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Open Population Mark-Recapture Models Including Ancillary Sightings

A thesis presented in partial
fulfilment of the requirements
for the degree of
Doctor of Philosophy
in Statistics
at Massey University

Richard J. Barker

1995

BARKER

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Abstract

A model is proposed for a mark-recapture experiment with ancillary observations obtained from marked animals any time between capture periods and throughout the geographic range of the animals. The model allows three types of emigration from the site where recaptures are made: (1) random emigration, where the probability an animal is at risk of capture at i does not depend on whether it was at risk of capture at $i - 1$, (2) permanent emigration where animals can leave the area where they are at risk of capture but not return, and (3) Markov emigration, where the probability an animal is at risk of capture at i depends on whether it was at risk of capture at $i - 1$. Under random emigration the likelihood function can be factored into a set of conditionally independent binomial terms used to estimate the parameters and a set of conditionally independent multihypergeometric terms that do not involve the parameters. Closed-form maximum likelihood estimators are derived under random emigration for models with age-dependence and a temporary marking effect. Contingency table based goodness-of-fit tests are derived from the multihypergeometric terms in the likelihood function. Contingency table tests of the age-dependence and temporary marking effect models are also derived. Explicit estimators do not appear to exist for permanent or Markov emigration.

It is shown that the estimator suggested by Jolly (*Biometrika* 52:239, 1965), and as a consequence the estimator suggested by Buckland (*Biometrics* 36:419-435, 1980), is only valid if there is no emigration from the study area or if emigration is random. The estimator suggested by Mardekian and McDonald (*Journal of Wildlife Management* 45:484-488, 1981) for joint analysis of recapture and tag-recovery data is also only valid under no emigration or random emigration.

By making appropriate constraints on parameters the models reduce to previously published models including the Jolly-Seber model (with age-dependence and a temporary marking effect), tag-resight models, tag-recovery models, and joint live-recapture/tag-recovery models. Thus, the model provides a common framework for most widely-used mark-recapture models and allows simultaneous analysis of data obtained in several ways. Advantages of the new models include improved

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precision of parameter estimates, and the ability to distinguish between different type of emigration. FORTRAN programmes are developed for fitting the models to data with an application to a data set for brown trout (*Salmo trutta*) tagged in spawning tributaries of Lake Brunner, Westland between 1987 and 1991.

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To John,
whose life's work has made this work possible.

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Chapter 1

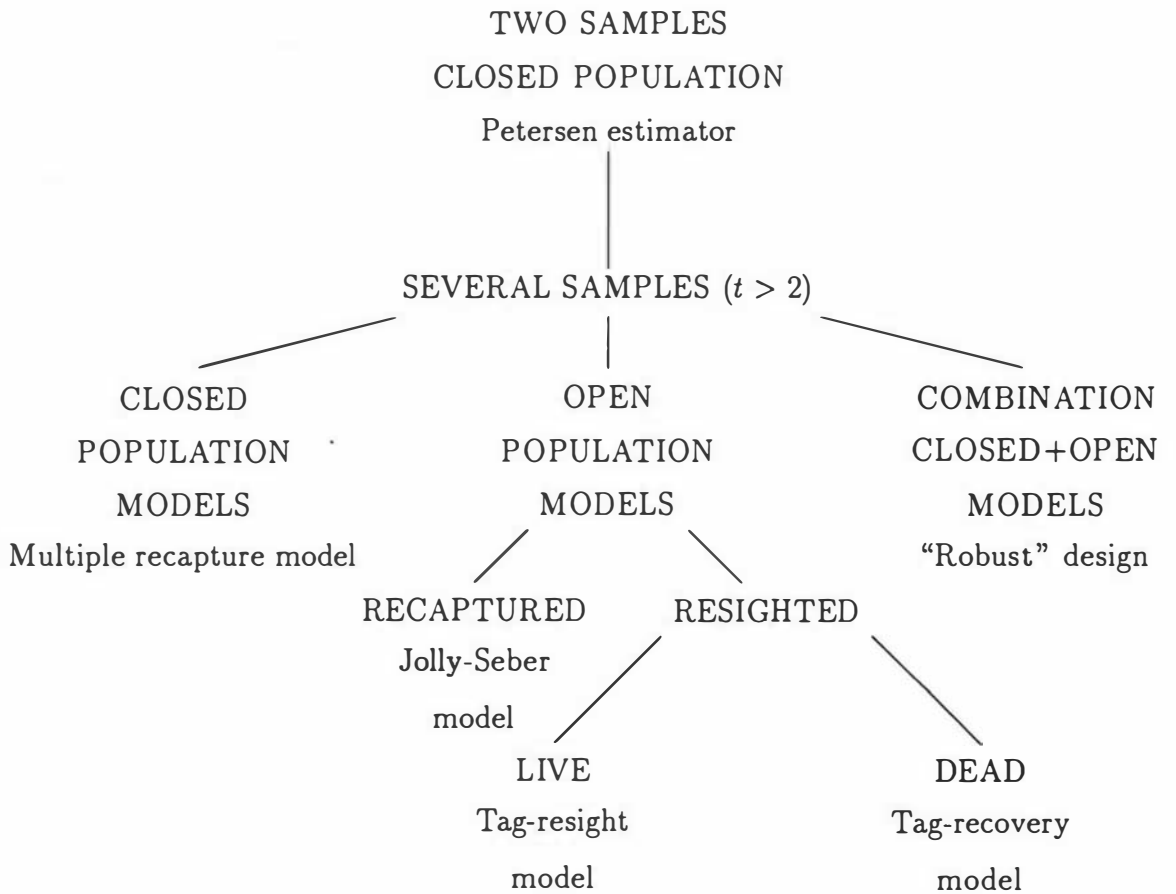
Mark-Recapture Overview

Estimates of population size obtained by marking a segment of the population and recording recaptures at later sampling occasions have a long history. The first recorded use of this technique has been attributed to Laplace who estimated the population of France in 1786 by recording the number of births in parishes with a known population and comparing these with birth registrations for the whole country (Cormack 1968).

There is an extensive mark-recapture literature with important reviews given by Cormack (1968,1979), Seber (1982,1986,1992), and Pollock et al. (1990). Mark-recapture models can be broadly divided into two categories: (A) models for populations which do not change during the study (closed population models), and (B) models for populations which may change during the course of the study (open population models). Open population models can also be categorized according to whether the recaptures are observations on live animals or dead animals. Within each broad category of mark-recapture models, individual models are classified according to their individual assumptions. An overview of these models indicating hierarchical relationships is given in Figure 1.

The description of the various models that follows roughly parallels the historical order of development with closed population models based on live recaptures considered first. Because of the separate development of the different types of models, each class has its own associated notation which we attempt to follow where pos-

Figure 1.1: Overview of the main classes of mark-recapture models and their inter-relationships. Adapted from Pollock et al. (1990).



sible. The final class of mark-recapture model that is described is the tag-recovery model of Chapter 2. In subsequent chapters we discuss developments that unify the various mark-recapture models. The notation is developed from that used to describe the tag-recovery models.

1.1 Closed-Population Mark-Recapture Models

The earliest mark-recapture models were for closed-populations. Such models lead to simpler mathematics than the open population models discussed in section 1.2. However, a major disadvantage is that their use is limited to short-term studies where the assumption of population closure is reasonable.

1.1.1 Petersen estimator

In the simplest method, referred to as the “Petersen method” or “Lincoln index” (Seber 1982), a sample of n_1 animals is caught, marked, and then released. These are allowed to mix with the remaining population and then a second sample of n_2 animals is obtained and the number of tagged animals, denoted m_2 recorded. Assuming that the proportion of marked animals in the sample is a good estimate of the proportion of marked animals in the population we obtain the intuitive Petersen estimator

$$\hat{N} = \frac{n_1 n_2}{m_2} \quad (1.1)$$

The method assumes:

- (i) The population is closed to additions and deletions.
- (ii) All animals are equally likely to be captured in both samples
- (iii) Animals do not lose marks between the two sample, and all marks are reported in the second sample.

If we also assume that the second sample is a simple random sample, then the exact conditional distribution of m_2 given n_1 and n_2 is hypergeometric (Seber 1982)

with probability function

$$Pr(m_2|n_1, n_2) = \frac{\binom{n_1}{m_2} \binom{N - n_1}{n_2 - m_2}}{\binom{N}{n_2}} \quad (1.2)$$

For this model the integer part of (1.1) is the maximum likelihood estimator (MLE). Because m_2 can be zero with non-zero probability the estimator \hat{N} has infinite bias, although this is of little practical importance. Of greater interest is bias in the case $m_1 > 0$. Chapman (1951) (cited in Seber 1982) investigated the properties of \hat{N} and found that it has a large bias in small samples. To reduce this bias he proposed a modified version

$$\hat{N}^* = \frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} - 1, \quad (1.3)$$

which is exactly unbiased for $n_1 + n_2 \geq N$ (Seber 1982). For the case where $n_1 + n_2 < N$ Robson and Regier (1964) recommend that $E[m_1^2] > 4$ to ensure that relative bias is small. Seber (1982) gives an approximately unbiased variance estimate for this estimator.

1.1.2 Multiple recaptures

An important extension of the Petersen estimator is to the case where recaptures are obtained on more than one occasion. A series of s recaptures of size n_1, \dots, n_s are made and examined for marks. Each animal is then released back into the population with previously unmarked animals receiving a mark. The first estimator for this situation was given by Schnabel (1938), however maximum likelihood estimators based on a generalized hypergeometric sampling model were developed by (Chapman 1952 - cited in Seber 1983) and (Darroch 1958).

If we let M_i denote the number of marked individuals in the population immediately before the i th sample (e.g. $M_1 = n_0$), and m_i the number of marked animals in the i th sample of size n_i , then by a straightforward extension of the

$s = 1$ Petersen model, the probability function under a hypergeometric formulation of the sampling model is given by

$$Pr(m_1, \dots, m_s | n_0, \dots, n_s) = \prod_{i=1}^s \frac{\binom{M_i}{m_i} \binom{N - M_i}{n_i - m_i}}{\binom{N}{n_i}}.$$

From Seber (1982:131) the MLE satisfies

$$\left(1 - \frac{M_{s+1}}{N}\right) = \prod_{i=1}^s \left(1 - \frac{n_i}{N}\right).$$

In the hypergeometric model, the random component of sampling arises through the activity of the experimenter. An alternative is to consider that the animals place themselves at risk of capture through their behaviour. Captures on the i th sampling occasion are assumed to occur at random with probability p_i . This leads to a multinomial distribution with index N and outcomes defined by the various possible recapture categories.

