quad = -\hat{S}_i^{st}\hat{f}_i^{st} \left[\frac{1}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})} \right]$$

$$\widehat{\text{cov}}(\hat{S}_i^{st}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \\ v=t \end{matrix} \quad = -\hat{S}_i^{st}\hat{p}_i^{st} \left[\frac{B_{\cdot i}^{st}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\widehat{\text{cov}}(\hat{M}_i^{s\cdot}, \hat{M}_j^{u\cdot}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = \sum_{w=1}^{b} (\hat{M}_i^{s\cdot}\hat{m}_i^{sw})^2 \left[\frac{(A_{\cdot i}^{sw})^2 + B_{\cdot i}^{sw}W_{\cdot i}^{sw}}{A_{\cdot i}^{sw}\,(A_{\cdot i}^{sw}+W_{\cdot i}^{sw})(A_{\cdot i}^{sw}+B_{\cdot i}^{sw})} \right] +$$

$$\hat{M}_i^{s\cdot}\hat{M}_i^{s\cdot} \left[\frac{1}{A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot}} - \frac{1}{N_i^{s}} - \frac{1}{T_i^{s\cdot}} \right]$$

Appendix 3.B (continued)

$$\widehat{\text{cov}}(\hat{M}_i^{s\cdot}, \hat{m}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = \hat{M}_i^{s\cdot}\hat{m}_i^{sv}\left[m_i^{sv}\frac{(A^{sv}_{\cdot i})^2 + B^{sv}_{\cdot i}W^{sv}_{\cdot i}}{A^{sv}_{\cdot i}\,(A^{sv}_{\cdot i}+W^{sv}_{\cdot i})\,(A^{sv}_{\cdot i}+B^{sv}_{\cdot i})} - \sum_{w=1}^{b}(m_i^{sw})^2\frac{(A^{sw}_{\cdot i})^2 + B^{sw}_{\cdot i}W^{sw}_{\cdot i}}{A^{sw}_{\cdot i}\,(A^{sw}_{\cdot i}+W^{sw}_{\cdot i})\,(A^{sw}_{\cdot i}+B^{sw}_{\cdot i})}\right]$$

$$\widehat{\text{cov}}(\hat{M}_i^{s\cdot}, \hat{f}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = -\hat{M}_i^{s\cdot}\hat{m}_i^{sv}\hat{f}_i^{sv}\left[\frac{B^{sv}_{\cdot i}W^{sv}_{\cdot i}}{A^{sv}_{\cdot i}\,(A^{sv}_{\cdot i}+W^{sv}_{\cdot i})\,(A^{sv}_{\cdot i}+B^{sv}_{\cdot i})}\right]$$

$$\widehat{\text{cov}}(\hat{M}_i^{s\cdot}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = -\hat{M}_i^{s\cdot}\hat{m}_i^{sv}\hat{p}_i^{sv}\left[\frac{B^{sv}_{\cdot i}W^{sv}_{\cdot i}}{A^{sv}_{\cdot i}\,(A^{sv}_{\cdot i}+W^{sv}_{\cdot i})\,(A^{sv}_{\cdot i}+B^{sv}_{\cdot i})}\right]$$

$$\widehat{\text{cov}}(\hat{m}_i^{st}, \hat{m}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \\ v=t \end{matrix} \quad = \hat{m}_i^{st}\hat{m}_i^{st}\left[\sum_{w=1}^{b}(m_i^{sw})^2\frac{(A^{sw}_{\cdot i})^2 + B^{sw}_{\cdot i}W^{sw}_{\cdot i}}{A^{sw}_{\cdot i}\,(A^{sw}_{\cdot i}+W^{sw}_{\cdot i})\,(A^{sw}_{\cdot i}+B^{sw}_{\cdot i})} + (1-2m_i^{sv})\frac{(A^{sv}_{\cdot i})^2 + B^{sv}_{\cdot i}W^{sv}_{\cdot i}}{A^{sv}_{\cdot i}\,(A^{sv}_{\cdot i}+W^{sv}_{\cdot i})\,(A^{sv}_{\cdot i}+B^{sv}_{\cdot i})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ j=i \\ v\neq t \end{matrix} \quad = \hat{m}_i^{st}\hat{m}_i^{sv}\left[\sum_{w=1}^{b}(m_i^{sw})^2\frac{(A^{sw}_{\cdot i})^2 + B^{sw}_{\cdot i}W^{sw}_{\cdot i}}{A^{sw}_{\cdot i}\,(A^{sw}_{\cdot i}+W^{sw}_{\cdot i})\,(A^{sw}_{\cdot i}+B^{sw}_{\cdot i})} - m_i^{st}\frac{(A^{st}_{\cdot i})^2 + B^{st}_{\cdot i}W^{st}_{\cdot i}}{A^{st}_{\cdot i}\,(A^{st}_{\cdot i}+W^{st}_{\cdot i})\,(A^{st}_{\cdot i}+B^{st}_{\cdot i})}\right.$$

$$\left. - m_i^{sv}\frac{(A^{sv}_{\cdot i})^2 + B^{sv}_{\cdot i}W^{sv}_{\cdot i}}{A^{sv}_{\cdot i}\,(A^{sv}_{\cdot i}+W^{sv}_{\cdot i})\,(A^{sv}_{\cdot i}+B^{sv}_{\cdot i})}\right]$$

Appendix 3.B (continued)

$$\widehat{\text{cov}}(\hat{m}_i^{st}, \hat{f}_j^{uv}) \quad \text{when} \quad \begin{array}{l} u=s \\ v=t \\ j=i \end{array} \quad = -\hat{f}_i^{st}\hat{m}_i^{st}(1-\hat{m}_i^{st}) \left[\frac{B_{\cdot i}^{st}W_{\cdot i}^{st}}{A_{\cdot i}^{st}\;(A_{\cdot i}^{st}+W_{\cdot i}^{st})\,(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\text{when} \quad \begin{array}{l} u=s \\ v\neq t \\ j=i \end{array} \quad = \hat{f}_i^{sv}\hat{m}_i^{st}\hat{m}_i^{sv} \left[\frac{B_{\cdot i}^{sv}W_{\cdot i}^{sv}}{A_{\cdot i}^{sv}\;(A_{\cdot i}^{sv}+W_{\cdot i}^{sv})\,(A_{\cdot i}^{sv}+B_{\cdot i}^{sv})} \right]$$

$$\widehat{\text{cov}}(\hat{m}_i^{st}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{array}{l} u=s \\ v=t \\ j=i \end{array} \quad = -\hat{p}_i^{st}\hat{m}_i^{st}(1-\hat{m}_i^{st}) \left[\frac{B_{\cdot i}^{st}W_{\cdot i}^{st}}{A_{\cdot i}^{st}\;(A_{\cdot i}^{st}+W_{\cdot i}^{st})\,(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\text{when} \quad \begin{array}{l} u=s \\ v\neq t \\ j=i \end{array} \quad = \hat{p}_i^{sv}\hat{m}_i^{st}\hat{m}_i^{sv} \left[\frac{B_{\cdot i}^{sv}W_{\cdot i}^{sv}}{A_{\cdot i}^{sv}\;(A_{\cdot i}^{sv}+W_{\cdot i}^{sv})\,(A_{\cdot i}^{sv}+B_{\cdot i}^{sv})} \right]$$

$$\widehat{\text{cov}}(\hat{f}_i^{st}, \hat{f}_j^{uv}) \quad \text{when} \quad \begin{array}{l} u=s \\ v=t \\ j=i \end{array} \quad = \hat{f}_i^{st}\hat{f}_i^{st} \left[\frac{1}{A_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} \right]$$

$$\widehat{\text{cov}}(\hat{f}_i^{st}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{array}{l} u=s \\ v=t \\ j=i \end{array} \quad = \hat{f}_i^{st}\hat{p}_i^{st} \left[\frac{B_{\cdot i}^{st}W_{\cdot i}^{st}}{A_{\cdot i}^{st}\;(A_{\cdot i}^{st}+W_{\cdot i}^{st})\,(A_{\cdot i}^{st}+B_{\cdot i}^{st})} \right]$$

$$\widehat{\text{cov}}(\hat{p}_i^{st}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{array}{l} u=s \\ v=t \\ j=i \end{array} \quad = \hat{p}_i^{st}\hat{p}_i^{st} \left[\frac{1}{A_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}} \right]$$

Appendix C
Exact tests in the Complete-Fidelity Model

3.C.1 Testing if the relative emigration rates at the time of release are homogeneous for all releases in the Complete-Fidelity Model.

$$H : m_i^{st} = m_{\cdot}^{st} \quad \text{assuming } f_i^{st} = \alpha_i^{s\cdot} f_1^{st}$$

$$A : m_i^{st} \text{ may vary among releases under the same assumption.}$$

The MSS under the null and alternate hypotheses are presented in Table 3.5.4.3a. Using the methods outlined in Chapter 1, the conditional distribution of the MSS(A) given MSS(H) used to construct a similar test is found to be:

$$\prod_{s=1}^{a} \frac{\displaystyle\prod_{i=1}^{k} \binom{R_{i\cdot}^{s\cdot}}{R_{i\cdot}^{s1} \;\cdots\; R_{i\cdot}^{sb}} \prod_{i=1}^{k} \binom{R_{\cdot i}^{s\cdot}}{R_{\cdot i}^{s1} \;\cdots\; R_{\cdot i}^{sb}} \prod_{t=1}^{b} (f_i^{st})^{R_{\cdot\cdot}^{st}} / (f_i^{s\cdot})^{R_{\cdot\cdot}^{s\cdot}}}{\displaystyle\prod_{i=1}^{k} \binom{T_i^{s\cdot}}{T_i^{s1} \;\cdots\; T_i^{sb}} \times P(R_{\cdot\cdot}^{st} \mid R_{\cdot\cdot}^{s\cdot},\ R_{\cdot i}^{s\cdot}\ i=1\ldots k,\ Z_i^{st}\ {}_{i=1\ldots l}^{t=1\ldots b})}$$

where

$$P(R_{\cdot\cdot}^{st} \mid R_{\cdot\cdot}^{s\cdot},\ R_{\cdot i}^{s\cdot}\ i=1\ldots k,\ Z_i^{st}\ {}_{i=1\ldots l}^{t=1\ldots b})$$

must be evaluated by enumerating all the configurations consistent with the conditioning. Note that this probability term will include a term including the band-recovery rates that will cancel with the term in the numerator, and so the test will be (as expected) a similar test.

Appendix 3.C (continued)

3.C.2 Testing if the relative emigration rates at the time of release are homogeneous over all pre-strata in the Complete-Fidelity Model.

$H : m_i^{st} = m_i^{\cdot t}$ assuming $f_i^{st} = \alpha_i^{s\cdot} f_i^{1t}$

$A : m_i^{st}$ may vary among pre-strata under the same assumption.

The MSS under the null and alternate hypotheses are presented in Table 3.5.4.3b. Using the methods outlined in Chapter 1, the conditional distribution of the MSS(A) given MSS(H) used to construct a similar test is found to be:

$$\prod_{i=i}^{k} \frac{\prod_{s=1}^{a}\binom{R_{i\cdot}^{s\cdot}}{R_{i\cdot}^{s1}\ \ldots\ R_{i\cdot}^{sb}} \prod_{s=1}^{a}\binom{R_{\cdot i}^{s\cdot}}{R_{\cdot i}^{s1}\ \ldots\ R_{\cdot i}^{sb}} \prod_{t=1}^{b} (f_i^{1t})^{R_{i\cdot}^{\cdot t}} / (f_i^{1\cdot})^{R_{i\cdot}^{\cdot\cdot}}}{\prod_{s=1}^{a}\binom{T_i^{s\cdot}}{T_i^{s1}\ \ldots\ T_i^{sb}} \times P\left(R_{i\cdot}^{\cdot t} \mid R_{i\cdot}^{\cdot\cdot},\ R_{i\cdot}^{s\cdot}\ s=1\ldots a,\ Z_i^{st}\ \begin{smallmatrix} t=1\ldots b \\ s=1\ldots a \end{smallmatrix}\right)}$$

where

$$P\left(R_{i\cdot}^{\cdot t} \mid R_{i\cdot}^{\cdot\cdot},\ R_{i\cdot}^{s\cdot}\ s=1\ldots a,\ Z_i^{st}\ \begin{smallmatrix} t=1\ldots b \\ s=1\ldots a \end{smallmatrix}\right)$$

must be evaluated by enumerating all the configurations consistent with the conditioning. Note that this probability term will include a term including the band-recovery rates that will cancel with the term in the numerator, and so the test will be (as expected) a similar test.

Appendix 3.D

Full-data representation for the Complete-Fidelity Model with sightings in the post-strata

The complete sighting and recovery history of an animal may be written as a $2x(l+1)$ matrix as in the Partial-Fidelity Model:

- the last column $(l+1)$ indicates the pre-stratum and year of release in rows 1 and 2 respectively;
- columns $1...l$ indicate the post-stratum and type of sighting or recovery of the band (either not seen, or recovered and sighted, or recovered but not sighted, or sighted without being recovered), in rows 1 and 2 respectively.

However, in the Complete-Fidelity Model, the post-strata of sightings and recovery must all be the same. Animals seen in two different post-strata are definite evidence against the Complete-Fidelity Model; however, the Complete-Fidelity Model may still be approximately valid if the number of such animals is small. Of course, no animals spotted in different post-strata does not prove that the Complete-Fidelity Model is valid.

An example of a four year history matrix is:

$$\begin{bmatrix} 0 & t & 0 & t & s \\ 0 & \begin{array}{c}\text{sighted}\\ \text{without being}\\ \text{recovered}\end{array} & 0 & \begin{array}{c}\text{recovered}\\ \text{but not}\\ \text{sighted}\end{array} & 1 \end{bmatrix} \qquad (D.1)$$

It indicates that the animal was released in pre-statum s in year 1, was not sighted or recovered in year 1, was sighted without being recovered in post-stratum t in year 2, was not sighted or recovered in year 3, and was recovered but not sighted in post-stratum t in year 4. Since complete-fidelity is being assumed, the animal is also assumed to have migrated to post-stratum t in years 1 and 3. Again, all columns corresponding to years after a band-recovery until the end of the experiment will be zero, as will all columns corresponding to years before the year of release.

The total number of distinct histories for animals released from pre-stratum s in year i can be computed as follows:

- there is one history for animals never sighted or recovered after being released
- if an animal is last sighted or recovered in post-stratum t in year j ($i \le j \le l$), then the animal can either be: not seen; or sighted without being recovered in post-stratum t in years $i \ldots j$-1. In year j, the animal is either: recovered and sighted; recovered but not sighted; or sighted without being recovered in post-stratum t, for a total of $(2)^{j-i}3b$ possible histories for $j=i \ldots l$.

Hence there are a total of

$$1 + \sum_{j=i}^{l} 3b(2)^{j-i} = 1 + 3b(2^{l-i+1}-1)$$

possible histories for animals released from pre-stratum s in year i.

The number of possible histories is of course smaller than in the Partial-Fidelity Model, but still can be large. While the data representation is simplified when fidelity to the post-strata occurs, it can still be complex. It is convenient to use the reduced-data array as presented in Section 3.6.

Since animals are assumed to act independently, and the histories are exclusive and exhaustive, the numbers of animals in each history follow a multinomial distribution under the assumptions of the complete-fidelity model. Each year's releases in each pre-stratum are independent, and so the likelihood of the data from the complete experiment can be written as:

$$L = \prod_{s=1}^{a} \prod_{i=1}^{k} \frac{N_{i}^{s}!}{\prod_{\omega \in \Omega_{i}^{s}} n_{i(\omega)}^{s}!} \prod_{\omega \in \Omega_{i}^{s}} (\pi_{\omega})^{n_{i(\omega)}^{s}}$$

where

ω is a history

Ω_{i}^{s} is the complete set of all possible histories for animals released from pre-stratum s in year i

$n_{i(\omega)}^{s}$ is the number of animals released from pre-stratum s in year i with history ω.

π_{ω} is the probability of the history ω.

The probability of history ω is computed in a manner similar to that of the reduced-data array in Section 3.6. For example, the probability of history (D.1) is computed as the product of:

- $M_{1}^{s\cdot} m_{1}^{st} (1-p_{1}^{st}) (1-f_{1}^{st})$ since the animal is known to have migrated to post-stratum t in year 1 but was not sighted or recovered;
- $S_{1}^{st}/(1-f_{1}^{st})$ since the animal is known to have survived in post-stratum t between years 1 and 2 conditional upon not being recovered;
- $p_{2}^{st}(1-f_{2}^{st})$ since the animal is known to have migrated back to post-stratum t and was sighted without being recovered in year 2;
- $S_{2}^{st}/(1-f_{2}^{st})$ since the animal is known to have survived in post-stratum t between years 2 and 3 conditional upon not being recovered;

- $(1-p_3^{st})(1-f_3^{st})$ since the animal is known to have migrated back to post-stratum t and was not sighted nor recovered in year 3;

- $S_3^{st}/(1-f_3^{st})$ since the animal is known to have survived in post-stratum t between years 3 and 4 conditional upon not being recovered;

- $p_4^{st}(1-f_4^{st})$ since the animal is known to have migrated back to post-stratum t and was sighted without being recovered in year 4.

Or:

$$\pi_\omega = M_1^{s\cdot} m_1^{st} (1-p_1^{st}) S_1^{st} p_2^{st} S_2^{st} (1-p_3^{st}) S_3^{st} p_4^{st} (1-f_4^{st}) \ .$$

The probability of the history corresponding to animals never sighted or recovered after being released is obtained by subtraction.

After simplification, the likelihood reduces to:

$$L = \prod_{s=1}^{a} \prod_{j=1}^{k} \frac{N_j^s!}{\prod_{\omega\in\Omega_j^s} n_{j(\omega)}^s!}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k} \left(M_j^{s\cdot}\right)^{A_{j\cdot}^{s\cdot}+B_{j\cdot}^{s\cdot}+W_{j\cdot}^{s\cdot}-W_{j\cdot\cdot}^{s\cdot\cdot}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{k} \prod_{t=1}^{b} \left(m_j^{st}\right)^{A_{j\cdot}^{st}+B_{j\cdot}^{st}+W_{j\cdot}^{st}-W_{j\cdot\cdot}^{stt}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(p_j^{st}\right)^{A_{\cdot j}^{st}+W_{\cdot j}^{st}} \left(1-p_j^{st}\right)^{B_{\cdot j}^{st}+Z_j^{st}-W_{\cdot j\cdot}^{stt}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l} \prod_{t=1}^{b} \left(f_j^{st}\right)^{A_{\cdot j}^{st}+B_{\cdot j}^{st}} \left(1-f_j^{st}\right)^{W_{\cdot j}^{st}-W_{\cdot j\cdot}^{stt}}$$

$$\prod_{s=1}^{a} \prod_{j=1}^{l-1} \prod_{t=1}^{b} \left(S_j^{st}\right)^{Z_j^{st}}$$

$$\prod_{s=1}^{a}\prod_{j=1}^{l-1}\prod_{t=1}^{b}\left(1-S_j^{st}\rho_{j+1}^{st}(1-f_j^{st})^{-1}(M_{j+1}^{st}m_{j+1}^{st})^{-1}\right)^{W_{\cdot j}^{st}-W_{\cdot j\cdot}^{stt}}$$

$$\prod_{s=1}^{a}\prod_{j=1}^{k}\left(1-\rho_j^{s\cdot}\right)^{N_j^s-A_{j\cdot}^{s\cdot}-B_{j\cdot}^{s\cdot}-W_{j\cdot}^{s\cdot}+W_{j\cdot\cdot}^{s\cdot\cdot}}$$

where ρ_j^{st} is the probability that an animal released in pre-stratum s in year j will be sighted or recovered in post-stratum t during the remainder of the banding experiment and is computed as:

$$\rho_l^{st} = M_l^{s\cdot}m_l^{st}(f_l^{st}+p_l^{st}-f_l^{st}p_l^{st}) \tag{D.2}$$

$$\rho_j^{st} = M_j^{s\cdot}m_j^{st}\{f_j^{st}+p_j^{st}-f_j^{st}p_j^{st}+S_j^{st}(1-p_j^{st})\rho_{j+1}^{st}(M_{j+1}^{s\cdot}m_{j+1}^{st})^{-1}\} \quad j=1\ldots l-1$$

$$\rho_j^{s\cdot} = \sum_{t=1}^{b}\rho_j^{st} \quad .$$

The MSS are easily derived, and are presented in Section 3.6.3. Since the dimension of the MSS equals the number of parameters, all parameters are identifiable. Using techniques similar to those presented in Chapter 2, the distribution of the MSS is found to be a product of the following conditionally independent multinomial or binomial distributions:

· the distribution of the number of animals released from pre-stratum s and recovered or sighted in post-stratum t in year j conditional upon the number of animals from pre-stratum s sighted or recovered in post-stratum t in year j or later which is a:

Multinomial(T_j^{st} animals sighted or recovered in post-stratum t in year j or later;

$A_{\cdot j}^{st}+B_{\cdot j}^{st}$ with probability $M_j^{s\cdot}m_j^{st}f_j^{st}\ /\ \rho_j^{st}$;

$W_{\cdot j}^{st}-W_{\cdot j\cdot}^{stt}$ with probability $M_j^{s\cdot}m_j^{st}p_j^{st}(1-f_j^{st})\{1-S_j^{st}(1-f_j^{st})^{-1}\rho_{j+1}^{st}(M_{j+1}^{s\cdot}m_{j+1}^{st})^{-1}\}/\rho_j^{st}$;

Z_j^{st} with probability $M_j^{s\cdot}m_j^{st}S_j^{st}\rho_{j+1}^{st}(M_{j+1}^{s\cdot}m_{j+1}^{st})^{-1}/\rho_j^{st}$).

for s=1...a, t=1...b, and j=1...l.

· the distribution of animals released from pre-stratum s and recovered and sighted in post-stratum t in year j or sighted or recovered after year j which is a:

Binomial ($A^{st}_{\cdot j}+B^{st}_{\cdot j}+Z^{st}_{j}$ animals recovered in year j, or sighted or recovered later;

$A^{st}_{\cdot j}+W^{stt}_{\cdot j \cdot}$ with probability p^{st}_{j};

$B^{st}_{\cdot j}+Z^{st}_{j}-W^{stt}_{\cdot j \cdot}$ with probability $(1-p^{st}_{j})$).

for s=1...a, t=1...b, and j=1...l.

· the distribution of the total unique animals released from pre-stratum s in year i and sighted or recovered during the experiment

Binomial(N^{s}_{i} total animals released ;

$A^{st}_{i\cdot}+B^{st}_{i\cdot}+W^{st}_{i\cdot}-W^{stt}_{i\cdot\cdot}$ with probability ρ^{st}_{i} for t=1...b;

$N^{s}_{i}-A^{s\cdot}_{i\cdot}+B^{s\cdot}_{i\cdot}+W^{s\cdot}_{i\cdot}-W^{s\cdot\cdot}_{i\cdot\cdot}$ with probability $1-\rho^{s\cdot}_{i}$).

for s=1...a, i=1...k.

The MLEs can be derived from the distribution of the MSS, or using the method of moments as outlined in Chapter 1, and are presented in Table 3.6.3; variances and covariances are shown in Appendix 3.E.

The distribution of the data conditional upon the MSS can be used as a general non-specific goodness-of-fit test in a similar fashion as in Pollock, Hines and Nichols (1985). Unfortunately, as in Pollock *et al.* (1985), and as in the partial-fidelity model, the large number of capture histories implies that most of the components of the test will involve small expected counts, require extensive pooling in the large sample contingency table approximations, and will likely have poor power.

More useful, is a goodness-of-fit test based upon the reduced-data array elements which are sufficient (but not minimal) statistics for the full likelihood. The distribution of the reduced-data array can be found using the techniques presented in Chapter 2. It is found to be the product of the following conditionally independent binomial or multinomial distributions:

- the distribution of the total unique animals released from pre-stratum *s* in year *i* and sighted or recovered during the rest of the experiment:

$$\text{Binomial}(\ N_i^s \text{ total animals released;}$$

$$A_{i\cdot}^{st}+B_{i\cdot}^{st}+W_{i\cdot}^{st}-W_{i\cdot\cdot}^{stt} \quad \text{with probability } \rho_i^{st} \text{ for } t=1\ldots b;$$

$$N_i^s-A_{i\cdot}^{s\cdot}+B_{i\cdot}^{s\cdot}+W_{i\cdot}^{s\cdot}-W_{i\cdot\cdot}^{s\cdot\cdot} \quad \text{with probability } 1-\rho_i^{s\cdot}\ )$$

for s=1...a, and i=1...k.

- the distribution of the animals released from pre-stratum *s* in year *i* and sighted or recovered in post-stratum *t* in year *j* conditional upon the animal being sighted or recovered in post-stratum *t* in year *j* or later:

$$\text{Multinomial}(\ \sum_{m=j}^{l}(A_{im}^{st}+B_{im}^{st}+W_{im}^{st}-W_{im\cdot}^{stt}) \text{ animals sighted or recovered in year } j \text{ or later;}$$

$$A_{ij}^{st} \quad \text{with probability } M_j^{s\cdot}m_j^{st}p_j^{st}f_j^{st}/\rho_j^{st}\ ;$$

$$B_{ij}^{st} \quad \text{with probability } M_j^{s\cdot}m_j^{st}(1-p_j^{st})f_j^{st}/\rho_j^{st}\ ;$$

$$W_{ij}^{st} \quad \text{with probability } M_j^{s\cdot}m_j^{st}p_j^{st}(1-f_j^{st})/\rho_j^{st}\ ;$$

$$\sum_{m=j+1}^{l}(A_{im}^{st}+B_{im}^{st}+W_{im}^{st}-W_{im\cdot}^{stt})-W_{\cdot j\cdot}^{stt} \quad \text{with probability } M_j^{s\cdot}m_j^{st}(1-p_j^{st})S_j^{st}\rho_{j+1}^{st}(M_{j+1}^{s\cdot}m_{j+1}^{st})^{-1}/\rho_j^{st}\ ).$$

for s=1...a, i=1...k, j=i...l-1.

- the distribution of the animals released from pre-stratum *s* in year *i* that are sighted without being recovered in post-stratum *t* in year *j* and are subsequently sighted or recovered after year j:

$$\text{Binomial}(\ W_{ij}^{st} \text{ animals sighted or recovered in year } j \text{ or later}$$

$$W_{ij\cdot}^{stt} \quad \text{with probability } S_j^{st}(1-f_j^{st})^{-1}\rho_{j+1}^{st}(M_{j+1}^{s\cdot}m_{j+1}^{st})^{-1};$$

$W^{st}_{ij} - W^{stt}_{ij\cdot}$ with probability $1 - S^{st}_{j}(1-f^{st}_{j})^{-1}\rho^{st}_{j+1}(M^{s\cdot}_{j+1}m^{st}_{j+1})^{-1})$

for $s=1\ldots a$, $t=1\ldots b$, $i=1\ldots k$, $j=i\ldots(l-1)$.

The goodness-of-fit test based upon the reduced array is constructed using the methods outlined in Chapter 1 and, after simplification, is based upon the conditional distributions:

$$\prod_{s=1}^{a}\prod_{t=1}^{b}\frac{\displaystyle\prod_{i=1}^{k}\prod_{j=i}^{l}\begin{pmatrix} \displaystyle\sum_{m=j}^{l}(A^{st}_{im}+B^{st}_{im}+W^{st}_{im}-W^{stt}_{im\cdot}) \\ A^{st}_{ij},\quad B^{st}_{ij},\quad W^{st}_{ij}-W^{stt}_{ij\cdot},\quad W^{stt}_{ij\cdot},\quad \displaystyle\sum_{m=j+1}^{l}(A^{st}_{im}+B^{st}_{im}+W^{st}_{im}-W^{stt}_{im\cdot})-W^{stt}_{ij\cdot}\end{pmatrix}}{\displaystyle\prod_{j=1}^{l}\begin{pmatrix} T^{st}_{j} \\ A^{st}_{\cdot j},\quad B^{st}_{\cdot j},\quad W^{st}_{\cdot j}-W^{stt}_{\cdot j\cdot},\quad W^{stt}_{\cdot j\cdot},\quad Z^{st}_{j}\end{pmatrix}} \times$$

$$\prod_{s=1}^{a}\prod_{t=1}^{b}\prod_{j=1}^{l-1}\frac{\displaystyle\prod_{i=1}^{k}\begin{pmatrix} A^{st}_{ij}+B^{st}_{ij} \\ A^{st}_{ij}\end{pmatrix}\begin{pmatrix} Z^{st}_{ij} \\ W^{stt}_{ij\cdot}\end{pmatrix}}{\begin{pmatrix} A^{st}_{\cdot j}+B^{st}_{\cdot j}+Z^{st}_{j} \\ A^{st}_{\cdot j}+W^{stt}_{\cdot j\cdot}\end{pmatrix}}$$

which is equivalent to:

$$\prod_{s=1}^{a}\prod_{t=1}^{b}\frac{\displaystyle\prod_{i=1}^{k}\prod_{j=i}^{l}\begin{pmatrix} \text{Total animals released from pre-stratum s } \textbf{in year i} \\ \text{and sighted or recovered in post-stratum t at or after year j} \\ \\ \substack{\text{Recovered} \\ \textbf{AND}\text{ sighted} \\ \text{in year j} \\ \text{in post-} \\ \text{stratum t}},\quad \substack{\text{Recovered }\textbf{BUT,} \\ \text{not sighted} \\ \text{in year j} \\ \text{in post-} \\ \text{stratum t}}\quad \substack{\text{Sighted for,} \\ \text{last time} \\ \text{in post-} \\ \text{stratum t} \\ \text{in year j}}\quad \substack{\text{Sighted }\textbf{WITHOUT,} \\ \text{being recovered} \\ \text{and subsequently} \\ \text{seen after year j} \\ \text{in post-stratum t}}\quad \substack{\text{Sighted or} \\ \text{recovered} \\ \text{in post-} \\ \text{stratum t }\textbf{only} \\ \text{after year j}}\end{pmatrix}}{\displaystyle\prod_{i=1}^{l}\prod_{j=i}\begin{pmatrix} \text{Total animals released from pre-stratum s } \textbf{in all years} \\ \text{and sighted or recovered in post-stratum t at or after year j} \\ \\ \substack{\text{Recovered} \\ \textbf{AND}\text{ sighted} \\ \text{in year j} \\ \text{in post-} \\ \text{stratum t}},\quad \substack{\text{Recovered }\textbf{BUT,} \\ \text{not sighted} \\ \text{in year j} \\ \text{in post-} \\ \text{stratum t}}\quad \substack{\text{Sighted for,} \\ \text{last time} \\ \text{in post-} \\ \text{stratum t} \\ \text{in year j}}\quad \substack{\text{Sighted }\textbf{WITHOUT,} \\ \text{being recovered} \\ \text{and subsequently} \\ \text{seen after year j} \\ \text{in post-stratum t}}\quad \substack{\text{Sighted or} \\ \text{recovered} \\ \text{in post-} \\ \text{stratum t }\textbf{only} \\ \text{after year j}}\end{pmatrix}} \times$$

$$\prod_{s=1}^{a}\prod_{t=1}^{b}\prod_{j=1}^{l-1}\frac{\displaystyle\prod_{i=1}^{k}\left(\begin{array}{c}\text{Animals recovered in}\\ \text{post-stratum t in}\\ \text{year j released in}\\ \text{year i}\\ \\ \text{Animals recovered and}\\ \text{sighted in post-}\\ \text{stratum t}\end{array}\right)\left(\begin{array}{c}\text{Animals recovered or sighted}\\ \text{after year j in post-stratum}\\ \text{t released in year i}\\ \\ \\ \text{Animals recovered or sighted}\\ \text{after year j in post-stratum}\\ \text{t and also sighted in year j}\end{array}\right)}{\displaystyle\prod_{j=1}^{l}\left(\begin{array}{c}\text{Animals recovered in post-stratum t in year j}\\ \text{or recovered or sighted in year j in post-strat t}\\ \\ \text{Animals sighted in year j}\\ \text{in post-stratum t}\end{array}\right)}\;.$$

Large-sample contingency tables that can be used for each component are presented in Tables 3.6.4.1a and 3.6.4.1b. Both components can be used to test if the reduced-data array may be combined over releases for each year of recovery to form the MSS. If the hypothesis of either component is rejected, it may indicate that the sighting, recovery, or survival rates in post-stratum t in year j are not the same for all releases.

Appendix 3.E

Estimators of non-zero covariances in the Complete-Fidelity Model with sightings in the post-strata

The estimators of the parameters are presented in Table 3.6.3.

$$\mathrm{cov}(\hat f_i^{st}, \hat f_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat f_i^{st}\hat f_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}}\right]$$

$$\widehat{\mathrm{cov}}(\hat f_i^{st}, \hat p_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat f_i^{st}\hat p_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat f_i^{st}, \hat S_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat f_i^{st}\hat S_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i-1 \end{matrix} \quad = -\hat f_i^{st}\hat S_{i-1}^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat f_i^{st}, \hat M_j^{u\cdot}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = \hat f_i^{st}\hat M_i^{s\cdot}\hat m_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat f_i^{st}, \hat m_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat f_i^{st}\hat m_i^{st}(1-\hat m_i^{st})\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v\neq t \\ j=i \end{matrix} \quad = -\hat f_i^{st}\hat m_i^{st}\hat m_i^{sv}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

Appendix 3.E (continued)

$$\widehat{\mathrm{cov}}(\hat{p}_i^{st}, \hat{p}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat{p}_i^{st}\hat{p}_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}}\right]$$

$$\widehat{\mathrm{cov}}(\hat{p}_i^{st}, \hat{S}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat{p}_i^{st}\hat{S}_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i-1 \end{matrix} \quad = -\hat{p}_i^{st}\hat{S}_{i-1}^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat{p}_i^{st}, \hat{M}_j^{u\cdot}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} \quad = \hat{p}_i^{st}\hat{M}_i^{s\cdot}\hat{m}_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat{p}_i^{st}, \hat{m}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat{p}_i^{st}\hat{m}_i^{st}(1-\hat{m}_i^{st})\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v\neq t \\ j=i \end{matrix} \quad = -\hat{p}_i^{st}\hat{m}_i^{st}\hat{m}_i^{sv}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

Appendix 3.E (continued)

$$\widehat{\mathrm{cov}}(\hat{S}_i^{st}, \hat{S}_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i-1 \end{matrix} = \hat{S}_{i-1}^{st}\hat{S}_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} = \hat{S}_i^{st}\hat{S}_i^{st}\left[\frac{1}{Z_i^{st}} + \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}}\right.$$

$$\left. - \frac{1}{T_{i+1}^{st}} + \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}} - \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st}} - \frac{1}{A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{\cdot,i+1}^{st}} + \frac{2(A_{\cdot i}^{st}+W_{\cdot i}^{stt})}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i+1 \end{matrix} = -\hat{f}_i^{st}\hat{m}_i^{st}\hat{m}_i^{sv}\left[\frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}} - \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st}} - \frac{1}{A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{\cdot,i+1}^{st}} + \frac{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}}{(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st})(A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{i+1}^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat{S}_i^{st}, \hat{M}_j^{u\cdot}) \quad \text{when} \quad \begin{matrix} u=s \\ j=i \end{matrix} = \hat{S}_i^{st}\hat{M}_i^{s\cdot}\hat{m}_i^{st}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ j=i+1 \end{matrix} = \hat{S}_i^{st}\hat{M}_{i+1}^{s\cdot}\hat{m}_{i+1}^{st}\left[\frac{-1}{T_{i+1}^{st}} + \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}} - \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st}} - \frac{1}{A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{\cdot,i+1}^{st}} + \frac{2(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt})}{(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st})(A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{i+1}^{st})}\right]$$

Appendix 3.E (continued)

$$\widehat{\mathrm{cov}}(\hat S_i^{st}, \hat m_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = \hat S_i^{st}\hat m_i^{st}(1-\hat m_i^{st})\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v\neq t \\ j=i \end{matrix} \quad = -\hat S_i^{st}\hat m_i^{st}\hat m_i^{sv}\left[\frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st}} + \frac{A_{\cdot i}^{st}+W_{\cdot i}^{stt}}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i+1 \end{matrix} \quad = \hat S_i^{st}\hat m_{i+1}^{st}(1-\hat m_{i+1}^{st})\left[\frac{-1}{T_{i+1}^{st}} + \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}} - \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st}} - \frac{1}{A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{\cdot,i+1}^{st}} + \frac{2(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt})}{(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st})(A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{i+1}^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v\neq t \\ j=i+1 \end{matrix} \quad = -\hat S_i^{st}\hat m_{i+1}^{st}\hat m_{i+1}^{sv}\left[\frac{-1}{T_{i+1}^{st}} + \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt}} - \frac{1}{A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st}} - \frac{1}{A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{\cdot,i+1}^{st}} + \frac{2(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{stt})}{(A_{\cdot,i+1}^{st}+W_{\cdot,i+1}^{st})(A_{\cdot,i+1}^{st}+B_{\cdot,i+1}^{st}+Z_{i+1}^{st})}\right]$$

$$\widehat{\mathrm{cov}}(\hat M_i^{s\cdot}\hat m_i^{st}, \hat M_j^{u\cdot}\hat m_j^{uv}) \quad \text{when} \quad \begin{matrix} u=s \\ v=t \\ j=i \end{matrix} \quad = (\hat M_i^{s\cdot}\hat m_i^{st})^2\left[\frac{1-\rho_i^{st}}{N_i^{s\cdot}\rho_i^{st}} - \frac{1}{T_i^{st}} + \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{stt}} - \frac{1}{A_{\cdot i}^{st}+W_{\cdot i}^{st}} - \frac{1}{A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_{\cdot i}^{st}} + \frac{2(A_{\cdot i}^{st}+W_{\cdot i}^{stt})}{(A_{\cdot i}^{st}+W_{\cdot i}^{st})(A_{\cdot i}^{st}+B_{\cdot i}^{st}+Z_i^{st})}\right]$$

$$\text{when} \quad \begin{matrix} u=s \\ v\neq t \\ j=i \end{matrix} \quad = -(\hat M_i^{s\cdot}\hat m_i^{st})(M_i^{s\cdot}m_i^{sv})\left[\frac{1}{N_i^{s\cdot}}\right]$$

The covariances of $M_i^{s\cdot}$, and m_i^{st} may be derived by a staightforward of the delta method using the immediately preceding results. No apparent algebraic simplication exists.

Appendix 3.F
Description of computer methods

Since the methods used to solve numerically for the MLEs and to obtain the variance-covariance matrix in restricted models is similar in both the Partial- and Complete-Fidelity Models, only the methods used in the Partial-Fidelity Model are described.

A commonly used procedure for obtaining MLEs when explicit solutions to the likelihood equations do not exist or are complicated, is the method of scoring (Rao, 1973, p. 366), i.e.:

$$\hat{\theta}_{i+1} = \hat{\theta}_i + I^{-1}(\hat{\theta}_i)g(\hat{\theta}_i)$$

where:

- θ is the unknown parameter vector
- $\hat{\theta}_i$ is the estimate for θ at the i^{th} iteration
- $g(\hat{\theta}_i)$ is the score statistic (first partials of the likelihood) evaluated at $\hat{\theta}_i$
- $I(\hat{\theta}_i)$ is the estimated information matrix.

Iterations continue until convergence is obtained.

There are three major problems in using the method of scoring directly in the Partial-Fidelity Model:

- the information matrix is extremely tedious to evaluate since the second partial derivatives of the likelihood with respect to the model parameters are extremely complicated.
- every restricted model will have a different form for the score statistic and the information matrix.
- the likelihood component for the external estimates of the pre-stratum population sizes and post-stratum band-reporting rates may

be required for some restricted models.

The first problem can be resolved by first finding a reparameterization of the model, in terms of which the score statistic and information matrix are trivial to compute and evaluate. Then using the chain rule, the score statistic and information matrix for the original parameters are easily derived. Specifically, let ξ be a 1-1 reparameterization of the underlying parameters θ. Then the score statistic in terms of θ can be obtained from the score statistic in terms of ξ:

$$g_\theta(\hat{\theta}) = \mathbf{P}\, g_\xi(\hat{\xi}) \qquad \text{(G.1)}$$

where $\mathbf{P}$ is the matrix of partial-derivatives of ξ with respect to θ.

Similarily, the information matrix in terms of θ can be obtained from the information matrix in terms of ξ by:

$$\mathbf{I}_\theta(\hat{\theta}) = \mathbf{P}\, \mathbf{I}_\xi(\hat{\xi})\, \mathbf{P}' \qquad \text{(G.2)}$$

In the Partial-Fidelity Model, a reparameterization that leads to simple evaluations of the score statistic and the estimated information matrix is obtained from the distribution of the MSS presented in Appendix 3.A. The set of ξ parameters is defined as:

$\rho_i^{s\cdot}$ i=1...k, s=1...a as defined in Appendix 3.A;

$\phi_i^{st} = S_i^{st}\rho_{i+1}^{s\cdot}(1-f_i^{st})^{-1}$ for i=1...(l-1), s=1...a, t=1...b;

$\psi_i^{lst} = M_i^{s\cdot} m_i^{st} p_i^{st} f_i^{st} / \rho_i^{s\cdot}$ for i=1...k, s=1...a, t=1...b;

$\psi_i^{2st} = M_i^{s\cdot} m_i^{st} (1-p_i^{st}) f_i^{st} / \rho_i^{s\cdot}$ for i=1...k, s=1...a, t=1...b;

$\psi_i^{3st} = M_i^{s\cdot} m_i^{st} p_i^{st} (1-f_i^{st}) / \rho_i^{s\cdot}$ for i=1...k, s=1...a, t=1....b;

$\psi_i^{1st} = S_k^{s\cdot} \ldots S_{i-1}^{s\cdot} M_i^{s\cdot} m_i^{st} p_i^{st} f_i^{st} / S_i^{s\cdot} \ldots S_{i-1}^{s\cdot} \rho_i^{s\cdot}$ for i=k+1...l, s=1..a, t=1...b

$\psi_i^{2st} = S_k^{s\cdot} \ldots S_{i-1}^{s\cdot} M_i^{s\cdot} m_i^{st} (1-p_i^{st}) f_i^{st} / S_i^{s\cdot} \ldots S_{i-1}^{s\cdot} \rho_i^{s\cdot}$ for i=k+1...l s=1...a, t=1...b

$\psi_i^{3st} = S_k^{s\cdot} \ldots S_{i-1}^{s\cdot} M_i^{s\cdot} m_i^{st} p_i^{st} (1-f_i^{st}) / S_k^{s\cdot} \ldots S_{i-1}^{s\cdot} \rho_i^{s\cdot}$ for i=k+1...l s=1...a, t=1...b

Now $\rho_i^{s\cdot}$ and ϕ_i^{st} are the parameters of a binomial distribution, and ψ_i^{1t}, ψ_i^{2st}, and ψ_i^{3st} are the parameters of a multinomial distribution and so the score statistics and Hessian under this parameterization are trivial. A subroutine is used to compute the partial-derivative matrix of this parameterization with respect to the parameters of interest (i.e., the migration, sighting, survival, and band-recovery rates), and the score statistic and information matrix are computed using (G.1) and (G.2).