Because of the multiple samples, a capture history can be built up for each animal. The usual representation of a capture history is an s dimension vector with a one in the i th position ($i = 1, \dots, s$) if the animal was captured in sample i or zero otherwise. For example the capture history (1011) from a four sample study signifies that the animal was captured in the first, third, and fourth samples but not in the second. From Seber (1982), let a_ω denote the number of animals with capture history ω and $\{a_\omega\}$ the set of observed a_ω 's and $\{n_i\}$ the set of observed n_i 's. Assuming

1. All animals have the same probability p_i of capture in the i th sample (the "homogeneous capture probabilities" assumption)

2. Captures in each sample are independent,

the joint probability of $\{a_\omega\}$ is given by

$$Pr(\{a_\omega\} | \{n_i\}) = \frac{N!}{\prod_{\omega} a_\omega! (N - M_{s+1})!} \prod_{i=1}^s p_i^{n_i} (1 - p_i)^{N - n_i}.$$

The MLE's for the hypergeometric and multinomial models are asymptotically equivalent. The main difference between the two models, apart from the issue of fixed vs random sample size, is the ease with which modifications can be made. Cormack (1979) argued in favour of the multinomial model as it is easier to modify the assumptions, for example to allow animals to have different catchabilities.

1.1.3 Generalizations

The homogeneous capture probabilities assumption may not always be appropriate. There are two main ways in which capture probabilities may differ among individuals:

1. Differences in capture probability that are an inherent feature of the animal. For example, young animals may have different probabilities of capture from old animals. Similarly, animals in poorer condition may be more vulnerable to capture.
2. Differences that are induced by the experiment. A “trap-happy” response occurs when animals are more likely to be recaptured as a consequence of the trapping experience. For example, if the traps are baited with food, animals that have been captured previously may be more likely to enter the trap. In contrast, “trap-shy” animals avoid being trapped, as a consequence of a previous unpleasant trapping experience.

To distinguish between the two possibilities we refer to the first as “heterogeneity” and the second as “trap response”.

Otis et al. (1978) considered a set of models that make different assumptions about the presence of temporal effects, trap response, or heterogeneity. They also developed a computer program called CAPTURE that provides estimates for some of these models. The following description of the models is based on the description given by Pollock et al. 1992:11-14.

M_0 The Equal Catchability Model:

This model assumes that capture probabilities are constant through time and are the same for all animals. CAPTURE provides a maximum likelihood estimator obtained by numerical methods. The model is sensitive to heterogeneity and a trap response but is robust to changes in capture probability over time (Pollock et al. 1992).

M_h The Heterogeneity Model:

This model assumes that each animal has its own capture probability drawn at random from an arbitrary probability distribution $F(p)$ over $(0,1)$ at the start of the experiment. Burnham and Overton (1978a) showed that regardless of the choice of $F(p)$ the set of capture frequencies for the M_{s+1} animals observed in the experiment is sufficient for the estimation of N .

Specifying a distribution for $F(p)$ then using maximum likelihood methods failed to produce satisfactory results and instead Burnham and Overton (1978a, 1978b) suggested a nonparametric estimator based on the "jackknife" method of bias reduction applied to the estimator $\hat{N} = M_{s+1}$. If no assumption is made about $F(p)$, M_{s+1} is in fact the MLE for N (Cormack 1979), and is very biased unless capture probabilities are close to 1, or s is large. The "jackknife" technique can be used to produce a series of estimators, and Burnham and Overton (1978a, 1978b) provided an objective method of choosing the estimator. The jackknife estimator and the objective selection method proposed by Burnham and Overton (1978) have been programmed into CAPTURE. Several simulation studies have indicated satisfactory performance of the jackknife estimator (e.g. Otis et al. 1978 and White et al. 1982). Cormack (1989:404) states that the jackknife estimator has a theoretical basis if bias of the initial estimator M_{s+1} can be expressed as a power series in $1/s$ but provides a proof that this is not possible for M_0 . "Thus, despite the simulation successes achieved by this estimator, standard theory does not prove that the jackknife estimator has any smaller bias than the initial estimator ..." (Cormack 1989) where the "initial estimator" is M_{s+1} .

One weakness of the jackknife estimator is that it usually underestimates N if many individuals have low capture probabilities (Chao 1987). Chao (1987) proposed an alternative estimation procedure for M_h . Her method uses the expected values of the capture frequencies to derive a minimum bound on N . Investigations using simulated data indicated improved performance of Chao's M_h estimator over the jackknife estimator for low average capture probabilities but the jackknife estimator performed better in studies with high average capture probabilities and a large number of captures. Chao (1989) proposed a similar estimator for the model M_t . Simulating using sparse (low p) data experiments she found her estimator showed little bias.

M_b The Permanent Trap Response Model:

The trap response model assumes that all unmarked animals have the same probability (p) of capture in all samples, and all marked animals have the same probability of capture (c) after they have been captured once. The MLE is computed numerically in program CAPTURE. An intuitive approach to estimation is discussed below for model M_{bh} . It should be noted that model rmM_b is in essence the removal method of Zippin (1951).

M_{bh} The Heterogeneity and Trap Response Model:

Model M_{bh} assumes that each animal has its own unique pair of capture probabilities ($p_i, c_i; i = 1, \dots, N$) which are assumed constant over all sampling times. Under the trap response model, the number of unmarked animals captured at i (u_i) has a linear regression on M_i , the cumulative catch up until sampling time i (i.e. the cumulative number of captured and marked animals immediately before i) or

$$E[u_i|M_i] = pN - pM_i .$$

Under M_{bh} the equivalent regression is given by

$$E[u_i|M_i] = \bar{p}_i N - \bar{p}_i M_i .$$

where \bar{p}_i is the average probability of capture in the i th sample for animals that have not been captured. If there is no heterogeneity then this remains constant from sample to sample, and the regression is linear. Under heterogeneity the high capture probability animals are captured sooner on average than the low capture probability animals. Hence, \bar{p}_i tends to diminish with i and the regression is non-linear. CAPTURE computes MLE's for this model.

M_t The Time-Dependent Multiple Recapture Model:

The multiple-recapture model described in section 1.1.2 allows capture probabilities to vary through time but allows no trap response and no heterogeneity. CAPTURE provides maximum likelihood estimates for this model.

Other Time-Dependent Models

Models M_h , M_b , and M_{bh} each have time specific generalizations M_{th} , M_{tb} , and M_{tbb} respectively, however it is difficult to find satisfactory estimates of population size for these models without additional assumptions. If individual capture probabilities are associated with known covariates, Pollock et al. (1984) showed how a relationship between capture probabilities and auxiliary variables can be incorporated into the model (also see Huggins 1989). A difficulty is that covariates for uncaptured animals are unknown, however Huggins (1989, 1991) and Alho (1990) independently reported a method of analysis where inference is conditional on the captured animals.

Finally, Chao et al. (1992) proposed an estimator for M_{th} based on the idea of sample coverage - the proportion of total individual capture probabilities of the captured animals. Using simulated data under M_{th} they found that their estimator outperformed the MLE for M_t and the jackknife estimator for M_h if there was large variation in capture probabilities among individuals and sample coverage was large. CAPTURE provides Chao's estimator and also includes an MLE for one version of model M_{tb} .

1.1.4 Log-linear models

Fienberg (1972) and Cormack (1979) showed how the multinomial model can be reparamaterized in terms of log-linear models based on representing mark-recapture data in terms of incomplete multi-way contingency tables. For the Petersen estimator we can form the 2×2 contingency table

First sample	Second sample		Total
	Present	Absent	
Present	m_2	$n_1 - m_2$	n_1
Absent	$n_2 - m_2$	-	-
	n_2	-	N

which is incomplete because we do not observe those animals who were absent in both samples. If this component were observed then we could test for independence of the two samples. In the Petersen estimator we take the reverse approach and assume independence in order to estimate the size of the unobserved component, and hence N . In the general case the counts of individuals with different capture histories form an $s + 1$ dimension contingency table, with the i th dimension a partition into categories of animals that were observed or not observed in sample i (Cormack 1994).

The model can be fitted to mark-recapture data using log-linear models with the number of animals observed with each distinct capture history as the counts. Note the last category corresponding to animals never observed is unobservable. An advantage of the contingency table approach is that various types of dependence are well understood in terms of log-linear models for count data. Determination of the different types of dependence in the model depends on which interaction terms are included in the model.

Cormack (1979) shows that M_i corresponds to the log-linear model with only main effects (i.e. samples are independent), and M_o is the case where all main effects are assumed equal (Cormack 1994). Models exhibiting different forms of dependence between samples can be formulated in a hierarchical series determined by the inclusion of the various interaction terms. For example, a temporary trap-

response extending only for one sampling period is modelled by including all first-order interactions. Because the count of animals who were seen in none of the samples is a structural zero (i.e. by definition this count is unobservable), the highest order interaction must be assumed to be zero.

1.1.5 Martingale estimators

The above models all assume that sampling is carried out at discrete points in time. Continuous time versions of M_t have been developed by Becker (1984) and Yip (1989) with estimators utilizing Martingale theory. Yip (1989) also gave a discrete time estimator for model M_t however this method has been criticized because the method is not invariant to the order in which samples are taken (Seber 1992:141). Lloyd and Yip (1991) and Lloyd (1992) extended the Martingale analysis to include model M_h by assuming beta distributed capture probabilities.

Wilson (1992) compared maximum likelihood (ML) based estimators with the martingale estimator for M_t . He used simulated data generated under M_t , M_{th} and M_{tbh} and found that the martingale estimator was less efficient than the ML estimators in all cases considered but obtained similar results for relative bias. Lloyd (1992) compared the martingale M_h estimator with the jackknife estimator using M_h data simulated under beta and non beta conditions and found the martingale estimator less biased under all the conditions he considered. However, Lloyd (1992) found it difficult to devise an interval estimator which has close to nominal coverage rates.

1.2 Open Populations

The assumption of a closed population in the models of section 1.1 is in practice very restrictive and may be violated in a number of ways. In certain cases population additions or losses may occur without serious consequence. For example, Seber (1982:152) shows that the multihypergeometric model of section 1.1.2 may be modified to allow known removals from the population on capture. This is par-

ticularly relevant when there is some known mortality associated with the capture process. Seber (1982) also shows that if mortality occurs between samples in the Petersen estimator then \hat{N} is still a valid estimate of the size of the population at time 1. If marked and unmarked animals have the same probability of surviving, denoted ϕ , then

$$E \left[\frac{m_2}{n_2} | n_1 \right] \approx \frac{\phi n_1}{\phi N}$$

and \hat{N} will be approximately unbiased for N . Similarly, if there is recruitment of animals into the population between the samples, with the number of recruits denoted R then

$$E \left[\frac{m_2}{n_2} | n_1 \right] \approx \frac{n_1}{N + R}$$

and \hat{N} will be approximately unbiased for $N + R$, the population size following recruitment. However, if there is both mortality and recruitment there is no useful interpretation of \hat{N} .