The second problem could be solved using methods similar to Conroy and Williams (1984). Briefly, they find the score statistic and information matrix for restricted models using methods similar to (G.1) and (G.2), execpt now the matrix $\mathbf{P}$ is a non-square matrix of the partial derivatives of the parameters of the restricted model with respect to the full model. Their method requires that both the restricted and full models have an explicit parameter set. This is not a problem when examining restricted models where, for example, parameters are homogeneous among post-strata, e.g., $f_i^{st}=f_i^{\cdot t}$. However, explicit parameters are difficult to find in some restricted models such as the one in which the harvest-derivation rates are restricted to be homogeneous among post-strata. For this reason, the methods outlined by Aitchison and Silvey (1958) and Don (1985) have been used.

In this method, we wish to find estimates of θ (the parameters of the unrestricted model) subject to the set of constraints $\mathbf{h}(\theta)=\mathbf{0}$. Aitkinson and Silvey (1958) showed that the method of scoring can be modified using the method of Lagrange Multipliers (the λ_i) as:

$$\begin{bmatrix} \hat{\theta}_{i+1} \\ \hat{\lambda}_{i+1} \end{bmatrix} = \begin{bmatrix} \hat{\theta}_{i} \\ \hat{\lambda}_{i} \end{bmatrix} + \begin{bmatrix} \mathbf{I}(\hat{\theta}_i) & [\mathbf{h}'(\hat{\theta}_i)]' \\ \mathbf{h}'(\hat{\theta}_i) & 0 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{g}(\hat{\theta}_i) \\ -\mathbf{h}(\hat{\theta}_i) \end{bmatrix} \qquad (G.3)$$

where $\mathbf{h}'(\theta)$ is the matrix of partial derivatives of $\mathbf{h}(\theta)$ with respect to θ. Due to the special pattern of the augmented Hessian, it is not necessary to actually invert the augmented matrix. Rather, Don (1985) obtained an expression for the updating formula for θ in terms of the components of the augmented Hessian. As well, if the matrix of contraints is singular, Moore-Penrose generalized inverses can be used. If the constraints are linear (such as in the case of simple restrictions on the parameters), (G.3) reduces to the ordinary method of scoring after the first iteration.

In summary of the resolution of the first two problems, let:

ξ be the set of parameters under the reparameterization above;

θ be the set of biologically interesting parameters for the partial-fidelity model;

$\mathbf{h}(\theta)=\mathbf{0}$ be the set of constraints upon the parameters;

$\mathbf{P} = \partial\xi/\partial\theta$ be a matrix of partial derivatives.

Then, the steps taken in one iteration of the method of scoring are:

- evaluate $\hat{\xi}_i$

- evaluate the score $g_\xi(\hat{\xi}_i)$
- evaluate the estimated information matrix $\mathbf{I}_\xi(\hat{\xi}_i)$
- compute $g_\theta(\hat{\theta}_i) = \mathbf{P}\, g_\xi(\hat{\xi}_i)$
- compute $\mathbf{I}_\theta(\hat{\theta}_i) = \mathbf{P}\, \mathbf{I}_\xi(\hat{\xi}_i)\, \mathbf{P}'$
- use (G.3) to update θ.

Initial starting values are obtained using the explicit estimators of the parameters for the general Partial-Fidelity Model given in Table 3.4.3.

The third problem typically occurs when tests of homogeneity of the derived parameters are required. For example, a test for homogeneous relative harvest derivation rates among post-strata should incorporate information from both the recoveries from the current study and the information from the external studies which gave rise to the external estimates of the pre-stratum population sizes and post-stratum band-reporting rates. This may be done in two ways:

- Use the delta-method to obtain the variance co-variance matrix of the derived estimates and then use a quadratic form to test for homogeneity as in Brownie *et al.* (1985, p. 180). Under the assumption that the derived estimates are asymptotically multivariate normal, the test statistic will have a chi-square distribution.
- create an approximate likelihood term for the external study and incorporate this term into the method of scoring as discussed earlier.

The first method, although conceptually easier, suffers from the disadvantage that it is difficult to implement a general solution in a computer program. The second method is more convenient once the relevant approximate likelihood has been created.

Without loss of generality, consider the case of a single external parameter, ϕ, that is estimated by an external study. Let $\hat{\phi}$ and $\hat{se}(\hat{\phi})$ represent the independent MLE and its estimated standard error from the external study. Technically, the total likelihood from the external study and the current study should be maximized to obtain the MLE of all parameters (internal and external). In the general model without restrictions on the parameters, the current study has no information on the external parameters, and vice-versa, and so the maximization can be done for each part of the likelihood separately. However, when certain restrictions on derived parameters are considered, both parts of the likelihood contain information on the derived parameters and cannot be maximized separately. The problem is, of course, that the likelihood function from the external study is unknown. However, the external MLEs are asymptotically sufficient for their parameters (Cox and Hinkley, 1974, p. 307), and all of the information from the external study is, asymptotically, contained in the MLE and its estimated standard error. If we assume that the MLE is asymptotically normally distributed about the true parameter value, and if we assume (for simplicity) that the true standard error is equal to the estimated standard error, an approximate log-likelihood from the external study can be constructed as:

$$.5*\log(2\pi) - \log(se(\hat{\phi})) - .5(\hat{\phi}-\phi)^2/se(\hat{\phi})^2.$$

This can now be incorporated into the method of scoring.

Chapter 4

The Non-Fidelity Model

Summary

In the Non-Fidelity Model, no assumptions are made about the fidelity of the animals to the pre-stratum of release or to the post-stratum of recovery. A stochastic model is developed for this model in an ordinary band-recovery context using matrix notation. Once again, ordinary band-recovery data are inadequate for inference; however, the complexity of the model specification precludes obtaining an explicit list of all identifiable parameters. The use of additional live sightings in the pre-strata and the post-strata is discussed, and the limitations of this approach are identified. It may be more cost-effective to employ radio-telemetry devices on fewer animals.

Chapter 4
The Non-Fidelity Model

4.1. INTRODUCTION

In the Non-Fidelity Model no assumptions are made about the fidelity of the animal either to the pre-stratum of banding or release, or to the post-stratum of recovery, or to both. Animals may migrate not only to a different post-stratum in each year, but may also return to a different pre-stratum other than where released. For example, in the Non-Fidelity Model, an animal that is banded and released in pre-stratum 1 in year 1 may: migrate to post-stratum 1 in year 1; migrate back to pre-stratum 2 by the time of banding in year 2; migrate to post-stratum 3 in year 2; migrate back to pre-stratum 1 by the time of banding in year 3; and migrate to post-stratum 2 in year 3 where the band is recovered. This differs from the Partial-Fidelity Model where animals are assumed to be faithful to their pre-stratum of release, and hence the location of a banded animal (assuming that it is alive) is known at banding time in every year following release. The concept of a pre-stratum is less well defined in the Non-Fidelity Model, since the pre-stratum of an animal at banding time is known only in the year of release; however it is still convenient to refer to the strata where banding and releases occur as pre-strata, and to the strata where recoveries occur as post-strata.

Brownie *et al.* (1985, Chapters 3 and 4) considered band-recovery models where pre-strata were defined by the age of the animal. In these models, animals can move among pre-strata (as they age), but only in a regimented, known fashion. Those models will be inappropriate where the movements among pre-strata are not known in advance. Arnason (1972, 1973) and Seber (1982, p. 555) considered the case of movement among strata in a capture-recapture context where captures occur at a point in time and occur in the same set of strata as releases. In exploited populations, a band-recovery context where recoveries occur over a period of time in strata typically different from those where releases occur, may be more pertinent. As well, Arnason (1972, 1973) assumed that any migration to strata outside the experiment was permanent; no such assumption is made in the Non-Fidelity Model.

This model can also be viewed as a compartmental-system model where the pre- and post-strata are different compartments, and the migration rates among the strata are viewed as the interchange rates among compartments. The methods used to analyze compartment-system models (Kalbfleisch, Lawless, and Vollmer, 1983; Kodell and Matis, 1976) are not applicable since these models assume: that sampling takes place at a point in time (rather than over an extended period); that all particles in a compartment are identified (rather than only a sample of animals); and that particles are indistinguishable so that individual movements cannot be followed (rather than some information being available as where the animals were released and recovered). If the entire movement history of a banded-animal is available, then the methods of inference in Markov-Chain models (Bartlett, 1958; Basawa and Rao, 1980) may be used; however, this data is unlikely to be available in ordinary band-recovery experiments unless radio-telemetry devices are used.

The formulation of the Non-Fidelity Model is greatly simplified by using matrix notation since the probability of recovery of a band in a post-stratum is a convolution of intermediate movements of an animal among pre-strata and the final movement of the animal to the post-strata, which is easily expressed as a product of matrices.

I start by outlining the notation used and the assumptions made in the Non-Fidelity Model. Next, a stochastic model is developed for data from an ordinary band-recovery experiment. Once again ordinary band-recovery data are inadequate for inferences in this model; however the complexity of the model precludes obtaining an explicit list of all identifiable parameters. The use of additional sightings of animals in the pre- and post-strata to overcome these deficiencies is discussed and the limitations of this approach are identified. Finally, a practical modification to the experimental design using radio-telemetry data that allows full inference about all parameters in this model is outlined. A detailed discussion of inference under this experimental design is omitted since the model can then be formulated as a Markov-chain model in which inferential techniques are well developed (Bartlett, 1955; Basawa and Rao, 1980).

4.2. NOTATION

All vectors and matrices are indicated by bold face. Individual elements within a matrix or a vector are indicated by the use of superscripts.

Parameters

a — the number of pre-strata where banding and releases take place. Pre-stratum $a+1$ represents the set of all other pre-strata where bandings and releases do not occur, but where animals are free to migrate.

b — number of post-strata where recoveries occur.

k — number of years of releases.

l — number of years of recoveries.

$\mathbf{N}_i$ — an $a \times 1$ vector whose s^{th} element (N_i^s) represents the number of animals released in pre-stratum s in year i.

$\mathbf{M}_i$ — an $a \times b$ matrix whose $(s,t)^{th}$ element represents the probability that an animal alive in pre-stratum s at the time of banding in year i decides to migrate to post-stratum t in the next year.

$\mathbf{M}_i^*$ — an $(a+1) \times b$ matrix whose first a rows are the matrix $\mathbf{M}_i$, and whose elements of the last row ($M_i^{*a+1,t}$) represents the probability that an animal alive at the time of banding in year i in other pre-strata (where banding does not occur) will migrate to post-stratum t in the next year.

$\mathbf{f}_i$ — an $a \times b$ matrix whose $(s,t)^{th}$ element (f_i^{st}) represents the probability that an animal alive in pre-stratum s at the time of banding in year i, and which decides to migrate to post-stratum t, will be recovered in post-stratum t in the next year.

f_i^* an $(a+1) \times b$ matrix whose first a rows are the matrix f_i, and where elements of the last row ($f_i^{*a+1,t}$) represent the probability that an animal alive in other pre-strata (where banding does not occur) at the time of banding in year i, and which decides to migrate to post-stratum t, will be recovered in post-stratum t in the next year.

S_i an $a \times (a+1)$ matrix whose $(s,u)^{th}$ element (S_i^{su}) represents the probability that an animal alive in pre-stratum s at the time of banding in year i will be alive and present in pre-stratum u at the time of banding in year $i+1$. These parameters include both a movement and survival component. The last column of the matrix (column $a+1$) represents movement/survival rates to pre-strata where banding does not occur.

S_i^* an $(a+1) \times (a+1)$ matrix whose first a rows are the matrix S_i and whose elements of the last row ($S_i^{*a+1,u}$) represent the probability than an animal alive in pre-strata where banding does not occur at the time of banding in year i, will be alive and present in pre-stratum u at the time of banding in year $i+1$

Statistics

R_{ij} an $a \times b$ matrix whose $(s,t)^{th}$ element (R_{ij}^{st}) represents the number of animals released in pre-stratum s in year i and recovered in post-stratum t in year j.

<u>Matrix operations and special matrices</u>

1 a vector whose every element is a 1.

x, + element by element multiplication and division.

For example if $\mathbf{A}=\begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix}$ and $\mathbf{B}=\begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix}$ then

$\mathbf{A} \mathbin{\mathbf{x}} \mathbf{B} = \begin{bmatrix} 5 & 12 \\ 21 & 32 \end{bmatrix}$ $\mathbf{A} + \mathbf{B} = \begin{bmatrix} 0.20 & 0.33 \\ 0.43 & 0.50 \end{bmatrix}$

D(**X**) the diagonal matrix formed by placing the elements of **X** on the diagonal.

4.3. ASSUMPTIONS

The usual assumptions made for band-recovery models as outlined in Section 1.3.3 are also made in the Non-Fidelity Model. As well it is assumed that:

- all migration decisions are Markovian in nature, i.e., the probability of migrating from a pre- to a post-stratum, or among pre-strata, does not depend upon previous migration patterns;
- animals behave independently with respect to migration and recovery, i.e., there is no schooling or flocking during migration, or if such behavior does occur, it does not influence the migration or recovery probabilities of the animal;
- for simplicity, banding occurs in the same set of pre-strata in each year of release and recoveries occur in the same set of post-strata in each year of recovery.

Note that it is not assumed that the animal must migrate only to the post-strata where recoveries occur, nor that they must migrate only among pre-strata where banding and releases occur. In Arnason (1972,

1973) and Seber (1982) any migration to strata outside the experiment was considered permanent and as another form of mortality. In the Non-Fidelity Model, animals may temporarily migrate to other pre-strata or other post-strata not part of the experiment, and return at a later time.

A crucial assumption in this model is the assumption of Markovian behavior in the choice of migration routes. This implies that the animals have "no memory" of where they migrated in past years when they choose their migration routes from the pre-strata to the post-strata or from the post-strata to the pre-strata. For species of animals with a homing instinct, this assumption will be violated, but these models may still be applicable if the degree of homing is small. This assumption can only be assessed on biological grounds when ordinary band-recovery data are available. If live sightings are available, it may be possible to compare subsequent recovery or sighting patterns among animals sighted in the same pre- or post-strata to assess the validity of the assumption.

4.4. STOCHASTIC MODEL USING ORDINARY BAND-RECOVERY DATA

The number of animals that are released in pre-stratum s in year i and are recovered in post-stratum t in year j can be displayed using matrices as shown in Figure 4.4a. For example, the matrix R_{13} contains the entire set of the number of recoveries of animals released in year 1 and recovered in year 3; the $(s,t)^{th}$ element (R_{13}^{st}) represents the number of recoveries released in pre-stratum s and recovered in post-stratum t.

Figure 4.4a

Symbolic representation of the number of animals released in pre-stratum s in year i and recovered in post-stratum t in year j in the case of $k=3$ years of releases and $l=4$ year of recoveries in the Non-Fidelity Model using ordinary band-recovery data

Year Released	Number Released	Number recovered by year 1	2	3	4
1	$\mathbf{N}_1$	$\mathbf{R}_{11}$	$\mathbf{R}_{12}$	$\mathbf{R}_{13}$	$\mathbf{R}_{14}$
2	$\mathbf{N}_2$		$\mathbf{R}_{22}$	$\mathbf{R}_{23}$	$\mathbf{R}_{24}$
3	$\mathbf{N}_3$			$\mathbf{R}_{33}$	$\mathbf{R}_{34}$

$$\mathbf{N}_i \text{ are } a \times 1 \text{ vectors } \begin{bmatrix} N_1^1 \\ N_1^2 \\ \cdot \\ \cdot \\ \cdot \\ N_1^a \end{bmatrix} \text{ and } \mathbf{R}_{ij} \text{ are } a \times b \text{ matrices } \begin{bmatrix} R_{ij}^{11} & R_{ij}^{12} & \cdots & R_{ij}^{1b} \\ R_{ij}^{21} & R_{ij}^{22} & \cdots & R_{ij}^{2b} \\ \vdots & & & \vdots \\ R_{ij}^{a1} & R_{ij}^{a2} & \cdots & R_{ij}^{ab} \end{bmatrix}$$

The number of animals never seen is not shown, but can be obtained by subtraction.

The set of elements in the s^{th} row of each of the matrices forming the i^{th} row of the table represents the entire set of recoveries for those animals released in pre-stratum s in year i. For example, the set of elements $\{\{R_{22}^{st},\ t=1\ldots b\},\ \{R_{23}^{st},\ t=1\ldots b\},\ \{R_{24}^{st},\ t=1\ldots b\}\}$ represents the recoveries of animals released in pre-stratum s in year 2 and recovered in years 2, 3 and 4 in one of the post-strata $t=1\ldots b$. I shall refer to this set of elements as the $(s_i)^{th}$ sub-row. The number of animals never recovered is not shown but can be found by subtraction.

Under the assumptions of the Non-Fidelity model, the $(s_i)^{th}$ sub-row can be modelled as a multinomial distribution, i.e., $\{R_{ij}^{st},\ j=i\ldots l,\ t=1\ldots b\}$ are multinomially distributed with index N_i^s. Simultaneous releases in different pre-strata are assumed to be independent, i.e., $\{R_{ij}^{ut},\ j=i\ldots l,\ t=1\ldots b\}$ is assumed to be independent of the previous distribution when $u \neq s$. Releases in successive years are also assumed to be independent.

The individual cell probabilities for these multinomial distributions are computed as a convolution of the intermediate movement rates among pre-strata $(\boldsymbol{S}_i)$ between the year of release and the year of recovery and the migration rates and band-recovery rates from the pre-strata to the post-strata ($\boldsymbol{M}_i$ and $\boldsymbol{f}_i$) in the year of recovery. The expressions for the individual cell probabilities are more easily computed using matrices as shown in Figure 4.4b. A numerical example showing the expected number of recoveries in the case of $a=2$ pre-strata where banding occurs, $b=3$ post-strata where recoveries occur, $k=3$ years

Figure 4.4b

The probabilities that an animal released in pre-stratum s in year i is recovered in post-stratum t in year j in the case of $k=3$ years of releases and $l=4$ years of recoveries in the Non-Fidelity Model using ordinary band-recovery data

Year Released	Number Released	Probabilities of recovery by year 1	2	3	4
1	$\boldsymbol{N_1}$	$\boldsymbol{M_1 x f_1}$	$\boldsymbol{S_1(M_2^* x f_2^*)}$	$\boldsymbol{S_1 S_2^*(M_3^* x f_3^*)}$	$\boldsymbol{S_1 S_2^* S_3^*(M_4^* x f_4^*)}$
2	$\boldsymbol{N_2}$		$\boldsymbol{M_2 x f_2}$	$\boldsymbol{S_2(M_3^* x f_3^*)}$	$\boldsymbol{S_2 S_3^*(M_4^* x f_4^*)}$
3	$\boldsymbol{N_3}$			$\boldsymbol{M_3 x f_3}$	$\boldsymbol{S_3(M_4^* x f_4^*)}$

$\boldsymbol{N_i}$ are a x 1 vectors $\begin{bmatrix} N_1^1 \\ N_1^2 \\ \cdot \\ \cdot \\ \cdot \\ N_1^a \end{bmatrix}$.

$\boldsymbol{M_i}$ are a x b matrices $\begin{bmatrix} M_i^{11} & M_i^{12} & \cdots & M_i^{1b} \\ M_i^{21} & M_i^{22} & \cdots & M_i^{2b} \\ \vdots & & & \vdots \\ M_i^{a1} & M_i^{a2} & \cdots & M_i^{ab} \end{bmatrix}$.

$\boldsymbol{M_i^*}$ are $(a+1)xb$ matrices $\begin{bmatrix} M_i^{11} & M_i^{12} & \cdots & M_i^{1b} \\ M_i^{21} & M_i^{22} & \cdots & M_i^{2b} \\ \vdots & & & \vdots \\ M_i^{a+1,1} & M_i^{a+1,2} & \cdots & M_i^{a+1,b} \end{bmatrix}$.

Figure 4.4b (continued)

$\boldsymbol{f}_i$ are $a \times b$ matrices $\begin{bmatrix} f_i^{11} & f_i^{12} & \cdots & f_i^{1b} \\ f_i^{21} & f_i^{22} & \cdots & f_i^{2b} \\ \vdots & & & \vdots \\ f_i^{a1} & f_i^{a2} & \cdots & f_i^{ab} \end{bmatrix}$;

$\boldsymbol{f}_i^*$ are $(a+1)xb$ matrices $\begin{bmatrix} f_i^{11} & f_i^{12} & \cdots & f_i^{1b} \\ f_i^{21} & f_i^{22} & \cdots & f_i^{2b} \\ \vdots & & & \vdots \\ f_i^{a+1,1} & f_i^{a+1,2} & \cdots & f_i^{a+1,b} \end{bmatrix}$.

$\boldsymbol{S}_i$ are $a \times (a+1)$ matrices $\begin{bmatrix} S_i^{11} & S_i^{12} & \cdots & S_i^{1,a+1} \\ S_i^{21} & S_i^{22} & \cdots & S_i^{2,a+1} \\ \vdots & & & \vdots \\ S_i^{a1} & S_i^{a2} & \cdots & S_i^{a,a+1} \end{bmatrix}$.

$\boldsymbol{S}_i^*$ are $(a+1)x(a+1)$ matrices $\begin{bmatrix} S_i^{11} & S_i^{12} & \cdots & S_i^{1,a+1} \\ S_i^{21} & S_i^{22} & \cdots & S_i^{2,a+1} \\ \vdots & & & \vdots \\ S_i^{a+1,1} & S_i^{a+1,2} & \cdots & S_i^{a+1,a+1} \end{bmatrix}$.

The probability of never recovering an animal is not shown, but can be obtained by subtraction.

Note that, for example, $\boldsymbol{S}_1\boldsymbol{S}_2^*$ means the usual matrix multiplication,

but, for example, $\boldsymbol{M}_3^* \times \boldsymbol{f}_3^*$ means element by element multiplication.

Figure 4.4c

A numerical example of the expected number of recoveries in the Non-Fidelity Model using ordinary band-recovery data in the case of *a=2* pre-strata where banding occurs, *b=3* post-strata where recoveries occur, *k=3* years of releases, and *l=4* years of recoveries using the parameter values given at the foot of the table.

Year Released	Number Released	Expected Number of Recoveries by year 1	2	3	4
1	$\begin{bmatrix}1000\\1000\end{bmatrix}$	$\begin{bmatrix}12.0 & 24.0 & 8.0\\20.0 & 12.0 & 12.0\end{bmatrix}$	$\begin{bmatrix}8.6 & 14.2 & 6.4\\12.2 & 8.8 & 8.2\end{bmatrix}$	$\begin{bmatrix}6.2 & 8.9 & 4.9\\7.8 & 6.5 & 5.8\end{bmatrix}$	$\begin{bmatrix}4.5 & 5.9 & 3.7\\5.2 & 4.8 & 4.1\end{bmatrix}$
2	$\begin{bmatrix}1000\\1000\end{bmatrix}$		$\begin{bmatrix}12.0 & 24.0 & 8.0\\20.0 & 12.0 & 12.0\end{bmatrix}$	$\begin{bmatrix}8.6 & 14.2 & 6.4\\10.0 & 8.8 & 8.2\end{bmatrix}$	$\begin{bmatrix}6.2 & 8.9 & 4.9\\7.8 & 6.5 & 5.8\end{bmatrix}$
3	$\begin{bmatrix}1000\\1000\end{bmatrix}$			$\begin{bmatrix}12.0 & 24.0 & 8.0\\20.0 & 12.0 & 12.0\end{bmatrix}$	$\begin{bmatrix}8.6 & 14.2 & 6.4\\10.0 & 8.8 & 8.2\end{bmatrix}$

where $\boldsymbol{M}_1^*=\boldsymbol{M}_2^*=\boldsymbol{M}_3^*=\boldsymbol{M}_4^* = \begin{bmatrix}0.30 & 0.40 & 0.20\\0.40 & 0.30 & 0.20\\0.20 & 0.20 & 0.40\end{bmatrix}$ and $\boldsymbol{M}_i$ are the first two rows of the corresponding matrix

$\boldsymbol{f}_1^*=\boldsymbol{f}_2^*=\boldsymbol{f}_3^*=\boldsymbol{f}_4^* = \begin{bmatrix}0.04 & 0.06 & 0.04\\0.05 & 0.04 & 0.06\\0.03 & 0.05 & 0.03\end{bmatrix}$ and $\boldsymbol{f}_i$ are the first two rows of the corresponding matrix

$\boldsymbol{S}_1^*=\boldsymbol{S}_2^*=\boldsymbol{S}_3^* = \begin{bmatrix}0.50 & 0.10 & 0.10\\0.05 & 0.55 & 0.10\\0.10 & 0.10 & 0.60\end{bmatrix}$ and $\boldsymbol{S}_i$ are the first two rows of the corresponding matrix

The rows of each matrix refer to the pre-strata; the columns refer to the post-strata.

The row-wise similarities are caused by assuming that parameters are constant over time.

of releases, and $l=4$ years of recoveries is shown in Figure 4.4c using the parameter values given at the foot of the table.

The band-recovery parameters, f_i^{st} and f_i^{*st}, represent the probability that the band is recovered from an animal that decides to migrate in year i from pre-stratum s to post-stratum t. The two sets of parameters are identical for pre-strata $s=1...a$; the only difference between the two sets is in the band-recovery rates for animals that migrate from other pre-strata where banding does not occur (represented by pre-stratum $a+1$) to the post-strata. These extra parameters are required since animals may temporarily migrate to pre-strata outside the experiment after being released. For example, in Figure 4.4c, the band-recovery rates $f_2^{13}=f_2^{*13}=0.04$ implies that, of the animals alive at banding time in year 2 in pre-stratum 1 that decide to migrate to post-stratum 3, only 4% of the bands will be recovered. The band-recovery rate $f_2^{*31}=0.03$ implies that, of the animals currently alive in pre-strata where banding does not occur in year 2 that decide to migrate to post-stratum 1, only 3% of the bands will be recovered. The band-recovery rates from pre-stratum 3 are not required to model the number of recoveries in the year of release (R_{11}, R_{22}, R_{33}) since these animals will not have had the opportunity to migrate to other pre-strata. Both sets of parameters are assumed not to depend upon the previous migration history of the animals. The band-recovery rates are allowed to vary among the pre-strata within a specific post-stratum for the same reasons as outlined in the Partial-Fidelity Model, except that in the Non-Fidelity Model, the pre-stratum refers to the actual location of the animal at banding time in year *i* which may not be the pre-stratum of release.

The migration parameters, M_i^{st} or M_i^{*st}, represent the net migration rates of animals alive at banding time in year *i* from pre-stratum *s* to post-stratum *t*. The two parameter sets are identical for pre-strata *s=1...a;* they differ only in the net migration rates for animals alive in other pre-strata (*s=a+1*) to post-stratum *t*. Again, these extra parameters are required since animals may temporarily migrate to other pre-strata after release. For example, in Figure 4.4c, the migration rates $M_2^{21}=M_2^{*21}= 0.40$ imply that, of the animals alive at banding time in year 2 in pre-stratum 2, 40% decided to migrate to post-stratum 3. The migration rate $M_2^{*32}=0.20$ implies that, of the animals alive at banding time in year 2 in all other pre-strata where banding does not occur, 20% decide to migrate to post-stratum 2. Both sets of parameters are assumed to be independent of the previous migration history of the animals. The total and relative migration rates are not introduced in this model, as they were in the Partial- and Complete-Fidelity Models, since the additional notation would be complex and they are easily derived from the net migration rates.

As in the Partial- and Complete-Fidelity Models, the timing of the migration decision is 'projected' back to the time of banding in year *i* so that all mortality from hunting in year *i* between release and recovery is incorporated into the band-recovery rates.

The parameters, S_i^{su} and S_i^{*su}, represent the net probability that an animal alive in pre-stratum s at the time of banding in year i will be alive and present in pre-stratum u at the time of banding in year $i+1$. These parameters incorporate both movement and mortality components; for convenience, they will be referred to as the survival rates. These parameters should not be confused with the post-stratum specific survival rates of the Partial- and Complete-Fidelity Models; rather these parameters are the extension of the net survival rates over all post-strata used in the Partial-Fidelity Model, except that the animals need not remain faithful to the pre-stratum of release. Both sets of parameters are identical for $s=1...a$; they differ only in the net probability that an animal alive in any other pre-stratum ($s=a+1$) at the time of banding in year i will survive and be present in pre-stratum u at the time of banding in year $i+1$. Both sets of parameters include the net probability that an animal alive in pre-stratum s at the time of banding in year i will be alive and present in the other pre-strata ($u=a+1$) at the time of banding in year $i+1$. For example, from Figure 4.4c, the survival parameter $S_2^{12}=0.10$ implies that, of the animals alive in pre-stratum 1 at the time of banding in year 2, 10% will survive and be present in pre-stratum 2 at the time of banding in year 3. Similarly, $S_2^{13}=0.10$ implies that 10% of the animals present in pre-stratum 1 at the time of banding in year 2 will be alive and present in other pre-strata outside the experiment at the time of banding in year 3, and $S_2^{32*}=0.10$ implies that 10% of the animals present in the other pre-strata at the time of banding in year 2, will be alive and present in pre-stratum 2 at the time of banding in year 3. The net survival parameters are assumed to be independent of the previous migration history of the animals.

Since migration rates from the pre-strata to the post-strata are already part of the model, why were migration rates from the post-strata back to the pre-strata not included? First, such an approach would require the individual post-stratum survival rates and the post-to pre-stratum migration rates for all post-strata, including an extra post-stratum ($t=b+1$) representing all other post-strata where recoveries do not occur. Introducing all these parameters will make the model even more complex, and the individual components will likely be nonidentifiable. Second, the net survival rates are themselves often of interest and in fact are a convolution of the pre- to post-strata migration rates, the post-stratum specific survival rates, and the post- to pre-strata migration rates.

The expected number of recoveries (or equivalently the cell probabilities) can be evaluated as shown in Figure 4.4c. The computation of the expected number of recoveries that takes place in the immediate year after release is straightforward. In this case, any migration among the pre-strata of the newly banded animals has not yet taken place. For example, the expected number of recoveries from animals released in pre-stratum 1 in year 1 and recovered in post-stratum 1 in year 1, $E(R^{11}_{11})$ is computed as:

$$E[\ R^{11}_{11}\ ] = N^{1}_{1} \times M^{11}_{1} \times f^{11}_{1} = 1000 \times 0.30 \times 0.04 = 12.0.$$

This implies that, of the 1000 animals released in pre-stratum 1, 30% decided to migrate to post-stratum 1, and of these 300 animals

(1000x0.30), 4% were recovered. Similarly:

$$E[\,R_{11}^{12}\,] = N_1^1 \times M_1^{12} \times f_1^{12} = 1000 \times 0.40 \times 0.06 = 24.0.$$

$$E[\,R_{11}^{13}\,] = N_1^1 \times M_1^{13} \times f_1^{13} = 1000 \times 0.20 \times 0.04 = 8.0.$$

Note that only 90% of the animals ($M_1^{11}+M_1^{12}+M_1^{13} = 0.30+0.40+0.20$) decided to migrate to post-strata 1...3; the remaining 10% migrated to other post-strata where no recoveries occur.

The computation of the expected number of recoveries is more complex in the second and subsequent years after release, since the animals released in a given pre-stratum may migrate to other pre-strata before being recovered. For example, the expected number of animals released in pre-stratum 1 in year 1 and recovered in post-stratum 1 in year 2, $E[R_{12}^{11}]$, is computed as a convolution of migration and survival after release in year 1 from pre-stratum 1 to pre-strata 1 and 2 (where banding occurred), and to pre-stratum 3 (representing all other pre-strata where banding does not occur), and the migration and recovery rates from these pre-strata to the post-stratum in year 2:

$$\begin{aligned} E[R_{12}^{11}] &= N_1^1 S_1^{11} M_2^{*11} f_2^{*11} + N_1^1 S_1^{12} M_2^{*21} f_2^{*21} + N_1^1 S_1^{13} M_2^{*31} f_2^{*31} \\ &= 1000 \times 0.50 \times 0.30 \times 0.04 + \\ &\ 1000 \times 0.10 \times 0.40 \times 0.05 + \\ &\ 1000 \times 0.10 \times 0.20 \times 0.03 \\ &= 6.0 + 2.0 + 0.6 = 8.6. \end{aligned}$$

These are more easily expressed in terms of matrices, in which case $E[R_{12}^{11}]$ is the $(1,1)^{th}$ element of the matrix product $\mathbf{D}(\boldsymbol{N}_1)\boldsymbol{S}_1(\boldsymbol{M}_2^* \mathbf{x}\ \boldsymbol{f}_2^*)$.

In subsequent years, additional terms must be computed representing the migration among pre-strata between release and recovery. For example, the expected number of recoveries in year 3 from those released in year 1 is computed as:

$$E[R_{13}] = D(N_1)S_1S^*_2\ (M^*_3 \times f^*_3).$$

The usual matrix product $(S_1S^*_2)$ computes the movement rates among pre-strata between the time of banding in years 1 and 3. The computation of individual elements is too tedious to be illustrated in detail.

4.5 INFERENCE USING ORDINARY BAND-RECOVERY DATA

In the Non-Fidelity Model with ordinary band-recovery data, there are $(a+1)bl$ migration parameters to the post-strata (M^*_i), $(a+1)bl$ band-recovery parameters (f^*_i), and $(a+1)(a+1)(l-1)$ survival parameters (S^*_i) for a total of $(a+1)(2bl+(a+1)(l-1))$ parameters. Because of the convolutions present in the expressions for the multinomial cell probabilities, the MSS is the entire set of observable counts, i.e., MSS=$\{R^{st}_{ij}$, $i=1...k$, $j=i...l$, $s=1...a$, $t=1...b\}$ with no reduction in dimensionality. As well, the complex structure of the likelihood makes it difficult to state explicitly a set of identifiable parameters; however, Figure 4.4b gives some insight into which parameters are confounded. As in the Partial-Fidelity Model with ordinary band-recovery data, the post-stratum migration rates and the band-recovery rates are confounded since only the products $M^{st}_i f^{st}_i$ or $M^{*st}_i f^{*st}_i$ appear in the likelihood. As well, confounding will take place between the pre-stratum survival, post-stratum migration, and the band-recovery rates in years $j=k+1...l$ since the elements of the matrix products $S^*_kS^*_{k+1}...S^*_{j-1}(M^*_j \times f^*_j)$ or $S_kS_{k+1}...S_{j-1}(M_j \times f_j)$ always appear together in the likelihood.

Of more serious concern, is the presence of parameters for the migration of the animals to and from pre-strata where no banding takes place, i.e., the last row of $\boldsymbol{M}_i^*$, $\boldsymbol{f}_i^*$, and $\boldsymbol{S}_i^*$, and the last column of $\boldsymbol{S}_i^*$ and $\boldsymbol{S}_i$. It is difficult, in the general case, to untangle the effects of the convolutions and these extra parameters upon the identifiability of the parameters. For example, consider the second year of recoveries of Figure 4.4b. Let the product $\boldsymbol{M}_2 \times \boldsymbol{f}_2$ be represented by θ_2, i.e., $\theta_2^{st} = M_2^{st} f_2^{st}$. Clearly, θ_2 is identifiable since a simple estimator is $\tilde{\theta}_2 = \boldsymbol{R}_{22} \div \boldsymbol{N}_2\mathbf{1}'$. Now, consider a moment estimator based upon $\boldsymbol{R}_{12}$. The first a rows of $\boldsymbol{M}_2^* \times \boldsymbol{f}_2^*$ are estimated by $\tilde{\theta}_2$. The method of moments will then lead to ab nonlinear equations (the number of elements in $\boldsymbol{R}_{12}$) in $a(a+1)+b$ unknowns (the number of elements in $\boldsymbol{S}_1$, plus the number of elements in the last row of $\boldsymbol{M}_2^* \times \boldsymbol{f}_2^*$). Depending upon the choice of a and b, the system of equations will have no solutions, one solution, or an infinite number of solutions; the last possibility would indicate additional problems of non-identifiability. The maximum likelihood estimators of the identifiable parameters must be determined numerically.

Hence, as in the Partial- and Complete-Fidelity Models, ordinary band-recovery data are inadequate for inference in the Non-Fidelity Model. The migration rates to the post-strata are confounded with the band-recovery rates. The survival rates may be estimated under certain circumstances depending upon the choice of the number of pre-strata in which banding occurs, and the number of post-strata in which recoveries occur. The experimental design must again be modified to allow full inference on all parameters.

4.6. MODIFICATIONS TO THE EXPERIMENTAL DESIGN

As in the Partial- and Complete-Fidelity Models, the experimental design must be modified in order to estimate all the parameters of the model.

The confounding of the pre- to post-stratum migration and post-stratum recovery rates can be resolved, as in previous models, by obtaining additional live sightings of the animals in the post-strata. The number of animals that are either: recovered and sighted; recovered but not sighted; and sighted without being recovered can be used to estimate the sighting and band-recovery rates, and consequently, to estimate the pre- to post-stratum migration rates from pre-strata where banding occurs (i.e., $\boldsymbol{f}_i$ and $\boldsymbol{M}_i$). As in the Partial-Fidelity Model, high sighting rates will be necessary to obtain estimates with good precision. The MLEs are not available in closed form and must be determined numerically.

However, these additional sightings in the post-strata do not resolve the problem of estimating the migration parameters from the other pre-strata where recoveries do not occur, nor the migration rates among the pre-strata. These parameters may be estimated in the general case by obtaining additional live sightings in the pre-strata at the time of banding. These sightings can be used to estimate the migration rates among the pre-strata using method analogous to Arnason (1972, 1973), and Seber (1982).

The use of additional sightings in both the pre- and post-strata introduces a large number of new parameters for the sighting rates making the model more complex to formulate and difficult to use. It is likely more cost-effective to employ radio-telemetry devices with a near 100% detectability in the pre- or post-strata. Note that it is not necessary to continuously track the animal; all that is required is that if the animal is present in the pre- or post-stratum, then there is a high probability that it will be detected. (This is very similar to employing sightings in the pre- or post-strata except that radio-telemetry devices are easier to 'sight'.) As a result, more complete movement histories for each animal are obtained and fewer animals need to be tagged with the devices. Some information will be missing if the animal migrates to post-strata or to pre-strata where no sampling effort takes place and the models for such data will be similar to the capture-recapture formulation of Arnason (1972, 1973) and Seber(1985). If the monitoring rates are close to 100% with only a small percentage of temporary out-migrations, the model can be approximated by a Markov-chain model in which case inference is particularly straightforward (Bartlett, 1958; Basawa and Rao, 1980). For this reason, a detailed discussion of inferences using this experimental design is not pursued.

4.7 SUMMARY

The Non-Fidelity Model is more complex than the Partial- or Complete-Fidelity Models because of possible temporary out-migration of animals to pre-strata where no banding takes place. Not surprisingly, ordinary band-recovery data are inadequate for inference in the Non-Fidelity Model. The migration rates to the post-strata and the band-recovery rates in the post-strata are confounded. Because of the complexity of the model formulation, it is difficult to state explicitly which survival rates are identifiable; this depends upon the number of pre-strata and post-strata where sampling effort takes place. Modifications to the experimental design, with additional live sightings in the post-strata, can be used to estimate the post-stratum migration rates; additional sightings in the pre-strata at banding time will be required to estimate the migration rates among pre-strata. Since a large experimental effort may be required, it may be more advantageous to use radio-telemetry devices and ensure that a high proportion of tagged animals that are alive and present in a pre- or post-stratum are detected.

A key assumption of this model is that migration patterns in one year are completely independent of the migration history in previous years. This assumption will not be valid for animal species that exhibit some degree of homing behavior and can only be tested if live sightings or telemetry data is available. In many cases, such tests are expected to have low power because of small sample sizes.

Chapter 5

The Internal-Transfer Model

Summary

In the Internal-Transfer Model, interest focuses upon the rate of interchange of the animals among a set of strata (e.g., among pre-strata) from banding time to banding time; other migrations (e.g., to post-strata) are ignored. Ordinary band-recovery data are theoretically adequate for infererence in this model. The model formulation is a simple matrix extension of the formulation in a simple band-recovery experiment. However, estimation is more difficult because of the convolution of parameters between release and recovery and this convolution causes estimates of the survival/migration parameters to have low precision with the individual parameters being, for practical purposes, nonidentifiable. The definition of the derived parameters of relative emigration, relative immigration, relative harvest derivation, and overall net survival must be modified since the concepts of pre- and post-strata are no longer used. Modifications to the experimental design by obtaining additional sightings at banding time or using radio-telemetry devices are discussed. With additional sightings at banding time, the model corresponds, in its migration/survival components, to that of Arnason (1972). This correspondence is developed, leading to more efficient estimators of these parameters.

Chapter 5
The Internal-Transfer Model

5.1 INTRODUCTION

In the Internal-Transfer Model, interest focuses upon the rates of interchange among a set of strata. For example, birds may be banded in their breeding areas, recoveries also occur in the breeding areas, and interest focuses upon the rates of interchange among the breeding areas from year to year. The concepts of pre- and post-strata are not meaningful since the releases and recoveries occur in the same set of strata. In a band-recovery context, animals are released at a point in time, but recoveries typically occur over the entire time period between two successive releases. Animals are tagged so that their individual histories of release and recovery can be recorded.

This model has been considered in a capture-recapture context by previous authors. Chapman and Junge (1956) and Darroch (1961) first considered the general problem of migration from pre- to post-strata between two sample times without mortality. In their formulation, animals are captured at the first sample time and released. Recaptures at the second sample time are used to estimate the net migration rates (including mortality) from the pre- to the post-strata. If mortality is present, then restrictions on the mortality rates are imposed to allow identification of the parameters. If the second sample is taken in the same set of strata as the first sample, then their models are an example of an Internal-Transfer Model in a capture-recapture context with only two sample times. Arnason (1972, 1973) and Seber (1982, p. 555) extended these models to the case of more than two sampling times and no restrictions on mortality, but remained within the capture-recapture setting. They compared the set of animals seen in years i and $i+2$ to those seen in years i and $i+1$, and seen in years $i+1$ and $i+2$ to estimate the migration rates among the strata between years i and $i+1$. The differences between these models and the model considered in this chapter are that: band recoveries are allowed to occur over the entire year between banding times, not just at a point in time; and an animal may be seen at most twice, at release and recovery, rather than being seen possibly at every sampling time. For exploited populations, the formulation in this chapter may be more pertinent.