1.3 Jolly-Seber Model

The earliest models for open populations considered population change to be deterministic (Cormack 1979), however our interest is in the case where population change occurs randomly. The most important development in mark-recapture models for open populations with stochastic population dynamics has been the so-called Jolly-Seber model first published in complete form by Jolly (1965) and Seber (1965), although the model for recaptures was anticipated by Cormack (1964).

The Jolly-Seber model allows different survival rates between samples, denoted S_i , and different capture probabilities, p_i , at each sample. Traditionally, emigration has been assumed permanent, in which case emigration is indistinguishable from death, and the joint probability that an animal survives between i and $i + 1$ and is at risk of capture at $i + 1$ (i.e. does not emigrate between i and $i + 1$) denoted by ϕ_i . Recently it has been pointed out that the Jolly-Seber model structure, at least for marked animals, is appropriate under a different type of emigration, where the probability that the animal is at risk of capture at $i + 1$ given that it was at risk of

capture at i is the same as the probability it is at risk of capture at $i + 1$ given that it was not at risk of capture at i (Burnham 1993). In this case, the parameter ϕ_i equals the true survival rate S_i , and the parameter p_i is the joint probability that a marked animal is at risk of capture and is captured at i .

1.3.1 Assumptions and notation

The following parameters and statistics are defined under permanent emigration:

Parameters

M_i = the number of marked animals in the population immediately prior to sample i ($i = 1, \dots, t$) (NB $M_1=0$).

N_i = the total number of animals in the population at i ($N_i = 1, \dots, t$).

U_i =the total number of unmarked animals in the population at time i .

B_i = the total number of new animals (recruits) entering the population between the i th and $(i + 1)$ th sample ($i = 1, \dots, t - 1$).

ϕ_i = the probability an animal alive and at risk of capture at time i is alive and at risk of capture at time $i + 1$ ($i = 1, \dots, t - 1$).

p_i = the probability an animal alive and at risk of capture at time i is captured at i ($i = 1, \dots, t$).

η_i = the probability an animal captured at i is released at i .

Statistics

$M_{i,j}$ = the number of marked animals released at time i next captured at time j ($i=1, \dots, t - 1$; $j=2, \dots, t$).

m_i = the number of marked animals captured in the i th sample ($i = 1, \dots, t$; $m_1 = 0$).

u_i = the number of unmarked animals captured in the i th sample ($i = 1, \dots, t$).

$n_i = m_i + u_i$, the total number of animals captured in sample i , ($i = 1, \dots, t$).

d_i = the number of the n_i that are lost on capture.

R_i = the number of the n_i that are released after sample i ($i = 1, \dots, t - 1$).

r_i = the number of the R_i that are ever captured again ($i = 1, \dots, t - 1$).

z_i = the number of marked animals not captured at i but that are captured at any time after i ($i = 2, \dots, t - 1$),

T_i = the number of marked animals at i that are captured at or after i ($T_i = z_i + m_i$).

The Jolly-Seber model assumes:

- (i) All animals in the population have the same probability of capture p_i at time i ,
- (ii) All animals in the population have the same probability ϕ_i of survival from time i until $i + 1$,
- (iii) Losses on capture are random, and every animal captured in the i th sample has the same probability of being released on capture.
- (iv) Animals do not lose their marks and all marks are correctly reported when encountered.
- (v) Recaptures are independent both between animals and between sampling times.
- (vi) Captures are made instantaneously at time i and each release is made immediately after the sample.

Under the assumption of random emigration, as discussed above, ϕ_i is redefined as the probability an animal alive at i is alive at $i + 1$, and p_i is the probability an animal is at risk of capture and is captured at i given that it is alive at i .

1.3.2 Intuitive estimators

Both Jolly (1965) and Seber (1965) formulated their models in terms of a multinomial distribution then obtained closed form MLE's. Jolly (1965) noted that the MLE's have a simple intuitive interpretation (see also Pollock et al. 1990:20-21).

The key difference between the closed and open population models is that we do not know M_i (apart from $M_1 = 0$) and as a consequence the M_i 's must be estimated. If the assumptions of the model are correct, then the proportion of marked animals not captured at i that are ever captured again should equal on average the proportion of marked animals captured at i that are ever captured again, or

$$\frac{z_i}{M_i - m_i} \sim \frac{r_i}{R_i}$$

which leads to the estimator

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i},$$

for $i=2, \dots, t-1$. Once we have an estimate of M_i , then we can estimate p_i as the estimated proportion of marked animals captured at i , or

$$\hat{p}_i = \frac{m_i}{\hat{M}_i}$$

for $i = 2, \dots, t-1$, and population size by the Petersen estimator substituting \hat{M}_i for M_i

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i}.$$

The intuitive estimator of survival rate is the proportion of marked animals in the population immediately after sampling time i that are still alive at sampling time $i + 1$

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i},$$

where $\hat{M}_i - m_i$ is the estimated number of marked animals not captured at i and R_i is the number of marked animals captured and released at i . Note that losses on capture are included in the analysis by conditioning on the releases R_i .

The obvious estimator of recruitment is then

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

which reduces to

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i \hat{N}_i$$

if all animals are released on capture.

Asymptotic variances and covariances are given by Pollock et al. (1990). Of particular relevance to later chapters are the asymptotic variances for \hat{p}_i and $\hat{\phi}_i$ given by

$$Var(\hat{p}_i | p_i) = [p_i(1 - p_i)]^2 \left(\frac{1}{E[r_i]} - \frac{1}{R_i} + \frac{1}{E[m_i]} + \frac{1}{z_i} \right)$$

and

$$Var(\hat{\phi}_i | \phi_i) = \phi_i^2 \left\{ \frac{1}{E[r_i]} - \frac{1}{R_i} + (1 - p_{i+1})^2 \left(\frac{1}{E[r_{i+1}]} - \frac{1}{R_{i+1}} \right) + p_{i+1}(1 - p_{i+1}) \frac{(R_{i+1} - E[r_{i+1}])^2}{R_{i+1}E[r_{i+1}](z_{i+1} + E[r_{i+1}])} \right\} .$$

Note that the above variances include only the variance due to estimation and would equal zero if all animals in the population were captured. Thus nonsampling variation due to the stochasticity of the birth and death processes is ignored. Variance and covariance estimates incorporating both components are given by Seber (1982:202-203). For example if the experimenter is interested in the underlying survival probability then from Pollock et al. (1990:22)

$$Var(\hat{\phi}_i) = Var(\hat{\phi}_i | \phi_i) + \frac{\phi_i(1 - \phi_i)}{M_i - E[m_i] + R_i} .$$

This will tend to zero when the number of marked animals is large.

1.3.3 The Jolly-Seber likelihood

The complete formulation of the Jolly-Seber model requires a model for the recaptures of released (i.e. marked) animals and a model for the captures of unmarked

animals. From Seber (1982) (see also Brownie et al. 1986) the likelihood for the observed sets of variables $\{u_i\}$, $\{d_i\}$, and $\{M_{i,j}\}$ can be factored into three components:

$$\begin{aligned} \mathcal{L}(\{u_i\}, \{d_i\}, \{M_{i,j}\}) &= \mathcal{L}_1(\{u_i\} | \{U_i\}, \{p_i\}) \times \mathcal{L}_2(\{d_i\} | \{u_i, M_{i,j}\}, \{\eta_i\}) \\ &\quad \times \mathcal{L}_3(\{M_{i,j}\} | \{R_i\}, \{\phi_i, p_i\}). \end{aligned}$$

From assumption (iii) the distribution of the d_i 's conditional on the n_i 's is binomial hence

$$\mathcal{L}_2 = \prod_{i=1}^t \binom{n_i}{d_i} (1 - \eta_i)^{d_i} \eta_i^{n_i - d_i}. \quad (1.4)$$

Model for recaptures of marked animals

A convenient method of summarizing the recaptures of marked animals in a mark-recapture experiment is the reduced m-array (Burnham et al. 1987). Let $M_{i,j}$ be the number of marked animals released at i that were next captured at j the reduced m-array has the form given in Table 1.1 The collection of animals released

Table 1.1: Reduced m-array summary of a mark-recapture data set with t years of capture.

Cohort	No. released	Time first recaptured				
		$j = 2$	3	4	...	t
$i = 1$	R_1	$M_{1,2}$	$M_{1,3}$	$M_{1,4}$...	$M_{1,t}$
2	R_2		$M_{2,3}$	$M_{2,4}$...	$M_{2,t}$
3	R_3			$M_{3,4}$...	$M_{3,t}$
.	.				.	.
.	.				.	.
.	.				.	.
$t - 1$	R_{t-1}					$M_{t-1,t}$

at i are referred to as a cohort. A member of the i th cohort can be *first* recaptured following release at i at just one of the times $j = i + 1, \dots, t$. As a consequence the

$M_{i,j}$'s ($j = i + 1, \dots, t$) are mutually exclusive and the recaptures for each cohort can be modelled as multinomial counts. On capture at time j , a marked animal contributes to $M_{i,j}$ then is re-released as a member of a new cohort, cohort j . Animals may appear in more than one cohort, but within each cohort each animal may appear in only one recapture cell. This emphasizes that we are conditioning on the releases in the Jolly-Seber model. Each pair of release-recapture events is considered independent of other release-recapture events which is justified because we know the animal is alive at the time of each release or recapture (Burnham 1991).

The probabilities for each multinomial "cell" are formulated using our knowledge of the fate of the animals between release and subsequent recapture. For example, for members of $M_{1,3}$ we know that these animals survived from time 1 to 2 and remained at risk of capture, which happened with probability ϕ_1 . Given that they were alive at time 2, they were not captured with probability $(1 - p_2)$, then they survived from time 2 until 3 and remained at risk of capture with probability ϕ_2 . Finally, given they were alive and at risk of capture at time 3 they were captured with probability p_3 . Therefore the multinomial cell corresponding to $M_{1,3}$ has probability $\phi_1(1 - p_2)\phi_2p_3$. The cell probability structure for the m-array in Table 1.1 is given in Table 1.2.

Table 1.2: Probability structure for the reduced m-array of Table 1.1 .