In some cases, the Internal-Transfer Model can be viewed as a compartment-system model with aggregate data (e.g., Kalbfleisch, Lawless, and Vollmer, 1983; Kodell and Matis, 1976). In these models, it is assumed: that sampling takes place at a point in time; that all marked particles in a compartment are counted at a sampling time; and that it is impossible to follow the movements of individual particles over time since all particles are homogeneous without unique labels (i.e., only aggregate data on the total number of particles in each compartment at each time point are available). In the Internal-Transfer Model considered in this Chapter, recoveries take place over a period of time, only a sample of animals present in a stratum are recovered, and some information is available about the movement of individual animals since the strata of release and recovery are known.

The Internal-Transfer Model considered here also differs from Markov-Chain models (e.g., Bartlett, 1955; Bawawa and Rao, 1980) where the location of every individual at each sampling time is recorded. In this Chapter, the location of the animal is known only at the time of release and recovery; the intermediate movements of individuals is unknown.

While ordinary band-recovery data (without sightings) is not adequate for inference about all parameters in the Partial-, Complete- and Non-Fidelity Models, it is theoretically adequate in the Internal-Transfer Model. The model formulation is a simple matrix extension to the model formulation in simple band-recovery experiments. However, estimation is more difficult because of the convolution of parameters between release and recovery and the typically low (about 3-10%) band-recovery rates. These cause estimates of the survival/migration parameters to have low precision and the individual survival/migration parameters to be almost nonidentifiable. As well, the definition of the derived parameters of relative emigration, relative immigration, relative harvest derivation, and overall net survival must be modified since the concepts of pre- and post-strata are no longer meaningful.

I begin with a discussion of the assumptions that are made in the Internal-Transfer Model. Next, I define and interpret a set of fundamental parameters, and then use these parameters to build a stochastic model. The modifications to the definition of the derived parameters are then examined. Inference under this model is described, and a numerical example illustrating the concepts is constructed. Finally, I discuss how inferences in this model can be improved through modifications to the experimental design.

5.2 NOTATION

Bold face letters will be used to represent matrices and vectors. Elements within a matrix or vector will be identified through the use of superscripts.

Matrix Operations and special matrices

$\mathbf{D}(X)$ transforms the column vector $\mathbf{X}$ into a matrix by placing the elements of $\mathbf{X}$ along the diagonal.

If $\mathbf{N} = \begin{bmatrix} 1000 \\ 1000 \end{bmatrix}$, then $\mathbf{D}(\mathbf{N}) = \begin{bmatrix} 1000 & 0 \\ 0 & 1000 \end{bmatrix}$

$\mathbf{x}, \div$ element by element multiplication or division.

If $\mathbf{A} = \begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix}$ and $\mathbf{B} = \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix}$ then

$\mathbf{A} \times \mathbf{B} = \begin{bmatrix} 5 & 12 \\ 21 & 32 \end{bmatrix}$ and $\mathbf{A} \div \mathbf{B} = \begin{bmatrix} 0.200 & 0.333 \\ 0.426 & 0.500 \end{bmatrix}$.

$\mathbf{1}$ a column vector of all ones.

$\mathbf{I}$ the identity matrix.

$\mathbf{J}$ a square matrix of all ones.

Fundamental Parameters

a the number of strata in which releases and recoveries take place

k the number of years of releases

l the number of years of recoveries

$\mathbf{N}_i$ an a x 1 vector whose s^{th} element (N_i^s) represents the number of animals released in stratum s in year i.

$\mathbf{N}_i^*$ an a x 1 vector whose s^{th} element (N_i^{s*}) represents the population size in stratum s at the time of banding in year i.

$\boldsymbol{f}_i$ an a x a matrix whose $(s,t)^{th}$ element (f_i^{st}) represents the probability that an animal present in stratum s at the time of banding in year i will be recovered in stratum t during the next year.

$\boldsymbol{S}_i$ an a x a matrix whose $(s,t)^{th}$ element (S_i^{st}) represents the probability that an animal alive in stratum s at the time of banding in year i will survive to and be present in stratum t at the time of banding in year $i+1$.

λ_i an a x a matrix whose $(s,t)^{th}$ element (λ_i^{st}) represents the band-reporting rate of animals alive in stratum s at the time of banding in year i and recovered in stratum t between the time of banding in year i and year $i+1$.

Derived Parameters

ρ_i an a x a matrix whose $(s,t)^{th}$ element (ρ_i^{st}) represents the total probability that an animal released in year i in stratum s will be recovered at some time during the rest of the experiment in stratum t.

$\rho_i = \boldsymbol{f}_i + \boldsymbol{S}_i\boldsymbol{f}_{i+1} + \ldots + \boldsymbol{S}_i\boldsymbol{S}_{i+1}\ldots\boldsymbol{S}_{l-1}\boldsymbol{f}_l$.

$\boldsymbol{m}_i$ an a x a matrix whose $(s,t)^{th}$ element (m_i^{st}) represents the relative emigration rate of animals alive in stratum s to stratum t between the time of banding in year i and year $i+1$.

$\mathbf{m}_i = \mathbf{S}_i + \mathbf{S}_i\mathbf{J}$

$\boldsymbol{I}_i$ an a x a matrix whose $(s,t)^{\text{th}}$ element (I_i^{st}) represents the relative immigration rate of animals into stratum t between the time of banding in year i and year $i+1$ from those animals alive in stratum s at the time of banding in year i.

$\boldsymbol{I}_i = \mathbf{D}(\boldsymbol{N}_i^*)\boldsymbol{S}_i + \mathbf{JD}(\boldsymbol{N}_i^*)\boldsymbol{S}_i.$

$\boldsymbol{D}_i$ an a x a matrix whose $(s,t)^{\text{th}}$ element (D_i^{st}) represents the relative harvest-derivation rate in stratum t between the time of banding in year i and the time of banding in year $i+1$ from the animals alive in stratum s at the time of banding in year i.

$\boldsymbol{D}_i = \mathbf{D}(\boldsymbol{N}_i^*)(\boldsymbol{f}_i+\boldsymbol{\lambda}_i) + \mathbf{JD}(\boldsymbol{N}_i^*)(\boldsymbol{f}_i+\boldsymbol{\lambda}_i)$

$\boldsymbol{S}_i^\bullet$ an a x 1 vector whose s^{th} element $(S_i^{s\bullet})$ represents the overall net probability that an animal alive in stratum s at the time of banding in year i will be alive and present in one of strata $1...a$ at the time of banding in year $i+1$.

$\boldsymbol{S}_i^\bullet = \boldsymbol{S}_i\boldsymbol{1}.$

Statistics

$\boldsymbol{R}_{ij}$ an a x a matrix whose $(s,t)^{\text{th}}$ element (R_{ij}^{st}) is the number of animals released in stratum s in year i that are recovered in stratum t in year j.

$\boldsymbol{R}_{i\bullet}$ an a x a matrix whose $(s,t)^{\text{th}}$ element $(R_{i\bullet}^{st})$ is the total number of animals released in stratum s in year i that are recovered in stratum t at any time at or after year i.

$$\boldsymbol{R}_{i\bullet} = \sum_{j=i}^{l} \boldsymbol{R}_{ij}$$

$\boldsymbol{R}_{\cdot j}$ an $a \times a$ matrix whose $(s,t)^{\text{th}}$ element $(R^{st}_{\cdot j})$ is the total number of animals released in stratum s in this or previous years that are recovered in stratum t in year j.

$$\boldsymbol{R}_{\cdot j} = \sum_{i=1}^{\min(j,k)} \boldsymbol{R}_{ij}$$

$\boldsymbol{T}_i$ an $a \times a$ matrix whose $(s,t)^{\text{th}}$ element (T^{st}_{i}) is the total number of animals released in stratum s and recovered in stratum t that were known to be alive in year i.

$$\boldsymbol{T}_1 = \boldsymbol{R}_{1\cdot}$$

$$\boldsymbol{T}_i = \boldsymbol{T}_{i-1} + \boldsymbol{R}_{i\cdot} - \boldsymbol{R}_{\cdot i-1} \qquad i = 2\ldots k$$

$$\boldsymbol{T}_i = \boldsymbol{T}_{i-1} \qquad\qquad - \boldsymbol{R}_{\cdot i-1} \qquad i = k+1\ldots l.$$

$\boldsymbol{Z}_i$ an $a \times a$ matrix whose $(s,t)^{\text{th}}$ element (Z^{st}_{i}) is the total number of animals released in stratum s and recovered in stratum t that were known to be alive after year i.

$$\boldsymbol{Z}_i = \boldsymbol{T}_i - \boldsymbol{R}_{\cdot i} = \boldsymbol{T}_{i+1} - \boldsymbol{R}_{i+1\cdot}$$

5.3 ASSUMPTIONS

The usual assumptions for band-recovery models as outlined Section 1.3.3 are also made here. As well, it is assumed that:

- no animals migrate temporarily to a stratum where recoveries and releases do not occur, returning after one or more years of absence. Animals may, of course, migrate out of the sampled strata permanently; such losses are indistinguishable from mortality. If temporary migration can occur, then, as found in the Non-Fidelity Model, inferences will be possible only under certain experimental combinations of the number of strata in which banding and releases occur, and the number of years of releases and recovery.

- all animals behave independently with respect to migration and recovery. Hence, it is assumed that flocking or schooling of animals after release does not occur, or does not influence the migration pattern of the animal.
- animals behave in a Markovian fashion in each year, i.e., the current migration patterns do not depend upon previous migration choices. This is a similar assumption to that made in the Partial- and Non-Fidelity Models.
- independent estimates of the stratum population sizes and the band-reporting rates are available along with estimates of their standard errors.

Note that no assumptions are made about the way in which animals move from stratum s in year i to stratum t in year $i+1$. The animals may move directly between the two strata or may make several intermediate movements to other strata before eventually reaching stratum t in year $i+1$. Hence, the $\boldsymbol{S}_i$ are net movement rates. In general, the actual number of migrations from one stratum to another is not uniquely determined by the net rates, e.g., a net migration of 2 animals from stratum 1 to stratum 2 may be the results of 5 animals moving from stratum 1 to stratum 2, and 3 animals moving from stratum 2 to 1; or a result of 8 animals moving from stratum 1 to stratum 2 and 6 animals moving from stratum 2 to stratum 1. More generally, the net migration rates in a Markov process compartment model are uniquely determined by the instantaneous migration intensities (or, equivalently, the absolute migration rates), but the converse is not necessarily true (Cuthbert, 1973).

5.4 THE STOCHASTIC MODEL

5.4.1 INTERPRETATION OF THE FUNDAMENTAL PARAMETERS

The band-recovery parameters f_i^{st} are interpreted as the probability that an animal alive in stratum *s* at the time of banding in year *i* will be recovered in stratum *t* between the time of banding in year *i* and the time of banding in year *i+1*. This parameter includes: a net migration component between stratum *s* and stratum *t*; and the usual harvest, band-retrieval, and band-reporting components of ordinary band-recovery models. These parameters are indexed by both stratum *s* and stratum *t* since it is likely that the migration components to stratum *t* will differ depending upon the stratum of origin even if subsequent harvest, band-retrieval, and band-reporting rates in stratum *t* are homogeneous. These parameters are assumed not to depend upon the migration patterns prior to year *i*.

An important implication is that the band-recovery rates are assumed to be equal for all animals that leave stratum s in year i and are recovered in stratum t in the next year, regardless of the route they choose. For example, birds that migrate from breeding area 1 to breeding area 2 via different wintering areas are assumed to have equal band-recovery rates in breeding area 2. If recoveries are obtained by hunting, all animals that migrate between two strata should arrive at the same time relative to the hunting season. If one subset arrives at the beginning of the season and another subset arrives halfway through the season (because of a longer migration route), the band-recovery rates will not be the same. If the rates are heterogeneous among subsets of animals migrating between strata s and t, then f_i^{st} can be thought of as an average rate. The multinomial model will no longer be valid; however, if the degree of heterogeneity is small, the results will still be (approximately) valid. If there is only one migration route between the two strata, or if a large majority of animals choose one route, this assumption is more likely to be (approximately) satisfied.

The survival/migration parameters, S_i^{st}, are interpreted as the probability that an animal alive in stratum s at the time of banding in year i will be alive and present in stratum t at the time of banding in year $i+1$. These parameters include a mortality component and a migration component. All permanent migration to strata where no recoveries or releases occur is indistinguishable from, and is treated as a another form of, mortality. It is assumed that these rates do not depend upon migration patterns prior to year i.

Again an implication is that the survival/migration rates are applicable to all animals regardless of the route chosen between strata. If there is considerable heterogeneity among subsets, then S_i^{st} can be thought of as an average survival/migration rate; however, as before, the multinomial model will no longer be valid.

Formal migration parameters, separate from the survival and band-recovery parameters, have not been introduced since it is impossible to achieve a meaningful separation of the survival and migration components unless the individual animal's behavior is modelled. Even if it is assumed that animals migrate directly between strata, it is still impossible to separate the migration and mortality rates. For example, consider the case with two strata. The transition rates among strata will consist of an ideal migration component (assuming that all birds survived) and a survival component for each group of animals choosing a specific migration route. Hence the net transition rate:

$$\mathbf{S} = \begin{bmatrix} 0.6 & 0.3 \\ 0.2 & 0.7 \end{bmatrix}$$

could be found as the element by element product of the absolute migration rates ($\mathbf{M}$) and the survival rates (ϕ), i.e.,:

$$\mathbf{S} = \mathbf{M} \times \phi.$$

For example,

$$\begin{bmatrix} 0.6 & 0.3 \\ 0.2 & 0.7 \end{bmatrix} = \begin{bmatrix} 0.65 & 0.30 \\ 0.22 & 0.75 \end{bmatrix} \times \begin{bmatrix} 0.923 & 1.000 \\ 0.909 & 0.933 \end{bmatrix}.$$

This would imply that 65% of the animals currently in stratum 1 decided to remain in stratum 1, 30% decided to migrate to stratum 2, and 5% decided to migrate (permanently) to other strata. Of those animals that decide to remain in stratum 1, 92.3% survive to the next year; of those animals that decide to migrate to stratum 2, 100% survive the journey. Unfortunately, there is an infinite number of pairs of $\mathbf{M}$ and ϕ that lead to the same final net transition matrix ($\mathbf{S}$). Moreover, there are problems associated with the timing of the migration relative to release and recovery times. Using the above example, if the migration does not occur immediately after banding time, how shall the mortality that occurs between the time of banding and the migration be apportioned?

5.4.2 THE LIKELIHOOD FUNCTION

The number of animals that are released in stratum s in year i and recovered in stratum t in year j can be displayed using matrices as shown in Figure 5.4.2a. Note the resemblance to the display of a simple band-recovery experiment (Brownie *et al., 1985*, pp. 13-17), except that now each element of the table is a matrix or a vector.

Under the assumptions given earlier, the number of animals released in stratum s in year i and recovered in stratum t in year j ($j=i\ldots l$, $t=1\ldots a$) can be modelled as a multinomial distribution. For example, from Figure 4.2a, the elements $\{R^{11}_{11}, R^{12}_{11}, R^{11}_{12}, R^{12}_{12}, R^{11}_{13}, R^{12}_{13}, R^{11}_{14}, R^{12}_{14}\}$ have a multinomial distribution with index N^1_1. Animals that are released in different strata in the same year are assumed to be independent of each other. Hence, the elements $\{R^{21}_{11}, R^{22}_{11}, R^{21}_{12}, R^{22}_{12}, R^{21}_{13}, R^{22}_{13}, R^{21}_{14}, R^{22}_{14}\}$ have a multinomial distribution with index N^2_1 independent of the previous set. Releases in successive years are also assumed to be independent.

The likelihood can then be written as a simple product of multinomial distributions; however, the individual probabilities are convolutions of the intermediate survival/migration rates and the band-recovery rates. The individual probabilities can be easily computed using matrices as illustrated in Figure 5.4.2b. Again note the similarity of the form of the cell probabilities to those from simple band-recovery experiments (Brownie *et al.*, 1985, pp. 13-17). The expected number of recoveries can then be computed from the elements of Figure 5.4.2b and are shown in Figure 5.4.2c using values of the parameters as shown at the foot of Figure 5.4.2c.

Figure 5.4.2a

Symbolic representation of the number of animals released in stratum *s* in year *i* and recovered in stratum *t* in year *j* in the case of *k=3* years of releases and *l=4* years of recoveries

Year Released	Number Released	Number recovered by year 1	2	3	4
1	$\mathbf{N}_1$	$\mathbf{R}_{11}$	$\mathbf{R}_{12}$	$\mathbf{R}_{13}$	$\mathbf{R}_{14}$
2	$\mathbf{N}_2$		$\mathbf{R}_{22}$	$\mathbf{R}_{23}$	$\mathbf{R}_{24}$
3	$\mathbf{N}_3$			$\mathbf{R}_{33}$	$\mathbf{R}_{34}$

$\mathbf{N}_i$ are $a \times 1$ vectors $\begin{bmatrix} N_1^1 \\ N_1^2 \\ \cdot \\ \cdot \\ \cdot \\ N_1^a \end{bmatrix}$ and $\mathbf{R}_{ij}$ are $a \times a$ matrices $\begin{bmatrix} R_{ij}^{11} & R_{ij}^{12} & \cdots & R_{ij}^{1a} \\ R_{ij}^{21} & R_{ij}^{22} & \cdots & R_{ij}^{2a} \\ \vdots & & & \vdots \\ R_{ij}^{a1} & R_{ij}^{a2} & \cdots & R_{ij}^{aa} \end{bmatrix}$

The number of animals never seen is not shown, but is easily obtained by subtraction.

Figure 5.4.2b

The probabilities that an animal released in stratum *s* in year *i* is recovered in stratum *t* in year *j* in the case of $k=3$ years of releases and $l=4$ years of recoveries

Year Released	Number Released	Probabilities of recovery by year 1	2	3	4
1	$\mathbf{N}_1$	$\mathbf{f}_1$	$\mathbf{S}_1\mathbf{f}_2$	$\mathbf{S}_1\mathbf{S}_2\mathbf{f}_3$	$\mathbf{S}_1\mathbf{S}_2\mathbf{S}_3\mathbf{f}_4$
2	$\mathbf{N}_2$		$\mathbf{f}_2$	$\mathbf{S}_2\mathbf{f}_3$	$\mathbf{S}_2\mathbf{S}_3\mathbf{f}_4$
3	$\mathbf{N}_3$			$\mathbf{f}_3$	$\mathbf{S}_3\mathbf{f}_4$

$$\mathbf{N}_i \text{ are } a \times 1 \text{ vectors } \begin{bmatrix} N_1^1 \\ N_1^2 \\ \vdots \\ N_1^a \end{bmatrix}.$$

$$\mathbf{f}_i \text{ are } a \times a \text{ matrices } \begin{bmatrix} f_{ij}^{11} & f_{ij}^{12} & \cdots & f_{ij}^{1a} \\ f_{ij}^{21} & f_{ij}^{22} & \cdots & f_{ij}^{2a} \\ \vdots & & & \vdots \\ f_{ij}^{a1} & f_{ij}^{a2} & \cdots & f_{ij}^{aa} \end{bmatrix}$$

$$\mathbf{S}_i \text{ are } a \times a \text{ matrices } \begin{bmatrix} S_{ij}^{11} & S_{ij}^{12} & \cdots & S_{ij}^{1a} \\ S_{ij}^{21} & S_{ij}^{22} & \cdots & S_{ij}^{2a} \\ \vdots & & & \vdots \\ S_{ij}^{a1} & S_{ij}^{a2} & \cdots & S_{ij}^{aa} \end{bmatrix}$$

The probability of never recovering an animal is not shown, but is easily obtained by subtraction.

Figure 5.4.2c

A numerical example of the expected number of recoveries in the case of $a=2$ strata, $k=3$ years of releases, and $l=4$ years of recoveries using the parameter values given at the foot of the table.

Year Released	Number Released	Expected Number of Recoveries by year			
		1	2	3	4
1	$\begin{bmatrix} 1000 \\ 1000 \end{bmatrix}$	$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 24.0 & 30.0 \end{bmatrix}$	$\begin{bmatrix} 18.3 & 21.3 \\ 17.4 & 21.0 \end{bmatrix}$	$\begin{bmatrix} 13.7 & 16.2 \\ 12.8 & 15.3 \end{bmatrix}$
2	$\begin{bmatrix} 1000 \\ 1000 \end{bmatrix}$		$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 21.0 & 26.0 \end{bmatrix}$	$\begin{bmatrix} 18.3 & 21.3 \\ 15.3 & 18.4 \end{bmatrix}$
2	$\begin{bmatrix} 1000 \\ 1000 \end{bmatrix}$			$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 21.0 & 26.0 \end{bmatrix}$

where $\boldsymbol{f}_1=\boldsymbol{f}_2=\boldsymbol{f}_3=\boldsymbol{f}_4= \begin{bmatrix} 0.03 & 0.03 \\ 0.03 & 0.04 \end{bmatrix}$

$$\boldsymbol{S}_1= \begin{bmatrix} 0.50 & 0.30 \\ 0.20 & 0.60 \end{bmatrix} \quad \boldsymbol{S}_2=\boldsymbol{S}_3= \begin{bmatrix} 0.50 & 0.30 \\ 0.20 & 0.50 \end{bmatrix}$$

$$\boldsymbol{N}_1^*= \begin{bmatrix} 100000 \\ 200000 \end{bmatrix} \quad \boldsymbol{N}_2^*= \begin{bmatrix} 100000 \\ 170000 \end{bmatrix} \quad \boldsymbol{N}_3^*= \begin{bmatrix} 100000 \\ 150000 \end{bmatrix}$$

$$\lambda_1=\lambda_2=\lambda_3= \begin{bmatrix} 0.50 & 0.60 \\ 0.60 & 0.40 \end{bmatrix}$$

The row-wise similarities are caused by assuming that $\boldsymbol{S}_2=\boldsymbol{S}_3$ and $\boldsymbol{f}_1=\boldsymbol{f}_2=\boldsymbol{f}_3=\boldsymbol{f}_4$.

The parameters $\boldsymbol{S}_3$ and $\boldsymbol{f}_4$ are not individually identifiable; only their product may be estimated.

It is necessary that $\boldsymbol{N}_2^* > \boldsymbol{N}_1^{*\prime}\boldsymbol{S}_1$ and $\boldsymbol{N}_3^* > \boldsymbol{N}_2^{*\prime}\boldsymbol{S}_2$ due to immigration from other strata and natural increases in the populations.

For example, of the 1000 animals released in stratum 2 in year 1 (N_1^2), the expected number of animals recovered in stratum 1 in year 1 is:

$$E(R_{11}^{21}) = N_1^2 \times f_1^{21} = 1000 \times 0.03 = 30.0.$$

Similarly, the expected number of these animals recovered in stratum 2 in year 1 is computed as:

$$E(R_{11}^{22}) = N_1^2 \times f_1^{22} = 1000 \times 0.04 = 40.0.$$

The situation is more complicated for those animals recovered in year 2. The expected number of animals released in stratum 2 in year 1 and recovered in stratum 1 in year 2 is composed of the expected number of animals that remained in stratum 2 in year 1 and then migrated to and were recovered in stratum 1 in year 2, plus the expected number of animals that migrated from stratum 2 to stratum 1 in year 1, and then remained in and were recovered in stratum 1 in year 2:

$$\begin{aligned} E(R_{12}^{21}) &= N_1^2 \times S_1^{22} \times f_2^{21} + N_1^2 \times S_1^{21} \times f_2^{11} \\ &= 1000 \times 0.6 \times 0.03 \ + 1000 \times 0.2 \times 0.03 \ = 18 + 6 = 24. \end{aligned}$$

Similarly,

$$\begin{aligned} E(R_{12}^{22}) &= N_1^2 \times S_1^{22} \times f_2^{22} + N_1^2 \times S_1^{21} \times f_2^{12} \\ &= 1000 \times 0.6 \times 0.04 \ + 1000 \times 0.2 \times 0.03 \ = 24 + 6 = 30. \end{aligned}$$

Of course, this is easily expressed in terms of matrices:

$$\begin{aligned} E(\boldsymbol{R}_{12}) &= \boldsymbol{D}(\boldsymbol{N}_1)\ \boldsymbol{S}_1\ \boldsymbol{f}_2 = \begin{bmatrix} R_{12}^{11} & R_{12}^{12} \\ R_{12}^{21} & R_{12}^{22} \end{bmatrix} \\ &= \begin{bmatrix} 1000 & 0 \\ 0 & 1000 \end{bmatrix} \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.6 \end{bmatrix} \begin{bmatrix} 0.03 & 0.03 \\ 0.03 & 0.04 \end{bmatrix} \\ &= \begin{bmatrix} 24.0 & 27.0 \\ 24.0 & 30.0 \end{bmatrix}. \end{aligned}$$

5.4.3 THE DERIVED PARAMETERS

Since the distinction between pre- and post-strata does not exist in the Internal-Transfer Model and since the migration and survival rates cannot be factored from the migration/survival parameters, the derived parameters of relative emigration, relative immigration, relative harvest-derivation, and overall net survival must be defined and interpreted carefully. In particular, they are defined using the net movement of animals from their current stratum at the time of banding in year *i*, and *include* any mortality in year *i*. This differs from the Partial- and Complete-Fidelity Models where a definite pre-stratum existed that did not change after release and where migration rates were free of any mortality component.

5.4.3.1 Relative emigration rates

The relative emigration rates are defined as the relative movement from stratum *s* to stratum *t* between the time of banding in year *i* and year *i+1*, *including any mortality*. Using the parameter values given at the foot of Figure 5.4.2c, the relative emigration rates in year 1 are computed as:

$$
\begin{aligned}
\boldsymbol{m}_1 &= \boldsymbol{S}_1 \div \boldsymbol{S}_1\boldsymbol{J} \\
&= \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.6 \end{bmatrix} \div \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.6 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \\
&= \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.6 \end{bmatrix} \div \begin{bmatrix} 0.8 & 0.8 \\ 0.8 & 0.8 \end{bmatrix} \\
&= \begin{bmatrix} 0.62 & 0.38 \\ 0.25 & 0.75 \end{bmatrix}
\end{aligned}
$$

This implies that, of the animals alive in stratum 1 in year 1 that survive to year 2 and remain in stratum 1 or 2, 62% will remain in and be alive in stratum 1 in year 2, and 38% will migrate to and be alive in stratum 2 in year 2.

5.4.3.2 Relative immigration rates

The relative immigration rates are defined as the relative movement into stratum t by the time of banding in year *i+1* based upon the number of animals alive at the time of banding in year *i*. The stratum population sizes in year *i* are required in order to compute these parameters. Using the parameter values given in Figure 5.4.2c, the relative immigration rates in year 2 are computed as:

$$
\begin{aligned}
\boldsymbol{I}_2 &= \mathbf{D}(\boldsymbol{N}^*_2)\boldsymbol{S}_2 + \mathbf{JD}(\boldsymbol{N}^*_2)\boldsymbol{S}_2 \\
&= \begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.5 \end{bmatrix} + \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.5 \end{bmatrix} \\
&= \begin{bmatrix} 50000 & 30000 \\ 34000 & 85000 \end{bmatrix} + \begin{bmatrix} 84000 & 115000 \\ 84000 & 115000 \end{bmatrix} \\
&= \begin{bmatrix} 0.60 & 0.26 \\ 0.40 & 0.74 \end{bmatrix}
\end{aligned}
$$

This implies that, of the animals alive and present in stratum 2 at the time of banding in year 2 that came from stratum 1 or 2, 26% came from stratum 1 and 74% came from stratum 2 from the previous year.

4.3.3 Relative harvest-derivation rates

The relative harvest derivation rates are defined as the fraction of animals harvested in year *i* that came from each stratum. They require the stratum population sizes and band-reporting rates in year *i*. Using the parameter values given in Figure 5.4.2c, the relative harvest-derivation rates in year 2 are computed as:

$$
\boldsymbol{D}_2 = \mathbf{D}(\boldsymbol{N}^*_2)\,(\boldsymbol{f}_2+\boldsymbol{\lambda}_2) + \mathbf{JD}(\boldsymbol{N}^*_2)\,(\boldsymbol{f}_2+\boldsymbol{\lambda}_2)
$$

$$
\begin{aligned}
= &\begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \left(\begin{bmatrix} 0.03 & 0.03 \\ 0.03 & 0.04 \end{bmatrix} + \begin{bmatrix} 0.5 & 0.6 \\ 0.6 & 0.4 \end{bmatrix} \right) + \\
&\begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \left(\begin{bmatrix} 0.03 & 0.03 \\ 0.03 & 0.04 \end{bmatrix} + \begin{bmatrix} 0.5 & 0.6 \\ 0.6 & 0.4 \end{bmatrix} \right)
\end{aligned}
$$

$$= \begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \begin{bmatrix} 0.06 & 0.05 \\ 0.05 & 0.10 \end{bmatrix} \div \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} 100000 & 0 \\ 0 & 170000 \end{bmatrix} \begin{bmatrix} 0.06 & 0.05 \\ 0.05 & 0.10 \end{bmatrix}$$

$$= \begin{bmatrix} 6000 & 5000 \\ 8500 & 17000 \end{bmatrix} \div \begin{bmatrix} 14500 & 22000 \\ 14500 & 22000 \end{bmatrix}$$

$$= \begin{bmatrix} 0.41 & 0.23 \\ 0.59 & 0.77 \end{bmatrix}$$

This implies that, of the animals harvested in stratum 1 in year 2 that came from stratum 1 or 2, 41% came from stratum 1 and 59% came from stratum 2.

5.4.3.4 Overall net survival rate

This rate is the overall survival rate of animals in stratum s from the time of banding in year i to year $i+1$ regardless of where they migrate, conditional upon the animal migrating to one of strata $1...a$. Migration to other strata is treated as another form of mortality. Using the parameter values from Table 5.2c,

$$\dot{S}_2 = S_2 1$$

$$= \begin{bmatrix} 0.5 & 0.3 \\ 0.2 & 0.5 \end{bmatrix} \begin{bmatrix} 1 \\ 1 \end{bmatrix} = \begin{bmatrix} 0.8 \\ 0.7 \end{bmatrix}$$

This implies that, of the animals in stratum 1 at the time of banding in year 2, 80% survive and are present in either stratum 1 or stratum 2 at the time of banding in year 3. Note that the overall net survival rate in the Internal-Transfer Model is analogous to the total migration rate in the Partial- and Complete-Fidelity Models.

5.4.4 REDUCED MODELS

As always, restrictions can be placed upon the parameters of the general model to obtain reduced models. There are a number of restrictions that may be of biological interest:

- the migration/survival parameters may be constant over time, i.e., $S_1 = S_2 = ... = S_{k-1}$.

- the recovery parameter matrices may be diagonal, i.e., $f_i^{st}=0$ if $s \neq t$. This model is meaningful if the recovery period is short and occurs prior to any mixing of the populations. In this case, the capture-recapture models of Arnason (1972, 1973) may be more useful.
- the band-recovery parameters may be independent of the stratum of origin, i.e., $f_i^{st}=f_i^{\bullet t}$ for all s. This would be meaningful if the recovery period occurs after most migration has taken place and the animals are otherwise indistinguishable in terms of harvest, band-recovery and band-reporting.

The definition and interpretation of the fundamental parameters and the derived parameters remains unchanged in the reduced models.

5.5 **INFERENCE**

5.5.1 ESTIMATION OF THE FUNDAMENTAL PARAMETERS

There are a total of $a^2(k-1)$ survival/migration parameters ($\mathbf{S}_1, \ldots, \mathbf{S}_{k-1}$), a^2k recovery rate parameters ($\mathbf{f}_1, \ldots, \mathbf{f}_k$), and $a^2(l-k)$ confounded parameters representing the product of survival and recovery in years $k+1 \ldots l$ ($\mathbf{S}_k\mathbf{f}_{k+1}, \ldots, \mathbf{S}_k\mathbf{S}_{k+1}\mathbf{S}_{k+2}\ldots\mathbf{S}_{l-1}\mathbf{f}_l$) for a total of $a^2(l+k-1)$ parameters. Again note the resemblance to simple band-recovery experiments where there are $(l+k-1)$ parameters. However, the analogy breaks down when the MSS are extracted from the likelihood. Because of the convolutions of the parameters, the MSS are the set of observed counts $\{R_{ij}^{st}, s=1\ldots a, t=1\ldots a, i=1\ldots k, j=i\ldots l\}$ with no reduction in dimensionality, i.e., the MSS has dimension $a^2(kl-k(k-1)/2)$. Since the dimension of the MSS exceeds the number of parameters, the method of moments used earlier in the Thesis will not necessarily lead to the MLEs. As well, the complex form of the likelihood implies that the MLEs must be found numerically.

A summary of how the MLEs were found using numerical methods is presented in Appendix 5.A. Since the variances and covariances must also be found numerically, it is difficult to give quantitative statements about the precision of the estimates. However, extensive simulations have shown that the precision of the estimated band-recovery rates is comparable to that in simple band-recovery experiments, but the precision of the estimated survival/migration rates is poor. This loss of precision is caused by the convolution of the intermediate survival/migration terms between release and recovery and the generally low band-recovery rates in practise (3-10%) which make it difficult to estimate them precisely. As well, similar to the findings of Kalbfleisch *et al.* (1983) who examined inference in compartmental models using aggregate data, there is a very high correlation among the estimated survival/migration rates which implies that these parameters are nearly nonidentifiable. An illustration of this is presented in the numerical example of Section 5.6.

The methods outlined in Aitchison and Silvey (1958) and Don (1985) and used in the Partial- and Complete-Fidelity Models are used to obtain MLEs when restrictions are placed upon the parameters.

A closed form moment-estimator of the parameters in the full model that is analogous to the estimators in simple band-recovery experiments can be constructed. It is easily shown that:

$$E(R_{i\bullet}) = D(N_i)[\ f_i + S_i f_{i+1} + \ldots + S_i S_{i+1} \ldots S_{l-1} f_l\ ] \qquad i=1\ldots k$$

$$E(T_i) = [\ D(N_1) S_1 \ldots S_{i-1} + D(N_2) S_2 \ldots S_{i-1} + \ldots + I\ ] \times [\ f_i + S_i f_{i+1} + \ldots + S_i S_{i+1} \ldots S_{l-1} f_l\ ] \qquad i=1\ldots k$$

$$E(Z_i) = [\ D(N_1) S_1 \ldots S_{i-1} + D(N_2) S_2 \ldots S_{i-1} + \ldots + I\ ] \times S_i \times [\ f_i + S_i f_{i+1} + \ldots + S_i S_{i+1} \ldots S_{l-1} f_l\ ] \qquad i=1\ldots k$$

$$E(R_{\bullet i}) = [\ D(N_1) S_1 \ldots S_{i-1} + D(N_2) S_2 \ldots S_{i-1} + \ldots + I\ ] \times f_i \qquad i=1\ldots k$$

$$E(R_{\bullet i}) = [\ D(N_1) S_1 \ldots S_{i-1} + D(N_2) S_2 \ldots S_{i-1} + \ldots + I\ ] \times S_k S_{k+1} \ldots S_{i-1} f_i \qquad i=k+1\ldots l$$

which leads to the moment-estimators (assuming all inverses exist):

$$\tilde{f}_i = D(N_i)^{-1} R_{i\bullet} T_i^{-1} R_{\bullet i} \qquad i=1\ldots k$$

$$\tilde{S}_i = D(N_i)^{-1} R_{i\bullet} T_i^{-1} Z_i R_{i+1,\bullet}^{-1} D(N_{i+1}) \qquad i=1\ldots k$$

$$S_k \ldots \tilde{S}_{i-1} f_i = D(N_i)^{-1} R_{k\bullet} T_k^{-1} R_{\bullet i} \qquad i=k+1\ldots l.$$

Although these estimators are simple matrix extensions of the results of Brownie *et al.* (1985, pp.13-17) and can be shown to reduce to the estimators of Arnason (1972) when transferred to a capture-recapture context with three sampling times (Appendix 5B), extensive simulations have shown that these estimators are generally unsatisfactory. They estimate the recovery rates reasonably well, but in many cases the estimates of the survival/migration parameters are negative or greater than 1.0. An example of this appears in the numerical example presented in Section 5.6.

5.5.2 ESTIMATION OF THE DERIVED PARAMETERS

The estimates of the derived parameters are found by simply replacing the fundamental parameters by their MLEs in the definition of the derived parameters, and using the external estimates of the stratum population sizes and band-reporting rates. Variances and covariance may be estimated using the delta-method in conjunction with the estimated variance-covariance matrix of the fundamental parameters and the estimated standard errors of the external estimates.

Since the estimates of the survival/migration rates have relatively poor precision and are highly correlated, it is expected that the same will occur with the estimates of the relative emigration, relative immigration, and relative harvest-derivation rates. However, the precision of the overall net survival rates is good. This is not unexpected, since the overall net survival rate can be estimated approximately by ignoring the strata, and treating the data as an ordinary band-recovery experiment pre-stratified at the time of release.

5.5.3 TESTING

Since the MSS remains fixed at the entire data array under most models of biological interest, the methods used in Chapter 2 cannot be used to derive test statistics to distinguish between models. Likelihood ratio tests, or the method of Rao (1973, p. 395) (since these are multinomial models) can be used to differentiate between models as illustrated in the Partial- and Complete-Fidelity Models. A goodness-of-fit test can be constructed using a likelihood ratio test comparing the full model to a saturated model where every cell in the recovery matrices has its own parameter. A numerical example illustrating the use of the likelihood ratio tests is presented in Section 5.6. The power of the tests to differentiate between models can also be approximated using the expected cell values of the alternate model as "data" as was done in the Partial- and Complete-Fidelity Models.

5.6 **NUMERICAL EXAMPLE**

Simulated data using the parameter values shown at the bottom of Figure 5.4.2c will be used to illustrate the concepts and problems discussed earlier. The purpose of this section is not to perform a definitive analysis of data, but rather to illustrate some of the methods and procedures to be followed when analyzing a set of data. The advantage of simulated data is that the true model that gave rise to the data is known. Since the recoveries from a known number of releases are assumed to follow a multinomial distribution, it is a simple matter to generate multinomial random variates and to construct the data arrays. As before, values for the external estimates of the population sizes and band-reporting rates are not used in generating the recovery arrays, but are needed to estimate the immigration and derivation rates. A set of simulated recovery data and external estimates is shown in Figure 5.6a in the same format as Figure 5.4.2a along with the column and row totals. In this case, the true model has constant band-recovery rates over time, but the survival/migration rates change between years 1 and 2

The log-likelihood (up to constant terms) for a saturated model where every cell in the recovery table has its own parameter is found to

Figure 5.6 a
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c

NUMBER OF YEARS OF RELEASES : 3
NUMBER OF YEARS OF RECOVERIES: 4
NUMBER OF STRATA : 2

ESTIMATED POPULATION SIZES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	STRATUM	POPULATION ESTIMATE	S.E.
1	1	100000.	25000.
1	2	200000.	40000.
2	1	100000.	20000.
2	2	170000.	35000.
3	1	100000.	30000.
3	2	150000.	30000.

ESTIMATED BAND-REPORTING RATES (OBTAINED FROM EXTERNAL STUDIES)

YEAR	STRATUM OF ORIGIN	ESTIMATES AND (S.E.) STRATUM 1	STRATUM 2
1	1	0.500 (0.050)	0.600 (0.060)
1	2	0.600 (0.060)	0.400 (0.040)
2	1	0.500 (0.050)	0.600 (0.060)
2	2	0.600 (0.060)	0.400 (0.040)
3	1	0.500 (0.050)	0.600 (0.060)
3	2	0.600 (0.060)	0.400 (0.040)

Figure 5.6 a (continued)
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c

RECOVERY MATRICES AND MARGINAL TOTALS

YEARS OF RECOVERY

YEAR	STR	NUMBER REL	1		2		3		4			
1	1	1000.	54.0	30.0	19.0	25.0	17.0	15.0	11.0	20.0	101.0	90.0
1	2	1000.	53.0	20.0	22.0	32.0	17.0	12.0	10.0	7.0	102.0	71.0
2	1	1000.	0.0	0.0	33.0	32.0	31.0	25.0	32.0	18.0	96.0	75.0
2	2	1000.	0.0	0.0	18.0	53.0	21.0	22.0	23.0	15.0	62.0	90.0
3	1	1000.	0.0	0.0	0.0	0.0	20.0	20.0	28.0	27.0	48.0	47.0
3	2	1000.	0.0	0.0	0.0	0.0	27.0	42.0	32.0	23.0	59.0	65.0
			54.0	30.0	52.0	57.0	68.0	60.0	71.0	65.0		
			53.0	20.0	40.0	85.0	65.0	76.0	65.0	45.0		

LOG-LIKELIHOOD FOR MODEL WITH NO STRUCTURE = -4081.39 WITH 36 PARAMETERS be -4081.39 and requires 36 parameters. This is used in assessing the goodness-of-fit of the data to the internal-transfer model.

The moment-estimators are used as starting values for the method of scoring and are shown in Figure 5.6b. As can be seen, the estimates for the band-recovery rates are reasonable and are close to the correct values. (Note that the estimates for f_4 in Figure 5.6b and others, are estimates of $S_3 f_4$ since the two individual parameters are not identifiable). However, the estimates for the survival/migration rates are poor, often giving estimates which are far from the true values and even negative or greater than 1.0.

The method of scoring converged in 28 iterations. This slow convergence is a consequence of the almost nonidentifiability of the survival/migration parameters. The final log-likelihood is -4090.03 with 24 parameters (Figure 5.6c). Different starting points (not shown) were also tried (e.g., letting S_i^{st}=0.5), and the iterative procedure converged to the same point.