Cohort	Time first recaptured				
	$j = 2$	3	4	...	t
$i = 1$	$\phi_1 p_2$	$\phi_1(1 - p_2)\phi_2 p_3$	$\phi_1(1 - p_2)\phi_2(1 - p_3)\phi_3 p_4$...	$\phi_{t-1} p_t \prod_{h=1}^{t-2} \phi_h(1 - p_{h+1})$
2		$\phi_2 p_3$	$\phi_2(1 - p_3)\phi_3 p_4$...	$\phi_{t-1} p_t \prod_{h=2}^{t-2} \phi_h(1 - p_{h+1})$
3			$\phi_3 p_4$...	$\phi_{t-1} p_t \prod_{h=3}^{t-2} \phi_h(1 - p_{h+1})$
.				.	.
.				.	.
.				.	.
$t - 1$.	$\phi_{t-1} p_t$

Each cohort also has a final cell corresponding to animals never seen again, and this cell has probability $1 - \lambda_i$ where

$$\lambda_i = \sum_{h=i+1}^t \pi_{i,j}$$

and $\pi_{i,j}$ denotes the probability of the event “released at i , next captured at j ”. The likelihood for recaptures conditional on the releases can then be written as

$$\mathcal{L}_3 \propto \prod_{i=1}^{t-1} (1 - \lambda_i)^{(R_i - r_i)} \prod_{h=i+1}^t \pi_{i,h}^{M_{i,h}}.$$

This form of the likelihood is not particularly convenient for deriving parameter estimates, however Burnham (1991) shows that \mathcal{L}_3 can be factored into the product of two sets of terms. The first set of terms involves the distribution of a set of minimally sufficient statistics, denoted $Pr(MSS)$. The second “residual” set of terms involves the distribution of various linear combinations of the $M_{i,j}$ ’s conditional on the MSS and does not involve the ϕ_i or p_i ’s. Hence the “residual” term is not involved in parameter estimation and we can write

$$\mathcal{L}_3 \propto Pr(MSS) = \prod_{i=1}^{t-1} \binom{R_i}{r_i} \lambda_i^{r_i} (1 - \lambda_i)^{(R_i - r_i)} \prod_{i=2}^{t-1} \binom{T_i}{m_i} \tau_i^{m_i} (1 - \tau_i)^{Z_i}, \quad (1.5)$$

where

$$\tau_i = \frac{\phi_{i-1} p_i}{\lambda_{i-1}}.$$

Model for captures of unmarked animals

The most common approach (e.g. Seber 1982:198) to modelling captures of unmarked animals is to assume binomial sampling and hence

$$\mathcal{L}_1 = \prod_{i=1}^t \binom{U_i}{u_i} p_i^{u_i} (1 - p_i)^{U_i - u_i}$$

In this parameterization the unmarked segment of the population U_i appears as a parameter to be estimated. Burnham (1991) adopts a slightly different model which explicitly incorporates the recruitment components into the likelihood.

Defining $b_{i,j}$ as the number of the B_i that are first captured at time j then the set of $b_{i,j}$ ’s conditional on the B_i ’s can be modelled as multinomial counts in a similar fashion to the $M_{i,j}$ ’s. The only conceptual difference is that the $b_{i,j}$ ’s are unobservable (except $b_{0,1} = u_1$). Noting that

$$u_j = \sum_{i=0}^{j-1} b_{i,j}$$

and defining

$$b_{i..} = \sum_{j=i+1}^t b_{i,j} \quad i = 0, \dots, t-1$$

$$u_i^* = u_i + u_{i+1} + \dots + u_t \quad i = 1, \dots, t-1$$

and the sums of lower triangular blocks of the $b_{i,j}$'s

$$b_i^* = b_{i..} + b_{i+1..} + \dots + b_{t-1..} \quad i = 0, \dots, t-1$$

then $u_i^* - b_i^*$ is a rectangular block of $b_{i,j}$'s exactly analogous to the $T_i = z_i + m_i$'s obtained from the reduced m-array. Burnham (1991) shows that \mathcal{L}_1 can be expressed as

$$\begin{aligned} \mathcal{L}_1 = & \begin{pmatrix} N_1 \\ u_1^* - b_1^* \end{pmatrix} (p_1 + (1-p_1)\lambda_1)^{u_1^* - b_1^*} (1-p_1 - (1-p_1)\lambda_1)^{N_1 - u_1^* + b_1^*} \\ & \times \begin{pmatrix} u_1^* - b_1^* \\ u_1 \end{pmatrix} \tau_1^{u_1^*} (1-\tau_1)^{u_1^* - b_1^* - u_1} \times \prod_{i=2}^{t-1} \begin{pmatrix} u_i^* - b_i^* \\ u_i \end{pmatrix} \tau_i^{u_i^*} (1-\tau_i)^{u_i^* - b_i^* - u_i} \end{aligned} \quad (1.6)$$

hence the likelihood is expressed explicitly in terms of the recruitment parameters b_2^*, \dots, b_{t-1}^* which depend on the B_i 's ($i = 2, \dots, t-1$).

Maximum-Likelihood Estimation

From equations 1.6, 1.4, and 1.5 the Jolly-Seber likelihood $\mathcal{L} = \mathcal{L}_1 \times \mathcal{L}_2 \times \mathcal{L}_3$ can be expressed as the product of $4t-3$ conditionally independent binomial terms with $4t-3$ estimable parameters: $\eta_1, \dots, \eta_t, \phi_1, \dots, \phi_{t-2}, p_2, \dots, p_{t-1}, b_0^*, b_2^*, \dots, b_{t-2}^*$ and the confounded pairs $\phi_{t-1}p_t$ and N_1p_1 . The likelihood can be maximized to obtain explicit MLE's for ϕ_i and p_i and these correspond to the intuitive estimators described in section 1.3.2. Note that the p_i and ϕ_i 's are 1-1 functions of the binomial parameters, the λ_i and τ_i 's, thus the MLE's and their asymptotic covariances are reasonably straight-forward to obtain. From the form of \mathcal{L}_1 explicit moment-type estimators of the b_i^* Burnham (1991) can be obtained leading to the estimates of B_2, \dots, B_{t-2} and N_2, \dots, N_{t-1} described in section 1.3.2.

Note \mathcal{L}_2 only provides information on the η_i 's hence can be ignored unless η_i is of particular interest. All information from losses on capture that is relevant to the estimation of ϕ_i is provided by conditioning on the releases R_i . Also, all information relevant to the estimation of ϕ_i and p_i is provided by \mathcal{L}_3 with \mathcal{L}_1 contributing information on U_i , hence N_i , making use of the assumption that capture probabilities are identical for marked and unmarked animals. If this assumption is invalid, $\hat{\phi}_i$ and \hat{p}_i remain valid estimators for marked animals and \mathcal{L}_1 contributes no useful information.

1.4 Hypergeometric Formulation of the Jolly-Seber Model

In the multinomial formulation used by Jolly (1965) and Seber (1965) binomial variation was assumed for the sample sizes. Robson (1969) treated the sample size as a fixed observable number and the number of survivors of a group with assumed equal survival treated as a fixed unknown parameter. Under this hypergeometric formulation, which is a natural extension of M_t the likelihood function can be written as

$$\mathcal{L} \propto \prod_{i=2}^t \left\{ \frac{\binom{M_i}{m_i} \binom{U_i}{u_i}}{\binom{N_i}{n_i}} \right\} \prod_{i=2}^{t-1} \left\{ \frac{\binom{M_i - m_i}{z_i} \binom{R_i}{r_i}}{\binom{M_i - m_i + R_i}{z_i + r_i}} \right\}.$$

Robson (1969) showed that the MLE's \hat{M}_i and \hat{N}_i under the hypergeometric model are identical to the Jolly-Seber estimates of M_i and N_i respectively. Because the hypergeometric models do not explicitly model the birth and death processes, survival and recruitment parameters do not appear in the likelihood. Instead, the estimator of ϕ_i is obtained by defining

$$\phi_i = \frac{M_{i+1}}{M_i - m_i + R_i}.$$

and estimates of the B_i are subsequently obtained as in section 1.3.2.

1.4.1 Log-linear models

Cormack (1979,1981,1989) showed that the log-linear model discussed in section 1.1.4 naturally extend to open populations with the presence of certain interactions equivalent to birth, death or trap dependence (Cormack 1994). In the log-linear analysis the counts of animals with particular capture histories are regarded as independent Poisson random variables. The expected number of animals with a particular capture history is expressed as the product of terms involving the size of the population and the parameters used to describe population dynamics and the sampling process (i.e. p_i , ϕ_i etc).

For open populations the most difficult aspect of log-linear modelling is to incorporate recruitment into the model. Cormack (1979, 1981) incorporates recruitment by considering a super-population of animals who are either alive at the start of the experiment or who are recruited into the population during the experiment. This device allows the recruitment process to be defined in terms of probabilities. Contrast this with the Jolly-Seber model where the number of recruits entering the population between i and $i + 1$ is a parameter to be estimated.

Cormack (1989) showed how a wide range of models can be fitted using program GLIM (Payne 1986). These models include M_o , M_t , M_b , M_{tb} , and the Jolly-Seber model. Sandland and Cormack (1984) and Cormack and Jupp (1991) examined the relationship between the Poisson and multinomial estimators and show that for large population sizes the different approaches are interchangeable with respect to parameter estimates, asymptotic covariances, and testing between models. Reduced parameter versions of the Jolly-Seber model obtained by omitting births or deaths can also be fitted in GLIM as can a model with capture probabilities constrained over time. A model with survival probabilities constrained over time cannot be fitted however.

The advantage of GLIM is the ease with which the various models can be fitted within a common framework and the availability of residual plots as a diagnostic tool. Also, parameter estimation can easily be constrained to ensure that only admissible estimates are possible. A disadvantage is that the estimates of the log-

linear model effects must be back-transformed to obtain estimates of the biological parameters. Cormack (1993) showed how variances of the biological parameters can be obtained from the sampling covariance matrix for the log-linear model parameter estimates.

1.4.2 Small sample bias

As noted by Seber (1982:204) \hat{N}_i and \hat{M}_i both involve ratios with denominators that may take the value zero with non-zero probability. Motivated by the modification of Chapman (1951) (cited in Seber 1982) to the Petersen estimator Seber suggested a bias-adjusted form for the Jolly-Seber estimators:

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

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

$$\tilde{\phi}_i = \frac{\tilde{M}_i}{\tilde{M}_i - m_i + R_i}$$

and

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

which are all approximately unbiased (Seber 1982). Gilbert (1973) and Carothers (1973) investigated the small sample bias of \tilde{N}_i . Gilbert (1973) reported “considerable” small sample bias under certain conditions which contrasted with the finding of Carothers (1973) that the small sample bias was small. Carothers noted that the cases with serious small sample bias observed by Gilbert appeared to coincide with a predicted coefficient of variation ≥ 1 . Carothers (1973) concluded that if an estimate has a sufficiently low estimated variance to be of practical use then it is unlikely to be subject to small sample bias. Seber (1982:507) suggests that in such cases the “bias-adjusted” estimators such as \tilde{N}_i may be unnecessary.