A goodness-of-fit test statistic to the Internal-Transfer Model can be computed using the log-likelihood values and has a value of 17.28=-2(-4090.03-(-4081.39)) with 12=36-24 degrees of freedom. The observed p-value is 0.14. There is little evidence against the Internal-Transfer Model. This is a correct decision since the data was generated using the Internal-Transfer Model. It should be noted that homogeneity of the rates was assumed for all animals alive in stratum s in year i and alive (or recovered) in stratum t in year $i+1$. These

Figure 5.6 b
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: FULL MODEL

STARTING VALUES FOR ITERATIONS

SURVIVAL AND MIGRATION RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	2
1	1	0.1278	0.5602
	2	0.3128	0.3060
2	1	2.1772	-0.7385
	2	2.3714	-1.2552

BAND RECOVERY AND CONFOUNDED RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	2
1	1	0.0540	0.0300
	2	0.0530	0.0200
2	1	0.0351	0.0207
	2	0.0222	0.0601
3	1	0.0248	0.0393
	2	0.0330	0.0835
4	1	0.0232	0.0077
	2	0.0260	-0.0185

Figure 5.6 c
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: FULL MODEL

ESTIMATES OF THE PARAMETERS

SURVIVAL AND MIGRATION RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	DESTINATION STRATUM 2
1	1	0.4816	0.1622
	2	0.1410	0.4993
2	1	0.6564	0.3394
	2	0.2117	0.4521

BAND RECOVERY AND CONFOUNDED RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	DESTINATION STRATUM 2
1	1	0.0540	0.0300
	2	0.0530	0.0200
2	1	0.0341	0.0325
	2	0.0221	0.0537
3	1	0.0244	0.0187
	2	0.0321	0.0395
4	1	0.0267	0.0251
	2	0.0310	0.0214

FINAL LOG-LIKELIHOOD= -4090.03 WITH 24 PARMS

Figure 5.6 d
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: FULL MODEL

ESTIMATES OF S.E. OF THE PARAMETERS

SURVIVAL AND MIGRATION RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM	
1	1	0.1869	0.2008
	2	0.1916	0.2224
2	1	0.3638	0.2766
	2	0.2997	0.2363

BAND RECOVERY AND CONFOUNDED RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM	
1	1	0.0072	0.0054
	2	0.0071	0.0044
2	1	0.0051	0.0056
	2	0.0042	0.0071
3	1	0.0043	0.0042
	2	0.0049	0.0060
4	1	0.0045	0.0045
	2	0.0049	0.0043

results do not relect the effects of departures from this assumption which could occur if the animals all do not get to stratum t from stratum s in the same way.

The MLEs are shown in Figure 5.6c and their estimated standard errors in Figure 5.6d. The estimated band-recovery rates are close to their true values and have good precision (estimated coefficients of variation of 10-15%). The estimated migration/survival rates are not close to their correct values and have poor precision (estimated coefficients of variation of 35-100%).

The estimated variance-covariance matrix was examined (not shown) and the estimated correlations among the parameter estimates was computed. These were generally low (less than 20%) except in the case of the correlation among the estimates of the survival/migration rates. For example:

$$\hat{\text{cor}}(\hat{S}_1^{11}, \hat{S}_1^{12}) = -0.94$$
$$\hat{\text{cor}}(\hat{S}_1^{21}, \hat{S}_1^{22}) = -0.94$$
$$\hat{\text{cor}}(\hat{S}_2^{11}, \hat{S}_2^{12}) = -0.95$$
$$\hat{\text{cor}}(\hat{S}_2^{21}, \hat{S}_2^{22}) = -0.95$$

These indicate that these parameters are nearly nonidentifiable and the estimates must be interpreted with care.

The estimates of the derived parameters are shown in Figure 5.6e. As expected, the estimated precision of the relative immigration rates is poor (estimated coefficients of variation around 50%) because of the poor precision of the estimated survival/migration rates. Note that the

Figure 5.6 e
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: FULL MODEL

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	FINAL & ORIGINAL STRATA		POPULATION EST (SE)	BAND-REPORTING EST (SE)	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	25000 (25000)	0.500 (0.050)	10801 (3243)	0.379 (0.094)	48164 (22235)	0.631 (0.323)
1	1	2	40000 (40000)	0.600 (0.060)	17669 (4606)	0.621 (0.094)	28205 (38726)	0.369 (0.323)
1	2	1	25000 (25000)	0.600 (0.060)	5001 (1620)	0.333 (0.100)	16217 (20489)	0.140 (0.155)
1	2	2	40000 (40000)	0.400 (0.040)	10001 (3148)	0.667 (0.100)	99861 (48750)	0.860 (0.155)
2	1	1	20000 (20000)	0.500 (0.050)	6814 (1833)	0.521 (0.102)	65637 (38680)	0.646 (0.337)
2	1	2	35000 (35000)	0.600 (0.060)	6262 (1864)	0.479 (0.102)	35987 (51483)	0.354 (0.337)
2	2	1	20000 (20000)	0.600 (0.060)	5416 (1527)	0.192 (0.060)	33944 (28484)	0.306 (0.200)
2	2	2	35000 (35000)	0.400 (0.040)	22837 (6030)	0.808 (0.060)	76854 (43178)	0.694 (0.200)
3	-1	1	30000 (30000)	0.500 (0.050)	4888 (1769)	0.378 (0.110)		
3	1	2	30000 (30000)	0.600 (0.060)	8030 (2172)	0.622 (0.110)		
3	2	1	30000 (30000)	0.600 (0.060)	3117 (1209)	0.174 (0.069)		
3	2	2	30000 (30000)	0.400 (0.040)	14794 (4000)	0.826 (0.069)		

relative immigration rates cannot be estimated in year 3 since the survival/migration rates can only be estimated in years 1 and 2. The estimates of the relative-harvest derivation rates are not as poorly estimated (estimated coefficients of variation around 30%) since the band-recovery rates are estimated fairly well.

A reduced model, where the survival/migration rates were assumed to be constant over time was also fit to the data, i.e., $S_i = S_{i+1}$ $i=1...k-1$. Note that the individual survival/migration and band-recovery parameters are not separately identifiable in years $k...1$. The parameter estimates from the full model were used as starting values for the iterative process after averaging the estimated survival/migration matrices. The MLEs for this restricted model are shown in Figure 5.6f, their estimated standard errors are shown in Figure 5.6g, and the estimates of the derived parameters and their standard errors are shown in Figure 5.6h. The log-likelihood of this reduced model was -4092.75 with 20 parameters.

A goodness-of-fit test for this reduced model has a test statistic of 22.72=-2(-4092.72-(-4081.39)) with 16=36-20 degrees of freedom. The observed p-value is 0.12 indicating little evidence that this reduced model is not appropriate. This is an incorrect decision, since the true survival/migration rates are not constant over time, but the change over time is small. When this model is compared to the full model, the likelihood ratio test statistic is 5.44=-2(-4092.75-(-4090.03)) with 4=24-20 degree of freedom. The observed p-value is 0.23 indicating that

Figure 5.6 f
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: SURVIVAL/MIGRATION CONSTANT OVER TIME

ESTIMATES OF THE PARAMETERS

SURVIVAL AND MIGRATION RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	2
1	1	0.2517	0.5213
	2	0.2520	0.4024
2	1	0.2517	0.5213
	2	0.2520	0.4024

BAND RECOVERY AND CONFOUNDED RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM 1	2
1	1	0.0534	0.0297
	2	0.0530	0.0200
2	1	0.0358	0.0315
	2	0.0201	0.0494
3	1	0.0228	0.0193
	2	0.0354	0.0391
4	1	0.0281	0.0272
	2	0.0327	0.0232

FINAL LOG-LIKELIHOOD= -4092.75 WITH 20 PARMS

Figure 5.6 g
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: SURVIVAL/MIGRATION CONSTANT OVER TIME

ESTIMATES OF S.E. OF THE PARAMETERS

SURVIVAL AND MIGRATION RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM	
1	1	0.1731	0.1680
	2	0.1527	0.1461
2	1	0.1731	0.1680
	2	0.1527	0.1461

BAND RECOVERY AND CONFOUNDED RATES

YEAR	STRATUM OF ORIGIN	DESTINATION STRATUM	
1	1	0.0071	0.0054
	2	0.0071	0.0044
2	1	0.0056	0.0054
	2	0.0040	0.0058
3	1	0.0046	0.0043
	2	0.0047	0.0052
4	1	0.0050	0.0049
	2	0.0045	0.0039

Figure 5.6 h
INTERNAL-TRANSFER MODEL
SIMULATED DATA USING VALUES OF PARAMETERS FROM FIGURE 5.4.2c
MODEL: SURVIVAL/MIGRATION CONSTANT OVER TIME

ESTIMATES OF HARVEST DERIVATION AND IMMIGRATION

YEAR	FINAL & ORIGINAL STRATA		POPULATION EST (SE)	BAND-REPORTING EST (SE)	HARVEST DERIVATION (SE)	RELATIVE DERIVATION (SE)	IMMIGRATION(SE)	RELATIVE IMMIGRATION(SE)
1	1	1	25000 (25000)	0.500 (0.050)	10684 (3209)	0.377 (0.093)	25170 (18420)	0.333 (0.189)
1	1	2	40000 (40000)	0.600 (0.060)	17682 (4606)	0.623 (0.093)	50407 (32161)	0.667 (0.189)
1	2	1	25000 (25000)	0.600 (0.060)	4946 (1604)	0.331 (0.100)	52126 (21259)	0.393 (0.124)
1	2	2	40000 (40000)	0.400 (0.040)	10009 (3149)	0.669 (0.100)	80479 (33368)	0.607 (0.124)
2	1	1	20000 (20000)	0.500 (0.050)	7152 (1951)	0.557 (0.104)	25170 (18029)	0.370 (0.195)
2	1	2	35000 (35000)	0.600 (0.060)	5692 (1734)	0.443 (0.104)	42846 (27417)	0.630 (0.195)
2	2	1	20000 (20000)	0.600 (0.060)	5249 (1476)	0.200 (0.062)	52126 (19769)	0.432 (0.123)
2	2	2	35000 (35000)	0.400 (0.040)	20999 (5404)	0.800 (0.062)	68407 (28559)	0.568 (0.123)
3	1	1	30000 (30000)	0.500 (0.050)	4565 (1711)	0.341 (0.105)		
3	1	2	30000 (30000)	0.600 (0.060)	8839 (2301)	0.659 (0.105)		
3	2	1	30000 (30000)	0.600 (0.060)	3210 (1241)	0.180 (0.070)		
3	2	2	30000 (30000)	0.400 (0.040)	14672 (3817)	0.820 (0.070)		

there is no evidence that this reduced model is inappropriate. Again, this is an incorrect decision.

This reduced model does have slightly more precise estimates of the band-recovery rates and survival/migration rates, but the estimated precision of the latter is still poor (estimated coefficient of variation from 30% to 90%). The convolutions of the survival/migration rates and the low band-recovery rates are still causing a problem in estimating the rates. The estimated correlations among the estimates of survival/migration rates are still over 90%. Because of the poor precision, the bias caused by using an incorrect model is not serious.

The power of these tests to detect differences among models can be estimated by computing the expected number of recoveries under an alternative model, and using these expected recoveries as "data" in fitting the full and reduced models in much the same way as in the Partial- and Complete-Fidelity Models. The likelihood ratio test statistics will then be the estimated value of the non-centrality parameter of a non-central chi-square distribution that can be used to estimate the power function.

The log-likelihood of the saturated model when the "expected values" were analyzed as data, had a value of -4111.94 with 36 parameters. The log-likelihood of the full model has a value of -4111.94 with 24 parameters. Hence, as expected since the data were generated assuming the model was valid, the non-centrality parameter of the goodness-of-fit test has a value of 0, which implies that this test is subject to Type I errors only. When the reduced model was fit to the "expected values", the log-likelihood has a value of -4112.24 with 20 parameters, and the non-centrality parameter for the test of the full vs. the reduced model is 0.6=-2(-4112.24-(-4111.94)) with 4 degrees of freedom. Hence the power to detect this change in the survival/migration rates is very small which explains why the earlier test did not reject the reduced model. A summary of the model fitting steps is shown in Figure 5.6i.

Any sequence of reduced models in the Internal-Transfer Model can be investigated in a similar fashion. However, since the estimates of the survival/migration rates are so poorly estimated and have such high correlations, the power to detect changes in the survival/migration rates is expected to be small for any reasonable experiment. The power to detect differences among the band-recovery rates is expected to be good; however, these are usually not of biological interest. In any case, the power of a proposed experiment to detect changes among the parameters can be investigated by generating the expected number of recoveries and performing the sequence of model tests. The sample sizes and recovery effort can be changed until reasonable power is obtained; however, it may be more feasible to modify the experimental design to overcome the confounding of the migration/survival parameters as discussed in the next section.

Figure 5.6i

Summary of the sequence of model fitting using the simulated data and using the "expected values" as data for the numerical example.

Simulated Data

Saturated Model
log-likelihood= -4081.30
with 36 parameters

Full Model
log-likelihood = -4090.03
with 24 parameters

Reduced Model
(Homogeneous survival/migration)
log-likelihood = -4092.75
with 20 parameters

Expected Values

Saturated Model
log-likelihood = -4111.94
with 36 parameters

Full Model
log-likelihood - -4111.94
with 24 parameters

Reduced Model
(Homogeneous survival/migration)
log-likelihood = -4112.24
with 20 parameters

5.7 DISCUSSION

In light of the fact that ordinary band-recovery data were inadequate for inference in the Partial- and Complete-Fidelity Models, it is surprising that ordinary band-recovery data is theoretically adequate in the Internal-Transfer Model. However, inference is not completely satisfactory, since the parameters of most biological interest, the survival/migration rates (S_i), are not estimated well. They have poor precision, and in many cases, are nearly nonidentifiable. This is caused by the convolution of these parameters between the time of release and recovery in the model formulation and the generally low band-recovery rates present in practise. As a consequence, the derived parameters of relative emigration, relative immigration, and relative harvest-derivation also have poor precision, and the power to differentiate among models is poor.

How can the experimental design be modified to solve these problems? Simply increasing the number of animals released or increasing the band-recovery rates will not be very satisfactory, since the expected improvements in precision are expected to be small. Rather more effort must be placed on obtaining additional information as to where the animal has migrated between release and recovery. As before this can be accomplished by additional sightings of the animal. In previous models, these additional sightings took place in the post-strata and at recovery time. In this model, additional sightings during the recovery period will also yield useful information since the number of S_i arrays that will be multiplied together in the likelihood to represent the (unknown) movement of the animal between releases, sightings, and recovery is reduced, i.e., it will reduce the complexity of the convolution terms. However, this solution is not entirely satisfactory since the sighting of an animal in a stratum during the recovery period does not give definite information about the location of the animal at the previous banding time (the animal may have migrated after the banding time but before the time of sighting). Since the parameters of most interest are the net movements from banding time to banding time, it is preferable to perform the additional sightings at *banding time*. In this case, the actual stratum of the animal at banding time in year i is then known, and more information is available to estimate the migration/survival rates. The effect of these additional sightings at banding time is again to reduce the complexity of the convolution terms. As well, the model is now closer in form to that of Arnason (1972, 1973) and Seber (1982) since sightings at banding time may be considered as "captures" and "releases" at a point in time. This solution differs from the previous models where sightings at banding time would give information on survival rates, but not on migration rates from the pre-strata to the post-strata. These modifications to the experimental design have not been explored in detail in this Thesis, since, unless the sighting rate is high, one will still have the problem of poor precision and high correlation. However, if the animal is sighted every year between release and recovery, then the complete migration history of the animal will be known, and the relatively simple method of inference in Markov chains (Bartlett, 1955; Basawa and Rao, 1980) can be used. If the animals are fitted with a radio-telemetry device, and the "sightings" take place in a small period of time, the methods of Arnason (1972, 1973) can be used since the "sighting" of an animal from its radio-telemetry device will be similar to a recapture and release in his capture-recapture formulation. Again, unless the "recapture rate" is high, the convolution of the parameters to represent the unknown movement of the animals between "captures" will cause similar problems of precision and nonidentifiability. With modern technology, inexpensive and reliable devices that permit the monitoring of an animal as it migrates among strata between release and recovery will be the most cost-effective method of obtaining good estimates of the survival/migration rates.

An important implication of the Internal-Transfer Model is that the band-recovery and migration/survival rates are homogeneous for all animals that migrate between stratum s and stratum t, regardless of the actual route used. In the presence of heterogeneity, the parameter values can be thought of as an average value; however, the multinomial model is no longer valid but will be a good approximation if the degree of heterogeneity is small.

Appendix 5.A
Maximum likelihood estimation in the Internal-Transfer Model

The likelihood is constructed as a simple product of multinomial distributions; however, the individual cell probabilities are complex because of the convolution of the intermediate survival/migration and band-recovery rates between release and recovery. The likelihood can be written as:

$$L = \prod_{i=1}^{k} \prod_{s=1}^{a} \frac{N_i^s!}{(N_i^s - R_{i\cdot}^{s\cdot})!} (1-p_{i\cdot}^{s\cdot})^{N_i^s - R_{i\cdot}^{s\cdot}} \prod_{j=i}^{l} \prod_{t=1}^{a} \frac{(p_{ij}^{st})^{R_{ij}^{st}}}{R_{ij}^{st}!}$$

where p_{ij}^{st} is the probability that an animal released in stratum s in year i is recovered in stratum t in year j. It is a convolution of the intermediate migration/survival and band-recovery rates, and its symbolic value can be obtained from Figure 5.4.2b.

Using the rules of matrix differentiation (Neudecker, 1967; Nel, 1980; Graybill, 1985) the first order conditions for the MLEs can be explicitly found and are given in Figure 5.A.1.

The Hessian is extremely complex to write out explicitly; however it can be computed using methods similar to those in Conroy and Williams (1984). For example, if θ represents the vector of fundamental parameters, the estimated information matrix can be computed as:

$$\sum_{i=1}^{k} \sum_{s=1}^{a} N_i^s \frac{1}{1-p_{i\cdot}^{s\cdot}} \frac{\partial p_{i\cdot}^{s\cdot}}{\partial \theta} \left(\frac{\partial p_{i\cdot}^{s\cdot}}{\partial \theta'} \right) + \sum_{i=1}^{k} \sum_{s=1}^{a} N_i^s \sum_{j=i}^{l} \sum_{t=1}^{a} \frac{1}{p_{ij}^{st}} \frac{\partial p_{ij}^{st}}{\partial \theta} \left(\frac{\partial p_{ij}^{st}}{\partial \theta'} \right)$$

where $\frac{\partial p_{ij}^{st}}{\partial \theta}$ is easily found using the rules for matrix differentiation.

Given initial starting values, the method of scoring may now be used to obtain the MLEs. The methods of Don (1985) and Aitchison and Silvey (1958) may be used to modify the method of scoring when restrictions are placed upon the parameters. As usual, the estimated information matrix at the last iteration may be used to estimate the asymptotic variances and covariances of the estimates.

Table 5.A.1
First order conditions for MLEs in the Internal-Transfer Model
using ordinary band-recovery data

$$\frac{\partial L}{\partial f_i} = 0 = \sum_{r=1}^{i} (\hat{S}_r \ldots \hat{S}_{i-1})' \Big(R_{ri} \div \hat{S}_r \ldots \hat{S}_{i-1} \hat{f}_i \quad - \quad [(N_r - R_r.1) \div (1 - \hat{\rho}_r) 1] 1' \Big)$$

$$\frac{\partial L}{\partial s_k s_{k+1} \ldots f_l} = 0 = \sum_{r=1}^{k} (\hat{S}_r \ldots \hat{S}_{k-1})' \Big(R_{ri} \div \hat{S}_r \ldots \hat{S}_{k-1} s_k s_{k+1} \hat{} \ldots f_i \quad - \quad [(N_r - R_r.1) \div (1 - \hat{\rho}_r 1)] 1' \Big)$$

$$\frac{\partial L}{\partial s_i} = 0 = \sum_{r=1}^{i} \sum_{c=i+1}^{l} (\hat{S}_r \ldots \hat{S}_{i-1})' \Big(R_{rc} \div \hat{S}_r \ldots \hat{S}_{c-1} \hat{f}_c \Big) (\hat{S}_{i+1} \hat{S}_{i+2} \ldots \hat{f}_c)' \quad -$$
$$\sum_{r=i}^{i} (\hat{S}_r \ldots \hat{S}_{i-1})' [(N_r - R_r.1) \div (1 - \hat{\rho}_r 1)] 1' \hat{\rho}_{i+1}$$

where $\hat{\rho}_i$ is the estimated probability of recovering an animal during the entire experiment after it is released in year i:

$$\hat{\rho}_i = \hat{f}_i + \hat{S}_i \hat{f}_{i+1} + \hat{S}_i \hat{S}_{i+1} \hat{f}_{i+2} + \ldots + \hat{S}_i \hat{S}_{i+1} \ldots \hat{S}_{k-1} S_k S_{k+1} \hat{} \ldots f_l$$

Appendix 5.B
Extension of moment-estimator to Capture-Recapture Experiments

The moment estimator for the full model in the Internal-Transfer Model can be extended to estimating migration rates in capture-recapture studies (Arnason, 1972, 1973; Seber, 1982, p. 555) in much the same way that the estimators from simple band-recovery experiments can be extended to capture-recapture studies (Brownie and Pollock, 1985). I will show that the extension of my moment estimator to capture-recapture studies uses more information than the one presented in Seber (1982, p. 555) and is, therefore, likely to be more efficient.

In capture-recapture studies, animals are released at a point in time and captured at a point in time, unlike band-recovery experiments where recoveries take place over a period of time. As well, an animal may be captured more than once in a capture-recapture study, but may be recovered only once in a band-recovery study. Nevertheless, by a suitable redefinition of the parameters, and a slight change in data representation, band-recovery methods may be used to estimate the migration parameters in capture-recapture studies.

Let the elements of $\boldsymbol{N}_i$ (N_i^s) represent the number of animals released at time i in stratum s. This will include those animals that were captured at time i and are being released.