A related problem is that of inadmissible estimates. Because parameters are not constrained to lie over their admissible range, estimates outside this range occur with non-zero probability. This usually manifests itself in survival rate estimates

greater than 1 or recruitment estimates less than 0. Buckland (1980) suggested a modified analysis that restricts the estimates to their admissible range. An alternative approach is to appropriately transform the parameters and is the approach used by the computer program SURVIV (White 1983). An argument against automatically restricting the parameters to their admissible range is that such estimates act as a flag that something may be wrong. Either the probability structure of the model may be incorrect, for example there may be non-random temporary emigration, or sample sizes may not be sufficiently large to ensure negligible small-sample bias.

1.4.3 Accuracy of Jolly-Seber variance estimates

Manly (1971a) examined the performance of the Jolly-Seber estimator using simulated data and found that when sample sizes are small confidence interval coverage rates may differ widely from their nominal value. Manly pointed out that this was a consequence of a high positive correlation between the estimated sampling variance of the parameter and the estimate when the estimates are substituted for the true values in the asymptotic variance formulae. The consequence is that underestimates appear more precise than is the actual case, and overestimates tend to understate the precision. Clearly, when sample sizes are small, the parameter estimates will tend to be imprecise, and the approximate variance estimates poor.

There have been a number of suggestions to improve confidence interval coverage rates. Manly (1977) investigated use of the generalized jackknife estimator (Gray and Shucancy 1972) to obtain confidence intervals and found that the resulting confidence intervals performed well. Buckland (1980) used a Monte Carlo confidence interval described in more detail in Buckland (1984). Buckland (1980) reported that the method compared favourably with the Jolly-Seber estimates, however, as the Monte Carlo simulations are based on the parameter estimates they will still suffer the problem discussed by Manly (1971a) of the variance estimate being correlated with the parameter estimate. To circumvent this problem, Manly (1971a) proposed logarithmic and reciprocal transformations of population size and survival

rate estimates and although these improved confidence interval coverage rates he commented that they cannot be relied upon in general. Manly (1984) proposed transformations based on the form of the variance formulae that give theoretically better results. Using simulation Manly (1984) verified the theoretical improvement, however he pointed out that the transformations are still somewhat arbitrary giving them an “ad hoc” appearance (Pollock et al. 1990).

1.4.4 Heterogeneous capture and survival probabilities

A key assumption of the Jolly-Seber model is the homogeneous capture and survival probabilities assumption. There have been several investigations of the performance of the Jolly-Seber model when the homogeneous capture probability assumption is violated. A good summary of these studies is provided by Pollock et al. (1990). In essence, if capture probabilities vary among individuals then the marked population will tend to be those individuals with high capture probabilities, and the proportion m_i/n_i will tend to overestimate the true proportion of marked animals in the population. This leads to underestimation of the population size.

Carothers (1973) and Gilbert(1973) evaluated the bias of the Jolly-Seber population size estimator resulting from heterogeneous capture probabilities using analytic approximations and computer simulation. They found that bias in \hat{N}_i was negative and often large. The extent of bias depended largely on the degree of variation in capture probabilities among individuals and the average capture probability. If average capture probabilities were reasonably high then heterogeneous capture probabilities did not lead to appreciable bias of \hat{N}_i leading Gilbert (1973) to suggest that the experimenter should design the experiment so that nearly all animals have capture probabilities ≥ 0.5 . As pointed out by Pollock et al. (1990), this may be difficult to achieve in practice. Carothers (1973) also looked at bias in the survival rate estimator in response to heterogeneous capture probabilities and found it to be an order of magnitude less than the bias of the capture probability estimator.

Differences in capture probability and/or survival rates may be induced as a

result of the experiment. A temporary trap response (say lasting for one sampling period) can lead to bias in the parameter estimates. However this may not be serious as a set of models have been developed that explicitly model such a response (section 1.5). A permanent trap response is more serious as it cannot be explicitly incorporated into the model without additional assumptions. The effect of a permanent trap-response in capture probability on the Jolly-Seber estimators has been investigated by Nichols et al. (1984). Under a permanent trap response of the type in the closed-population model M_b , all marked animals have the same capture probability and the homogeneous capture probability assumption is valid for marked animals. Thus \hat{p}_i and $\hat{\phi}_i$ remain valid estimators for the capture and survival probabilities respectively for marked animals. Clearly in this case no valid estimate of population size is possible. Under a trap-happy response, marked animals have a higher capture probability than unmarked animals leading to an underestimate of N_i . Conversely, under a trap-shy response marked animals have a lower capture probability than unmarked animals leading to overestimation of N_i .

The usefulness of $\hat{\phi}_i$ depends on whether the assumption that marked and unmarked animals share the same survival rate is valid. The precision of the survival rate estimator is affected however. Under a trap-happy response the values of T_i and r_i are increased leading to increased precision of the survival rate estimator. In contrast, a trap-shy response leads to reduced precision of the survival rate estimator. If there is a permanent trap-response in survival rate, then the survival rate may be seriously biased. The most likely response is where marking reduces subsequent survival and is particularly relevant where the tags are large relative to the animal, or where the animal is injured in some way by the application of the tag. As with capture probabilities, a temporary trap-response in survival rates is less serious as this response can be explicitly modelled (see section 1.5).

Because of the sensitivity of the Jolly-Seber population size estimator to heterogeneous capture probabilities and the relative lack of sensitivity in the survival rate estimator, recent emphasis has shifted toward experiments in which survival rate estimation is the primary focus (Lebreton et al. 1992).

1.4.5 Special cases of the Jolly-Seber model

Following Jolly (1965) and Seber (1965) an important area of research has been the development of restricted parameter models that obtain greater precision of the parameter estimates by making more restrictive assumptions. Alternatively a number of models have been developed which relax the assumptions of the Jolly-Seber model. Pollock et al. (1990) provide a comprehensive review of these developments.

Deaths-only model

Jolly (1965:241-242) showed that incorporating the constraint $B_1 = B_2 = \dots = B_{t-1} = 0$ leads to

$$\hat{N}_i = \frac{R_i z'_i}{r_i} + n_i \quad i = 1, \dots, t-1,$$

and

$$\hat{p}_i = \frac{n_i}{\hat{N}_i}$$

where z'_i is the total number of animals (marked or unmarked) that are not captured at i but are captured after i ($z'_i = z_i + \sum_{j=i+1}^t u_j$). Note that an estimate of N_1 is available under the deaths only model.

The survival rate estimator is given by

$$\hat{\phi}_i = \frac{\hat{N}_{i+1}}{\hat{N}_i - n_i + R_i} \quad i = 1, \dots, t-2.$$

Because there is no need to estimate the number of recruits, there is a gain in the precision of the \hat{N}_i and $\hat{\phi}_i$'s. The asymptotic variances are given by

$$Var(\hat{N}_i | N_i) = (N_i - E[n_i])(N_i - E[n_i] + R_i) \left(\frac{1}{E[r_i]} - \frac{1}{R_i} \right)$$

$$Var(\hat{p}_i | p_i) = [p_i(1 - p_i)]^2 \left\{ \frac{1}{E[r_i]} - \frac{1}{R_i} + \frac{1}{N_i - E[n_i]} + \frac{1}{E[z'_i]} \right\}$$

and

$$Var(\hat{\phi}_i | \phi_i) = \phi_i^2 \left\{ \frac{(N_{i+1} - E[n_{i+1}])(N_{i+1} - E[n_{i+1}] + R_{i+1})}{N_{i+1}^2} \left(\frac{1}{E[r_{i+1}]} - \frac{1}{R_{i+1}} \right) + \frac{N_i - E[n_i]}{N_i - E[n_i] + R_i} \left(\frac{1}{E[r_i]} - \frac{1}{R_i} \right) \right\}.$$

The additional precision in the estimators over the Jolly-Seber estimators, and the availability of an estimator for p_1 , result from the fact that we know that all animals captured during the course of the experiment were alive on the first sampling occasion. Both the deaths-only and births only models described in the following section were first considered by Darroch (1959) for the special case of no losses on capture. Also, in the 2-sample case with no losses on capture $R_1 = n_1$, $z'_1 = u_1$ and $r_1 = m_2$, and

$$\hat{N}_1 = \frac{n_1(m_2 + u_2)}{m_2}$$

is simply the Petersen estimator as noted by Seber (1982:71) and discussed at the beginning of section 1.2.

Births only model

Jolly (1965) also considered the case where there are no deaths during the study and just births. In this case the population size is the Petersen estimator applied at each sample as noted by Seber (1982:71) for the 2-sample case. The estimators are given by

$$\hat{N}_i = \frac{n_i M_i}{m_i}$$

and

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

with asymptotic variances given by Jolly (1965) and Pollock et al. (1990) as

$$Var(\hat{N}_i | N_i) = N_i(N_i - E[n_i]) \frac{N_i - M_i}{N_i E[m_i]}$$

and

$$Var(\hat{B}_i | B_i) = Var(\hat{N}_{i+1} | N_{i+1}) + Var(\hat{N}_i | N_i).$$

Constant survival and capture

An early criticism of the Jolly-Seber model was that it involved a large number of parameters and lacked parsimony (Cormack 1979). Jolly (1982) introduced a series of three models:

Model B: Survival is constant but all remaining parameters are time specific,

Model C: Capture probabilities are constant but all remaining parameters are time specific,

Model D: Capture and survival probabilities are constant throughout the experiment.

Only the Jolly-Seber model (Model A) has explicit MLE's and numerical methods must be used to fit the sequence of models. Several computer packages are available which incorporate these models, for example JOLLY (Pollock et al. 1990 with the exception of Model C). The flexible program SURVIV (White 1983) can be used to fit all four models for the recapture component of the model and allows intermediate cases to be fitted as well. For example a model with constant survival for groups of sampling times is easy to fit in SURVIV.

Jolly (1982) used a Poisson likelihood and like Cormack (e.g. 1979) conceptualized a super-population in order to model recruitment. Brownie et al. (1986) used a multinomial model to obtain Jolly's results and showed how to construct goodness-of-fit tests and comparisons between models that were more efficient than those suggested by Jolly (1982). Specifically they showed that the goodness-of-fit tests for each model could be easily constructed from the goodness-of-fit test for Model A and the test of the restricted model against Model A. Their procedure is discussed in more detail in section 5.5.

Crosbie and Manly (1985) also used a multinomial likelihood to fit reduced parameter models, however they achieved flexibility by specifically modelling both the birth and death processes. To model the birth process they also envisaged a super-population of animals containing all animals present in the population during the course of the experiment. Estimation procedures for the models of Crosbie and Manly (1985) are complex and are carried out numerically.

1.5 Generalizations of the Jolly-Seber Model

Because of the sensitivity of the Jolly-Seber estimators to heterogeneous capture probabilities in particular, there have been a number of generalizations of the model which relax the homogeneity assumption. A detailed discussion of the generalizations discussed below is given by Pollock et al. (1990). We also discuss a generalization which relaxes the assumption of permanent (or random) emigration.

Temporary trap-response model

Robson (1969) introduced a model that allowed marking to have a short-term (usually lasting 1 capture period) effect on survival probabilities. Independently Manly (1971b) developed a similar model. Pollock (1975) extended Robson's (1969) model to include a short term effect on capture probabilities. In the Jolly-Seber model the population is divided into two groups of animals: marked and unmarked, with the assumption that all animals, whether marked or unmarked, have the same time-specific capture and survival probabilities. This assumption allows inference to be made about the population. Robson (1969) and Pollock (1975) consider the population immediately after each sample as comprising three groups: unmarked, newly marked, and previously marked. Newly marked is usually taken as first marked at the most recent sample, with the response lasting just one sampling period, however a longer-lasting response is also possible under their model. The assumption that the trap-response "wears off" after the short term (i.e. capture and survival probabilities for previously marked and unmarked animals are equal) means that inference can still be made about the population based on the sample of marked animals.

The estimators have the same form as the Jolly-Seber estimators with the difference that estimates are made just using the subset of animals that are not newly marked (Pollock et al. 1990). As a consequence they are less precise than the corresponding Jolly-Seber estimates. Pollock (1975) and Brownie and Robson (1983) also derived straight-forward contingency tables which test the Jolly-Seber model

against the alternative trap-response model.

Age-dependent model

A likely source of heterogeneity is parameters differing by age-class. Manly (1970) showed that age-dependent mortality can lead to bias in the Jolly-Seber estimates. Pollock (1981a) proposed a model for the situation where the population comprises age class 0 through l animals, with parameters varying among classes. Sampling is assumed to occur on the anniversary dates of the animals. Stokes (1984) extended this model to allow sampling between, as well as on, the anniversary dates.

Using the same notation as the Jolly-Seber model but introducing the superscript ν to denote age-class occupied at the time of sampling, Pollock (1981) shows that the MLE's are given by

$$\hat{N}_i^{(\nu)} = \frac{n_i^{(\nu)} \hat{M}_i^{(\nu)}}{m_i^{(\nu)}} \quad \nu = 1, \dots, l-1$$

$$\hat{N}_i^{(l)} = \frac{n_i^{(l)} (\hat{M}_i^{(l)} + M_i^{(l+1)})}{m_i^{(l)}}$$

$$\hat{M}_i^{(\nu)} = m_i^{(\nu)} + \frac{R_i^{(\nu)} z_i^{(\nu)}}{r_i^{(\nu)}} \quad \nu = 1, \dots, l-1$$

$$\hat{M}_i^{(l)} + \hat{M}_i^{(l+1)} = m_i^{(l)} + \frac{R_i^{(l)} z_i^{(l)}}{r_i^{(l)}}$$

$$\hat{M}_i^{(l)} = \frac{T_i^{(l)}}{T_i^{(l)} + T_i^{(l+1)}} (\hat{M}_i^{(l)} + \hat{M}_i^{(l+1)})$$

$$\hat{\phi}_i^{(\nu)} = \frac{M_{i+1}^{(\nu+1)}}{M_i^{(\nu)} - m_i^{(\nu)} + R_i^{(\nu)}} \quad \nu = 0, \dots, l-1$$

$$\hat{\phi}_i^{(l)} = \frac{M_{i+1}^{(l+1)}}{M_i^{(l)} + M_i^{(l+1)} - m_i^{(l)} + R_i^{(l)}} .$$

Note for unmarked animals we can only distinguish the age-classes $0, \dots, l$ but for marked animals we can distinguish $l + 1$ age classes -those animals aged exactly $0, \dots, l$, and those animals at least age $l + 1$. Identification of this additional age-class is needed for parameter estimation. In addition to the above estimators, Pollock et al. (1990) show that it is possible to partition recruitment into $B_i^{1(\nu)}$ and $B_i^{11(\nu)}$ where

$B_i^{1(\nu)}$ = the number of survivors at $i + 1$ of members of age class $(\nu - 1)$ at i ,

$B_i^{11(\nu)}$ = the number of animals immigrating between i and $i + 1$ that are present and of age ν at time $i + 1$.

These are estimated by

$$\hat{B}_i^{1(\nu)} = \hat{\phi}_i^{(\nu-1)} (\hat{N}_i^{(\nu-1)} - n_i^{(\nu-1)} + R_i^{(\nu-1)}) \quad \nu = 2, \dots, l$$

$$\hat{B}_i^{11(\nu)} = N_{i+1}^{(\nu)} - \hat{B}_i^{1(\nu)} \quad \nu = 2, \dots, l - 1$$

$$\hat{B}_i^{11(l)} = N_{i+1}^{(l)} - \hat{\phi}_i^{(l)} (\hat{N}_i^{(l)} - n_i^{(l)} + R_i^{(l)}) - \hat{B}_i^{1(l)}$$

and

$$\hat{B}_i^{(\nu)} = \hat{B}_i^{1(\nu)} + \hat{B}_i^{11(\nu)} \quad \nu = 2, \dots, l.$$

Asymptotic variances for $\hat{N}_i^{(\nu)}$, $\hat{M}_i^{(\nu)}$, and $\hat{\phi}_i^{(\nu)}$ are given by Pollock (1981a).

Pollock (1981a) presented a straightforward test based on contingency tables for testing between the Jolly-Seber model and the age-dependent model. A general goodness-of-fit test for the age-dependence model was described by Pollock et al. (1990) and is based on the general goodness-of-fit test for the Jolly-Seber model developed by Pollock et al. (1985). Brownie et al. (1986) developed reduced parameter models which are age-dependent analogues of Jolly's (1982) Model B and Model D for a 2-age study. The general 2-age model, the reduced parameter versions, and testing procedures, were incorporated in a computer package JOLLYAGE by Pollock et al. (1990).

Combination open and closed population models

The Jolly-Seber model assumes that samples are obtained instantaneously. In practice this is impossible and to ensure that the assumption is valid the experimenter should sample over an interval that is short relative to the between-captures period. For example a study may be based on daily captures made over a one week period (secondary samples) with one year between the start of each capture period (primary samples). Pollock (1981b) suggested that a useful design in this type of situation might be to consider the whole experiment as series of short-term studies. Closed population models could be used to estimate N_i using the data from secondary samples which allow unequal catchability. The secondary capture data can then be pooled to form a data set for the primary capture periods and open population models used to estimate survival rate using these pooled data. A full description of the design is given by Pollock (1982) and Pollock et al. (1990).

Pollock's "robust design" has several advantages over the Jolly-Seber model. In particular: it relaxes the equal catchability assumption, all parameters are estimable including N_1 , N_t , ϕ_{t-1} and B_1 , and it allows separate estimation of immigration and *in situ* recruitment numbers for a two or more age class model (Pollock et al. 1993). Kendall and Pollock (1992) compared the robust design estimators with the Jolly-Seber estimators using simulated data. They reported mixed results. Under varying degrees of heterogeneity the robust estimator was preferred, based on a mean square error (MSE) or bias criterion, in half of their comparisons. In contrast the Jolly-Seber survival estimator performed better both in terms of bias and MSE in all cases. Pollock and Kendall (1992) found the robust design recruitment estimator outperformed the Jolly-Seber estimator in almost all cases. They concluded that evidence supported the use of the Jolly-Seber survival estimator but that choice of estimator for survival and recruitment was scenario dependent. Because the number of estimable parameters is increased and because there is added control over bias and precision they recommended the use of the robust design whenever possible.

1.5.1 Stationary Markov movement model

The two models: “random emigration” and “permanent emigration” are special cases of a more general movement model that can be developed using the Jolly-Seber structure. Sandland and Kirkwood (1981) developed a model which allowed first-order Markov dependence of capture probabilities. The motivation for their model was an abalone (*Haliotis laevis*) population where at times the animals could move from relatively open areas where they were subject to observation to crevices where they could not be observed. This movement was not permanent, however, as later during the study the abalone were able to move back out into the open. Sandland and Kirkwood (1981) considered only the estimation of survival rates from their model and did not explicitly consider the problem of estimating population size. Independently, Whitehead (1990) developed a similar model for a closed population. Since his population was closed, Whitehead (1990) focused on the estimation of population size but indicated that his method could be easily extended to open populations. In fact, his work was anticipated by Sandland and Kirkwood (1981).

Let

μ = the probability an animal at risk of capture at time i is at risk of capture at time $i + 1$.

λ = the probability an animal not at risk of capture at time i is at risk of capture at time $i + 1$.

then the permanent emigration model corresponds to the constraint $\lambda = 1$, and the random emigration model corresponds to the constraint $\lambda = \mu$. Neither of these constrained models (i.e. the Jolly-Seber model) permit estimation of the emigration parameters however both parameters are identifiable in the unconstrained model. However this depends on the stationarity assumption. If μ and λ are allowed to differ among capture periods then the model is no longer identifiable.

1.6 General Multi-Strata Movement Models

The age- and trap- dependence models are special cases of a more general class of models with multiple strata. In the case of age- and trap-dependence movement of animals between strata is deterministic, and in the case of age-dependence the movement is unidirectional.

Cormack (1979) commented on the shortage of models that incorporate local migration and that development of models allowing such movement would be an important area of future research. The earliest work on this problem was in the context of a population closed to births and deaths. Chapman and Junge (1956) derived method of moments estimators and Darroch (1961) maximum likelihood estimators for the Petersen (two sample, closed population) estimator for a geographically stratified population with movements between strata. A detailed summary of their results is given by Seber (1982:431-434).