The elements of $\boldsymbol{R}_{ij}$ (R_{ij}^{st}) now represent the number of animals released in stratum s at time i and *next* captured in stratum t at time j. In capture-recapture studies, $\boldsymbol{R}_{ii}$ must, by definition, be zero. If an animal is captured at time j, it then becomes a member of $\boldsymbol{N}_j$ and is 'removed' from the $\boldsymbol{N}_i$ cohort (just as a recovery of an animal removes it from the $\boldsymbol{N}_i$ cohort in band-recovery studies). Hence only the first recaptures of animals released from $\boldsymbol{N}_i$ contribute to $\boldsymbol{R}_{i,i+1}$, $\boldsymbol{R}_{i,i+2}$, ... $\boldsymbol{R}_{i,l}$. But an animal that is captured $v+1$ times contributes to exactly v of the $\boldsymbol{R}_{ij}$ and to $v+1$ of the $\boldsymbol{N}_i$. The symbolic data representation of the matrices in the case of four sampling times is shown in Figure 5.B.1. Note that captures at the first sample time are required only to provide a set of marked animals that will be released back to the population.

Capture-recapture studies require the use of two new parameter matrices, ϕ_i and $\mathbf{p}_i$. The elements of ϕ_i (ϕ_i^{st}) represent the probability that an animal alive in stratum s at time i is also alive in stratum t at time $i+1$. Hence ϕ_i contain both migration and mortality components. Again, it is assumed that if animals migrate to other strata, they do so permanently. The elements of $\mathbf{p}_i$ (p_i^s) represent the probability that an animal alive in stratum s at time i will be captured. All animals in stratum s at time i, regardless of previous migrations or previous captures, are assumed to have the same probability of capture.

The expected number of recoveries in the capture-recapture formulation in the case of four sample times is displayed in Figure 5.B.2. As in the Internal-Transfer Model examined earlier, the expected number of recoveries involves a convolution of the intermediate survival/migration and capture probabilities between recaptures.

Figure 5.B.1

Symbolic representation of the number of animals released in stratum *s* at time *i* and captured for the next time in stratum *t* at time *j* in the case of four sampling times in a capture-recapture context.

Time Released	Number Released	Number captured for the next time at sampling time 1	2	3	4
1	$\boldsymbol{N}_1$	-	$\boldsymbol{R}_{12}$	$\boldsymbol{R}_{13}$	$\boldsymbol{R}_{14}$
2	$\boldsymbol{N}_2$		-	$\boldsymbol{R}_{23}$	$\boldsymbol{R}_{24}$
3	$\boldsymbol{N}_3$			-	$\boldsymbol{R}_{34}$

$$\boldsymbol{N}_i \text{ are } a \times 1 \text{ vectors } \begin{bmatrix} N_1^1 \\ N_1^2 \\ \vdots \\ N_1^a \end{bmatrix} \text{ and } \boldsymbol{R}_{ij} \text{ are } a \times a \text{ matrices } \begin{bmatrix} R_{ij}^{11} & R_{ij}^{12} & \cdots & R_{ij}^{1a} \\ R_{ij}^{21} & R_{ij}^{22} & \cdots & R_{ij}^{2a} \\ \vdots & & & \vdots \\ R_{ij}^{a1} & R_{ij}^{a2} & \cdots & R_{ij}^{aa} \end{bmatrix}$$

The number of animals never recaptured is not shown, but is easily obtained by subtraction.

Figure 5.B.2

The probabilities that an animal released in stratum s at time i is captured for the next time in stratum t at time j in the case of four sampling times in a capture-recapture context.

Time Released	Number Released	Probability of recapture at this sampling time 1	2	3	4
1	N_1	-	$\phi_1 D(p_2)$	$\phi_1 D(1-p_2)\phi_2 D(p_3)$	$\phi_1 D(1-p_2)\phi_2 D(1-p_3)\phi_3 D(p_4)$
2	N_2		-	$\phi_2 D(p_3)$	$\phi_2 D(1-p_3)\phi_3 D(p_4)$
3	N_3			-	$\phi_3 D(p_4)$

$$N_i \text{ are } a \times 1 \text{ vectors } \begin{bmatrix} N_1^1 \\ N_1^2 \\ \cdot \\ \cdot \\ \cdot \\ N_1^a \end{bmatrix}; \; p_i \text{ are } a \times 1 \text{ vectors } \begin{bmatrix} p_1^1 \\ p_1^2 \\ \cdot \\ \cdot \\ \cdot \\ p_1^a \end{bmatrix}.$$

$$\phi_i \text{ are } a \times a \text{ matrices } \begin{bmatrix} \phi_{ij}^{11} & \phi_{ij}^{12} & \cdots & \phi_{ij}^{1a} \\ \phi_{ij}^{21} & \phi_{ij}^{22} & \cdots & \phi_{ij}^{2a} \\ \vdots & & & \vdots \\ \phi_{ij}^{a1} & \phi_{ij}^{a2} & \cdots & \phi_{ij}^{aa} \end{bmatrix}$$

The probability of never recapturing an animal is not shown, but is easily obtained by subtraction.

If we compare Figure 5.B.2 with Figure 5.4.2b, we note that the diagonal elements of Figure 5.B.2 are all zero, but the table has the same general form as Figure 5.4.2b. Figure 5.B.3 is a reformulation of Figure 5.B.2 using the band-recovery notation and from it the following equivalences can be made:

$$\boldsymbol{f}_i = \phi_{i-1}\mathbf{D}(\mathbf{p}_i)$$

$$\boldsymbol{S}_i = \phi_{i-1}\mathbf{D}(\mathbf{1}-\mathbf{p}_i)$$

By writing out the expected value of the row and column totals, the following moment estimators can be developed:

$$\tilde{\mathbf{f}}_i = \mathbf{D}(\mathbf{N}_{i-1})^{-1}\mathbf{R}_{i-1,\cdot}(\mathbf{T}_i-\mathbf{R}_{i\cdot})^{-1}\mathbf{R}_{\cdot i}$$

$$\tilde{\mathbf{S}}_i = \mathbf{D}(\mathbf{N}_{i-1})^{-1}\mathbf{R}_{i-1,\cdot}(\mathbf{T}_i-\mathbf{R}_{i\cdot})^{-1}(\mathbf{Z}_i-\mathbf{R}_{i\cdot})\mathbf{R}^{-1}_{\cdot i}\mathbf{D}(\mathbf{N}_i)\,.$$

Note that the estimators have a slightly different form from those presented in Section 5.4.2; this is caused by the empty main diagonal of the data in Figure 5.B.1.

Now, using the equivalences above, we obtain the moment estimators:

$$\tilde{\boldsymbol{\phi}}_{i-1} = \tilde{\mathbf{S}}_i + \tilde{\mathbf{f}}_i \qquad i = 2\ldots k \tag{B.1}$$

$$\tilde{\mathbf{p}}_i = \tilde{\boldsymbol{\phi}}_{i-1}^{-1}\,\tilde{\mathbf{f}}_i\,\mathbf{1}.$$

In the case of sampling on three occasions, the above estimators reduce to those of Arnason (1973, Equation 1.11). Seber (1982, pp. 555-559) suggested that if the experiment has more than three sample times, the estimators of Arnason (1973) be applied to successive groups of three sample time, i.e., use times 1, 2, and 3 to estimate ϕ_1; use

Figure 5.B.3

The probabilities that an animal released in stratum *s* at time *i* is captured for the next time in stratum *t* at time *j* in the case of four sampling times in a capture-recapture context reformulated using band-recovery notation.

Time Released	Number Released	Probability of recapture at this sampling time 1	2	3	4
1	$\mathbf{N}_1$	-	$\mathbf{f}_2$	$\mathbf{S}_2\mathbf{f}_3$	$\mathbf{S}_2\mathbf{S}_3\mathbf{f}_4$
2	$\mathbf{N}_2$		-	$\mathbf{f}_3$	$\mathbf{S}_3\mathbf{f}_4$
3	$\mathbf{N}_3$			-	$\mathbf{f}_4$

$\mathbf{N}_i$ are $a \times 1$ vectors $\begin{bmatrix} N_1^1 \\ N_1^2 \\ \vdots \\ N_1^a \end{bmatrix}$.

$\mathbf{f}_i$ are $a \times a$ matrices $\begin{bmatrix} f_{ij}^{11} & f_{ij}^{12} & \cdots & f_{ij}^{1a} \\ f_{ij}^{21} & f_{ij}^{22} & \cdots & f_{ij}^{2a} \\ \vdots & & & \vdots \\ f_{ij}^{a1} & f_{ij}^{a2} & \cdots & f_{ij}^{aa} \end{bmatrix}$; $\mathbf{S}_i$ are $a \times a$ matrices $\begin{bmatrix} S_{ij}^{11} & S_{ij}^{12} & \cdots & S_{ij}^{1a} \\ S_{ij}^{21} & S_{ij}^{22} & \cdots & S_{ij}^{2a} \\ \vdots & & & \vdots \\ S_{ij}^{a1} & S_{ij}^{a2} & \cdots & S_{ij}^{aa} \end{bmatrix}$

The probability of never recapturing an animal is not shown, but is easily obtained by subtraction.

times 2, 3, and 4 to estimate ϕ_2; etc. However, that method ignores all information on captures outside of the selected sampling times while my new estimators do not. As a consequence, it is expected that my proposed estimators will be more efficient.

One could obtain MLEs of the capture-recapture parameters by using the computer program developed for the Internal-Transfer Model by finding $\hat{f}_i$ and $\hat{S}_i$ of Figure 5.B.3, and then using the equivalence relations 5.B.1 to obtain the MLEs for ϕ_{i-1} and $\mathbf{p}_i$. However, this procedure is not recommended due to the potential numerical difficulties caused by the high sampling correlations in the estimates. Numerical procedures should be used to obtain the MLEs of the capture-recapture parameters directly.

Chapter 6

Considerations in using the models of this Thesis

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Considerations in using the models of this Thesis

General guidelines on performing a banding study have been given by Brownie *et al.* (1985, Chapter 9); more specific guidelines on the use of banding data in determining migration rates has been given by Crissey (1955). They discuss, among other things, the need to ensure that the banded sample is representative of the population, how to determine the sample sizes required for a given level of precision, and the need for stratification to correct for heterogeneity in the parameters within a population. For the most part, their guidelines are applicable to the models considered in this Thesis; experimenters should review their guidelines while planning a banding study. Consideration should also be given to two important assumptions of the models of this Thesis: the assumption of fidelity to strata or the assumption of Markovian behavior in the choice of strata; and the assumption of independence between sightings and recoveries.

6.1 **REPRESENTATIVENESS**

A study must be carefully designed to ensure that the banded animals are representative of the population; otherwise, any results from the study may not be applicable to the population of interest. Brownie *et al.* (1985) and Crissey (1955) recommend that the banding of animals should only take place when the populations are relatively sedentary, and that effort should be distributed over the entire banding site. If banding is performed when the populations are not sedentary, it is possible to band transient animals which may have different parameter values than the rest of the population. Distributing the banding effort over the entire site will guard against unforeseen local effects that could bias the estimates, e.g., increased mortality on local groups caused by an outbreak of a disease.

As well, the experimenter should ensure that the banding procedure itself does not introduce biases through non-random sampling. For example, in some species, certain age or sex classes are more easily captured and banded. These classes may have different survival and band-recovery rates than the rest of the population. Some degree of non-random sampling can be corrected by stratification or by a modification of the experimental model. However, as indicated by Brownie *et al.* (1985, p. 184), there is no satisfactory method of dealing with experiments that band young animals only (as opposed to young and adult animals) without restrictive and potentially unrealistic assumptions.

6.2 **SAMPLE SIZE PLANNING**

Brownie *et al.* (1985, Chapter 9) develop explicit formulae for a specified level of precision for each estimate. This is too unwieldy for the models of this Thesis, and it is easier to simply choose typical values for the parameters (based upon prior information or other related studies), generate the array of expected recoveries and/or sightings with these parameter values, and then use these expected values as data to the computer programs described earlier to obtain approximate precisions (Section 1.4). The proposed effort in the experiment can then be varied until suitable precision is obtained. This approach can also be employed to investigate the relative allocation of effort among releases in pre-strata and recoveries and/or sightings in post-strata.

A similar procedure can be used to examine the power of a particular study to detect a specified degree of heterogeneity in the values of the parameters among pre- or post-strata or over time as outlined in Section 1.4.

6.3 **HETEROGENEITY**

It is well known that animals within a population have different survival and band-recovery rates. As shown by Pollock and Ravelling (1982) and Nichols *et al.* (1982), homogeneity in the survival rates and heterogeneity in the band-recovery rates within a population lead to unbiased estimates of the survival rates and of the average band-recovery rates. Other combinations of heterogeneity in the survival and band-recovery rates lead to bias in both estimates. The usual remedy for heterogeneity is stratification, i.e., partitioning the population into strata so that animals within a stratum have more homogeneous parameter values. With ordinary band-recovery data, the stratification can only take place at the time of release, e.g., by sex, by age, or by banding site. As indicated by Pollock and Raveling (1982, p. 291), heterogeneity is often caused, in practise, by differences in migration routes, differences in wintering areas, and differences in hunting pressures - events that take place after banding. The models of this Thesis provide additional flexibility to the experimenter by allowing both pre- and post-release stratification (Chapter 2), and by explicitly modelling the migration process (Chapters 3,4 and 5). By using these models, heterogeneity among animals within strata can be reduced, and biases in the estimates reduced.

Of course, pre- and post-release stratification will still not completely eliminate heterogeneity among animals within a stratum for any real animal population. In particular, the experimenter should check that the following assumptions are approximately satisfied before using the models of this Thesis:

- In the general post-stratification model (Chapter 2), all animals belonging to a specific post-stratum have the same band-recovery and survival rates.
- In the Complete-, Partial-, and Non-Fidelity Models (Chapters 3 and 4), all animals migrating between specific pre- and post-strata have the same post-stratum specific band-recovery, sighting, and survival rates.
- In the Internal-Transfer Model (Chapter 5), all animals migrating between two strata have the same survival/migration and band-recovery rates regardless of the actual route used between the two strata.

The effect of residual heterogeneity will be similar in the models of this Thesis as in ordinary band-recovery models - heterogeneity in the band-recovery or sighting rates, but homogeneity in the survival rates will lead to unbiased estimates of survival. The reason for this is that sighting and recovery information can be combined into one new type of "recovery" and the prior results are now directly applicable. The effect of heterogeneity on the estimates of band-recovery, sighting, or migration rates is difficult to quantify since it depends upon the type of heterogeneity in both the sighting and recovery rates. However, it is expected that any bias in the estimates of the migration rates will be small relative to their standard errors for most studies.

All of the goodness-of-fit tests considered in this Thesis, search for some evidence of heterogeneity in the band-recovery and survival rates. Usually, a component of the test examines if subsequent recovery patterns of newly released and previously released animals are similar. Common causes for rejection are age or banding effects. For example, if banded animals are a mixture of ages and the survival rates decline with age, then the "average" survival rate of a previously banded cohort will be less than that of a newly banded cohort. Or newly banded animals may have a reduced survival rate (compared to previously banded animals) caused by the stress of being captured and banded. Unfortunately, the power of these tests to detect heterogeneity is likely to be low due to small sample sizes. If such effects as given above are suspected, the models of this Thesis could be modified to incorporate age classes or one year effects of banding in a similar fashion to those in Brownie *et al.* (1985, Section 2.5, Chapters 3 and 4).

6.4 THE FIDELITY AND MARKOVIAN ASSUMPTIONS

Each of the models in this Thesis makes assumptions about the fidelity of animals to either or both of the pre- and post-strata. In particular:

- In the general post-stratification model (Chapter 2), it was implicitly assumed that animals were faithful to their post-strata. Models 2a and 1 can still be used in certain partial-fidelity situations.
- In the Complete-Fidelity Model (Chapter 3), it was assumed that animals were faithful to both the pre-stratum of release and the post-stratum of recovery.
- In the Partial-Fidelity Model (Chapter 3), it was assumed that animals were faithful to the pre-stratum of release, but may choose a new post-stratum in each year. Indeed, it was assumed that animals displayed a Markovian behavior (i.e., lack of memory) in their choice of post-stratum.
- In the Non-Fidelity Model (Chapter 4), it was assumed that animals were faithful to neither strata, i.e., animals displayed Markovian behavior in both their choice of post-stratum when leaving a pre-stratum, and their choice of pre-stratum when returning from a post-stratum.
- In the Internal-Transfer Model (Chapter 5), it was assumed that animals were not faithful to strata, and again displayed Markovian behavior in their choice of migration routes each year.

The experimenter has, of course, little control over the behavior of the animals, and the validity of the fidelity and Markovian assumptions usually must be assessed on biological grounds. In some cases, information from the experiment does provide some information on these assumptions.

The fidelity assumption implies that the animals must remember the migration destination (either to the post-stratum or back to the pre-stratum) from year to year. Violations of the fidelity assumption are usually caused by factors external to the animal or by behavioral aspects of the animal. For example, unusual weather patterns may disrupt the usual migration route. Pair bonding may occur, in which case, one member of the pair now follows the other to the latter's migration destination. The occurrence of one animal that violates the fidelity assumption is enough, in theory, to refute the assumption. However, since these occurrences may be the biological equivalents of "outliers", the experimenter should obtain stronger evidence before rejecting the fidelity assumption. Conversely, the absence of any animal violating the fidelity assumption, does not prove the assumption is true; the experimental effort may not be large enough to detect violations that occur.

The Markovian assumption implies that animals forget completely their migration destination of previous years. All animals alive at a point in time at a location behave in a similar manner regardless of their past history. Violation of the assumption of Markovian behavior in one segment of the migration route may be caused by a homing instinct, by age effects, or by banding effects. For example, an animals may always start a migration in an initial direction and then choose randomly from the destinations only along that route rather than randomly from all destinations in all directions. Older animals may develop habits and prefer to return to certain destinations. Newly banded animals may be stressed in the year of banding, and behave differently than previously banded animals. The Markovian assumption can be assessed by comparing the subsequent migration and recovery patterns of two cohorts of animals alive at a common location but having different previous histories. For example, a component of the goodness-of-fit tests compares the subsequent behavior of newly banded and previously banded animals. In models with live sightings, the subsequent recovery and sighting pattern of two cohorts of animals (sighted in the same stratum in the same year but with difference prior migration patterns) are compared. However, it is likely that such tests will have low power due to small sample sizes.

There is always the danger that despite biological assessments and formal statistical tests, the incorrect fidelity and Markovian assumptions will be made. The effect of model mis-specification errors in a sequence of nested models (i.e., where model A is the same as Model B except that certain parameters are subject to restrictions) is well known. In nested models, choice of a too general model usually does not lead to serious bias in the estimates (compared to the correct model), but does give larger estimated standard errors. Choice of a too specific model may lead to serious bias, but more importantly, the estimated standard errors are too small giving a false sense of precision. Testing procedures to choose among nested models are well developed as illustrated in this Thesis. The Non-, Partial-, and Complete-Fidelity Models are, unfortunately, not a sequence of nested models since the more restrictive models are not obtained from the more general models by a simple restriction on the parameters. The effects of incorrect model specification can be assessed in a general sense by generating "data" corresponding to the expected recoveries and sighting under the correct model, and analyzing this "data" using the incorrect model. For example, by comparing the expected recoveries computed using the same values of the parameters in the Partial-Fidelity Model (Figure 3.4.2c) and the Complete-Fidelity Model (Figure 3.6.2c), it can be seen that they are very similar. Consequently, as the simulations in Section 3.7 indicate, the parameter estimates from either model will be comparable, but the estimated standard errors in the Complete-Fidelity Model are much smaller. Unfortunately, there is no simple test in non-nested specifications of which model is "better". The test statistics from the goodness-of-fit tests could be used, but this approach will likely have low power.

6.5 INDEPENDENCE BETWEEN SIGHTINGS AND RECOVERIES

In all the models that employ sightings, a crucial assumption is that sightings and recoveries are independent events. In most banding studies, the experimenter has little control over the recovery effort, but is in direct control of sighting effort. As noted in Sections 3.4 and 3.6, a high sighting rate give good precision in the estimates. In some cases, special bands that are easily spotted can be used, or pigments applied to the animals to increase visibility. The experimenter must be careful that any special banding technique does not make the animals more susceptible to recovery. The timing and placement of the sighting effort should also be planned carefully. Violation of the independence assumption will occur if:

- sightings take place after recoveries. If this occurs, then it is impossible to obtain any animals that are both sighted and recovered. The sighting effort should take place prior to or at the same time as recoveries. However, if sightings take place too far in advance of recoveries, there is a danger that the animals sighted will have left the recovery area before recoveries start.
- sightings take place on different sub-populations than recoveries. This can occur, as noted above, if sightings take place far in advance of recoveries and the sighted sub-population has left the recovery area. As well, sightings and recoveries should not occur on two separate geographical areas unless the experimenter is sure that animals traverse both areas.

Since various ratios of the numbers of animals that are recovered and sighted, recovered but not sighted, and sighted without being recovered form the basis of the estimates of the recovery and sighting rates (and hence the migration and survival rates), serious violation of this independence assumption will lead to biases in the estimators. In the most severe case, some parameters may again be nonidentifiable. The goodness-of-fit test to the models do incorporate a component for testing the independence assumption; however, small sample sizes may give tests with lower power. This assumption is best assessed on biological and methodological grounds prior to the study.

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