1.6.1 The Petersen estimator for s strata

At time 1 a sample denoted by a $(s \times 1)$ vector \mathbf{n}_1 , where $\mathbf{n}_1 = (n_{1,1}, \dots, n_{1,s})'$, is captured from a population partitioned into s strata with stratum population sizes of N_1, \dots, N_s . The vector of population sizes at time 1 is denoted \mathbf{N}_1 . Following capture the sample \mathbf{n}_1 is marked, and released. Between sampling times 1 and 2 the population randomly mixes, with $\phi_{i,j}$ denoting the probability that an animal makes the transition from stratum i at time 1 to stratum j at time 2. The matrix of transition probabilities is denoted Φ . At time 2 a random sample is taken of \mathbf{n}_2 animals and the $(s \times s)$ matrix \mathbf{M} observed, where the i, j th element $m_{i,j}$ denotes the number of marked animals that were released in stratum i and recaptured in stratum j . Let $D(\mathbf{x})$ denote the diagonal matrix with the vector \mathbf{x} on the diagonal, and $\mathcal{E}[\mathbf{A}]$ the expectation operator with the i, j th element of the matrix produced by $\mathcal{E}[\mathbf{A}]$ the expected value of the i, j th element of \mathbf{A} . If all members in stratum i are captured with probability p_i then

$$\mathcal{E}[\mathbf{M}] = D(\mathbf{n}_1)\Phi D(\mathbf{p}) \quad (1.7)$$

and assuming that marked and unmarked animals have the same probability in each stratum

$$\mathcal{E}[D(\mathbf{n}_2)] = D(\mathbf{N})D(\mathbf{p}) \quad (1.8)$$

If $\frac{1}{[\mathbf{x}]} = (1/x_1, \dots, 1/x_s)'$ and $\mathbf{1}$ an $(s \times 1)$ vector of ones then

$$\begin{aligned} \frac{1}{[\mathbf{p}]} &= \mathbf{M}^{-1}D(\mathbf{n}_1)\Phi\mathbf{1} \\ &= \mathbf{M}^{-1}\mathbf{n}_1 . \end{aligned}$$

This follows because Φ is a transition matrix hence $\Phi\mathbf{1} = \mathbf{1}$. Substituting back into equations (1.7) and (1.8) and solving for Φ and \mathbf{N} respectively we obtain

$$\hat{\Phi} = D^{-1}(\mathbf{n}_1)MD(\mathbf{M}^{-1}\mathbf{n}_1) ,$$

and

$$\hat{\mathbf{N}} = D(\mathbf{n}_2)\mathbf{M}^{-1}D(\mathbf{n}_1)\mathbf{1}$$

hence an estimate of the total number of animals in the population $N = \mathbf{N}'\mathbf{1}$ is

$$\hat{N} = \mathbf{n}_2'\mathbf{M}^{-1}\mathbf{n}_1$$

as given by equation (13) of Chapman and Junge (1956). Seber (1982) shows that the above estimates are maximum likelihood estimators under the assumption of multinomial sampling at time 2.

1.6.2 Open population movement models

As with the single stratum Petersen estimator, the assumption of population closure for the multi-stratum estimator can be relaxed to allow mortality between sampling times (Darroch 1961, Seber1982:439). Although in their model it is still possible to estimate the size of the population at time 1, the remaining parameters are identifiable only with certain restrictions on the survival rates.

Arnason (1972, 1973) derived method of moments estimates for the three-sample case and multiple strata with animals subject to mortality between sampling occasions. He assumed:

- (i) all individuals alive and in stratum n ($n = 1, \dots, s$) have the same probability of capture in the i th sample,
- (ii) all individuals alive and in stratum n at i have the same probability of survival until time $i + 1$,
- (iii) animals migrate freely between strata with the probability of moving from stratum m to stratum n the same for all animals in stratum m ,
- (iv) if animals leave the study area they do so permanently,
- (v) all animals behave independently with respect to capture, survival, and migration
- (vi) there is no recruitment.

His method was extended to the general t -sample case by Seber (1982:555-559). Let $M_{i,j}$ denote the matrix of observed number of animals released at i and next recaptured at j . From Seber (1982) equation 13.80 we have

$$\hat{\Phi}_j = D^{-1}(\mathbf{n}_j)(M_{j,j+2}M_{j+1,j+2}^{-1}D(\mathbf{n}_{j+1})M_{j,j+1}) \quad (1.9)$$

thus Seber's t -sample extension of Arnason's estimator will not be fully efficient for $k > 3$ as it ignores information provided by $M_{j,j+h}$, $h = 3, 4, \dots, k - 1$.

Schwarz et al. (1993) described the likelihood for the above models of Arnason (1973) and Seber (1982), thus allowing maximum likelihood estimators to be obtained. Because all the data can be used the resulting estimators are fully efficient. Brownie et al. (1993) extended the model further, allowing capture probability to depend on time and strata, thus completed the full multivariate extension of the Jolly-Seber model. Explicit moment estimators were provided by Brownie et al. (1993) and are simple matrix analogues of the Jolly-Seber survival and capture probability estimators.

The data can be represented by a multivariate m -array formed in a similar fashion to the univariate m -array but where the $m_{i,j}$ are now matrices, say $\mathbf{m}_{i,j}$ with m, n th element $m_{i,j}^{m,n}$, the number of animals last released in stratum m at

Table 1.3: Multivariate reduced m-array for a study with t years of capture.

Release cohort	No. released	year next captured			
		$j = 2$	3	...	t
$i = 1$	\mathbf{R}_1	$\mathbf{m}_{1,2}$	$\mathbf{m}_{1,3}$...	$\mathbf{m}_{1,4}$
2	\mathbf{R}_2		$\mathbf{m}_{2,3}$...	$\mathbf{m}_{2,4}$
.
.
.
$t - 1$	\mathbf{R}_{t-1}				$\mathbf{m}_{t-1,t}$

time i that are next captured in stratum m and time j . The numbers released at i are summarized in the vector \mathbf{R}_i with m th element R_i^m , the number of animals released at time i in stratum m . A multivariate m-array for a study with t years of capture is given in Table 1.3. Following Brownie et al. 1993, let

$\phi_i^{m,n}$ = the probability an animal alive and in stratum m at time i is alive and in stratum n at time $i + 1$,

$p_i^{m,n}$ = the probability an animal alive and in stratum m at time $i - 1$ is captured in stratum n at i

and define the matrices

$$\mathbf{A}_i = \begin{bmatrix} \phi_i^{1,1}(1 - p_{i+1}^{1,1}) & \phi_i^{1,2}(1 - p_{i+1}^{1,2}) & \dots & \phi_i^{1,s}(1 - p_{i+1}^{1,s}) \\ \phi_i^{2,1}(1 - p_{i+1}^{2,1}) & \phi_i^{2,2}(1 - p_{i+1}^{2,2}) & \dots & \phi_i^{2,s}(1 - p_{i+1}^{2,s}) \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \phi_i^{s,1}(1 - p_{i+1}^{s,1}) & \phi_i^{s,2}(1 - p_{i+1}^{s,2}) & \dots & \phi_i^{s,s}(1 - p_{i+1}^{s,s}) \end{bmatrix}$$

Table 1.4: Multinomial cell probabilities corresponding to the multivariate m-array of Table 1.3

Release				
cohort	$j = 2$	3	...	t
$i = 1$	B_1	$A_1 B_2$...	$B_{t-1} \prod_{h=1}^{t-2} A_h$
2		B_2	...	$B_{t-1} \prod_{h=2}^{t-2} A_h$
.			.	.
.			.	.
.			.	.
$t - 1$				B_{t-1}

and

$$B_i = \begin{bmatrix} \phi_i^{1,1} p_{i+1}^{1,1} & \phi_i^{1,2} p_{i+1}^{1,2} & \dots & \phi_i^{1,s} p_{i+1}^{1,s} \\ \phi_i^{2,1} p_{i+1}^{2,1} & \phi_i^{2,2} p_{i+1}^{2,2} & \dots & \phi_i^{2,s} p_{i+1}^{2,s} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \phi_i^{s,1} p_{i+1}^{s,1} & \phi_i^{s,2} p_{i+1}^{s,2} & \dots & \phi_i^{s,s} p_{i+1}^{s,s} \end{bmatrix}$$

then for marked animals the multinomial cell probabilities corresponding to the multivariate m-array in Table 1.3 are given in Table 1.4. This is model JMV of Brownie et al. (1993) and represents a full multivariate extension of the Jolly-Seber model for marked animals. To model the unmarked captures additional assumptions about the distribution of unmarked animals between strata are required. Thus population size and hence recruitment estimates are not possible for model JMV.

The model considered by Arnason (1973), Seber (1982), and Schwarz et al. (1993) incorporates the constraint $p_i^{1,n} = p_i^{2,n} = \dots = p_i^{m,n} = p_i^n$. This means we can write

$$A_i = \Phi_i D(1 - p_{i+1})$$

$$B_i = \Phi_i D(p_{i+1})$$

where Φ_i is the matrix with m, n th element given by $\phi_i^{m,n}$, p_i is the vector $(p_i^1, \dots, p_i^n)'$, $(1 - p_i)$ the vector $((1 - p_i^1), \dots, (1 - p_i^n))$. This model, referred to as the Arnason-Schwarz model by Brownie et al. (1993), allows estimation of population size under the assumption that stratum specific capture probabilities are the same for unmarked and unmarked animals.

The full multivariate extensions of the Jolly-Seber model (model JMV of Brownie et al. 1993) and the restricted version considered by Arnason (1973), Seber (1982) and Schwarz et al. (1993) all assume Markovian transitions - i.e. the transition matrix is indexed only by time, and does not depend on the previous state. Brownie et al. (1993) also consider the memory model of Hestbeck et al. (1991) in which the transition probabilities at time i also depend on the location of the animals at time $i - 1$. In principle the full likelihood for the memory model can be written but it must be written separately for all capture histories. Because this is labourious Brownie et al. (1993) recommend against this and instead proposed maximizing a conditional likelihood, rather than the full likelihood, with consequent loss of efficiency.

Chapter 2

Tag Recovery Models

An important restricted version of the Jolly-Seber model is where all animals are removed from the population on recapture. This restriction reduces the number of estimable parameters as discussed below. Several early methods of analysis were proposed but made various restrictive assumptions (see Seber 1970 for a brief review). An important early contribution was made by Seber (1962) in the context of a mark-recapture study where releases and recaptures operate independently with all animals removed from the population on capture. In this model, referred to as the “multi-sample single recapture” model, recaptures occur at discrete points in time, as in the Jolly-Seber model, and Jolly (1965) shows that the maximum-likelihood estimators of p_i and ϕ_i are equivalent under the two models. In fact Jolly (1965:243) points out that in the Jolly-Seber model there does not need to be any relationship between the captures and the releases as assumed by Seber in his 1962 model.

2.1 Seber-Robson-Youngs Model

Seber (1970) and Robson and Youngs (1971) (cited in Seber 1982) independently provided an important extension to the multi-sample single recapture model by allowing recaptures to occur continuously through time. We refer to this model as the “time-specific tag-recovery” model. This model has proven an extremely

important basis for the analysis of tag returns from dead animals. Batches of tagged animals are released at time i and tags from dead animals are reported at any time in the future, up to time l . The parameters are the probability that an animal alive at i is alive at $i+1$, and the probability that an animal alive at i has its tag recovered between i and $i+1$, denoted f_i . Because there are no live recaptures it is not possible to estimate population size or recruitment.

2.1.1 Notation, assumptions, and data structure

Parameters

f_i = the probability an animal alive at time i dies and has its tag recovered and reported to the experimenter between i and $i+1$ ($i = 1, \dots, l$).

S_i = the probability an animal alive at time i is alive at time $i+1$ ($i = 1, \dots, l-1$).

Statistics

N_i = the number of animals released at time i , $i = 1, \dots, t \leq l$.

M_i = the number of marked (tagged) animals in the population immediately before release i .

$M_{i,j}$ = the number of tags recovered between times j and $j+1$ from animals released at i .

R_i = the total number of tag recoveries from animals released at i
 $(R_i = \sum_{j=i}^l M_{i,j})$

C_j = the total number of tag recoveries at time j ($C_j = \sum_{i=1}^j M_{i,j}$)

T_i = the total number of tag recoveries between times i and l inclusive from animals released at or before i .

The assumptions of the time specific tag-return model are:

- (i) all animals have the same probability of survival between i and $i + 1$,
- (ii) all animals have the same tag-recovery probability between i and $i + 1$,
- (iii) the time of recovery is correctly reported,
- (iv) animals do not lose their tags,
- (v) the fate of each tagged animal is independent of the fate of other individuals.

Assumptions (i) and (ii) are respectively the homogeneous survival and recovery probability assumptions. From the homogeneity assumption and assumption (iv) the tag recoveries for each release cohort will be multinomial random variables as each animal can only be recovered once, or never at all.

Tag recoveries are usually obtained in one of two ways. First, in non-game animals tag-returns are usually obtained from members of the public who find the dead animal. For this to occur some time during year i several events must occur. The animal must die, which happens with probability $(1 - S_i)$, the tagged animal must be found given that it is dead, with probability θ_i , say, then the tag must be reported, given that the animal has been found dead, with probability λ_i . Thus

$$f_i = (1 - S_i)\theta_i\lambda_i .$$

The second method of tag-recovery is through tag-returns reported by hunters from gamebird species. For tag recovery to occur the animal must be killed, with harvest rate h_i ($0 < h_i < 1 - S_i$), the animal must be recovered given that it has been killed, with probability $(1 - c_i)$, then the tag must be reported with probability λ_i . Thus,

$$f_i = h_i(1 - c_i)\lambda_i$$

and the two forms of recovery are identical as far as modelling is concerned.

The most convenient means of representing the data is in terms of a recovery array analogous to the reduced m-array of section 1.3.3. The recovery array for a

study with $t = 4$ years of release and $l = 6$ years of recovery is illustrated in Table 2.1. The corresponding probability structure is given Table 2.2 for the model with time specific recovery and survival rates.

Table 2.1: Recovery array for a tag-recovery experiment with 4 years of release and 6 years of recovery, where $M_{i,j}$ is the number of tag recoveries at time j from animals released at time i .

Cohort	No. released	Time first recaptured					
		$j = 1$	2	3	4	5	6
$i = 1$	N_1	$M_{1,1}$	$M_{1,2}$	$M_{1,3}$	$M_{1,4}$	$M_{1,5}$	$M_{1,6}$
2	N_2		$M_{2,2}$	$M_{2,3}$	$M_{2,4}$	$M_{2,5}$	$M_{2,6}$
3	N_3			$M_{3,3}$	$M_{3,4}$	$M_{3,5}$	$M_{3,6}$
4	N_4				$M_{4,4}$	$M_{4,5}$	$M_{4,6}$

Table 2.2: Probability structure for the recovery array in Table 2.1

Cohort	Time tag recovered					
	$j = 1$	2	3	4	5	6
$i = 1$	f_1	$S_1 f_2$	$S_1 S_2 f_3$	$S_1 S_2 S_3 f_4$	$S_1 S_2 S_3 S_4 f_5$	$S_1 S_2 S_3 S_4 S_5 f_6$
2		f_2	$S_2 f_3$	$S_2 S_3 f_4$	$S_2 S_3 S_4 f_5$	$S_2 S_3 S_4 S_5 f_6$
3			f_3	$S_3 f_4$	$S_3 S_4 f_5$	$S_3 S_4 S_5 f_6$
4				f_4	$S_4 f_5$	$S_4 S_5 f_6$

Note that the joint probability an animal survives from i to $i + 1$, and does not have its tag recovered is given by S_i , since the probability that the tag is not recovered given the animal is alive is 1. Also, f_5 always occurs in the product $S_4 f_5$ and f_6 in the product $S_4 S_5 f_6$, hence S_4 , S_5 , f_5 , and f_6 are not individually identifiable and we can only estimate the products $S_4 f_5$ and $S_4 S_5 f_6$.

2.1.2 Intuitive estimators

As with the Jolly-Seber model we can easily derive intuitive estimators. The proportion C_i/T_i is an estimate of the probability an animal has its tag recovered

between i and $i + 1$ given that it is alive at i and its tag is recovered after i . Similarly, the proportion R_i/N_i is an obvious estimate of the probability that an animal alive at i has its tag recovered after i . Thus we can estimate f_i by

$$\hat{f}_i = \frac{R_i C_i}{N_i T_i}$$

for $i=1, \dots, t$. To estimate the confounded parameters $S_t f_{t+1}$, $S_t S_{t+1} f_{t+2}$ etc we simply note that C_{t+j}/T_t ($j = 1, \dots, l - t$) is an estimate of the probability an animal has its tag recovered at $t + j$ given that it is alive at t , and hence

$$f_{t+j} S_t \cdots S_{t+j-1} = \frac{R_t C_{t+j}}{N_t T_t}.$$

If the assumptions of the model are correct, then the proportion of animals released before i that ever have their tags recovered should equal on average the proportion of animals released at i that are have their tags recovered, or

$$\frac{T_i - R_i}{M_i} \sim \frac{r_i}{R_i}$$

hence

$$\hat{M}_i = \frac{N_i(T_i - R_i)}{R_i},$$

We then estimate the survival rate by the estimated proportion of marked animals in the population immediately after release i that are still alive at time $i + 1$, or

$$\begin{aligned} S_i &= \frac{M_{i+1}}{M_i + N_i} \\ &= \frac{N_{i+1} R_i T_{i+1} - R_{i+1}}{N_i R_{i+1} T_i} \\ &= \frac{N_{i+1} R_i T_i - C_i}{N_i R_{i+1} T_i}. \end{aligned}$$

for $i=1, \dots, t - 1$, corresponding to the MLE's given by Seber (1970:314).

2.1.3 The tag-return model likelihood

As with the recapture component of the Jolly-Seber likelihood we can write the likelihood in the form

$$\mathcal{L} \propto \prod_{i=1}^{t-1} (1 - \lambda_i)^{(N_i - R_i)} \prod_{j=i+1}^t \pi_{i,j}^{M_{i,j}},$$

where $1 - \lambda_i = f_i + S_i f_{i+1} + \dots + S_i \dots S_{l-1} f_l$ is the probability that an animal never has its tag recovered following release at i and $\pi_{i,j}$ is the multinomial cell probability for $M_{i,j}$.

Following Burnham (1991) the likelihood can be expressed in the more useful form:

$$\mathcal{L} \propto Pr(MSS) = \prod_{i=1}^t \binom{N_i}{R_i} \lambda_i^{R_i} (1 - \lambda_i)^{(N_i - R_i)} \prod_{i=1}^{l-1} \binom{T_i}{C_i} \tau_i^{C_i} (1 - \tau_i)^{T_i - C_i} \quad (2.1)$$

where

$$\tau_i = \frac{f_i}{\lambda_i} \quad i = 1, \dots, t$$

or

$$\tau_i = \frac{f_i S_t \dots S_{i-1}}{\lambda_t - \sum_{h=t}^{i-1} f_h S_t \dots S_{h-1}} \quad i > t.$$

As with the recapture component of the Jolly-Seber likelihood the tag-recovery likelihood can be expressed as the product of independent binomial terms with MLE's and their asymptotic covariances obtained by straightforward algebraic manipulation.

The asymptotic variances for \hat{f}_i and \hat{S}_i are given by

$$Var(\hat{f}_i) = [f_i]^2 \left\{ \frac{1}{E[R_i]} - \frac{1}{N_i} + \frac{1}{E[C_i]} - \frac{1}{T_i} \right\} \quad i = 1, \dots, t$$

and

$$Var(\hat{S}_i) = [S_i]^2 \left\{ \frac{1}{E[R_i]} - \frac{1}{N_i} + \frac{1}{E[R_{i+1}]} - \frac{1}{N_{i+1}} + \frac{1}{T_i - E[C_i]} - \frac{1}{T_i} \right\} \quad i = 1, \dots, t-1.$$

2.1.4 Heterogeneous survival and recovery rates

Pollock and Ravelling (1982) and Nichols et al. (1982) investigated the effects of heterogeneous recovery and survival probabilities on the tag-return model estimators. Pollock and Raveling (1982) found that if there is heterogeneity in recovery

but not survival rates there is no bias in \hat{f}_i as an estimator of average recovery rate. However, if there is heterogeneity in both recovery and survival rates then the recovery rate estimators at the beginning and end of the study have no bias for $E[f_i]$ but those in the middle are negatively biased. If recovery rates are heterogeneous but not survival rates, the survival rate estimator is unbiased. If survival rates are heterogeneous the survival rate estimators as estimates of $E[S_i]$ generally have a negative bias which is most severe for high survival species and short duration studies.

Nichols et al. (1982) extended the work of Pollock and Ravelling (1982) by looking at the case where survival and recovery rates were positively correlated. and found that survival rate estimates were positively biased for $E[S_i]$. They argued that such a positive relationship would be expected when the banding and recovery periods were separated by time spans not negligible with respect to mortality. Because these studies suggested that bias induced by heterogeneity was likely to be small relative to the standard errors of survival rate estimates, Barker (1992) repeated the studies of Pollock and Ravelling (1982) and Nichols et al. (1982) but looked at confidence interval coverage rates in the presence of heterogeneity. He found that coverage rates were lowest when survival and recovery rates were positively correlated among animals and when banded sample sizes were large. These studies illustrate that unmodelled heterogeneity can lead to biased point estimates and interval estimate coverage rates that are much less than the nominal values.

As with the Jolly-Seber model, trap-response may lead to differences in recovery rates and survival rates among animals. A temporary trap-response in recovery rates may occur if dispersal of newly tagged animals away from the study site is slow and if tag reporting rates differ near the study site. This is particularly relevant in waterfowl studies where tag returns are obtained by hunters. Such a temporary response in recovery rates can be explicitly incorporated into the model (see section 2.1.5). A temporary response for both recovery and survival rates cannot be modelled however (Brownie et al. 1985:79). In this case, the tag-return model will lead to biased estimation (Pollock et al. 1982) as will a permanent

response in survival rates.

2.1.5 Restricted and generalized tag-return models

There have been several important restricted parameter and generalized versions of the Seber-Robson-Youngs tag-return model. Most of these are covered in the comprehensive work of Brownie et al. (1985).

Reduced parameter models

Brownie et al. (1985) provided a series of reduced parameter models that can be fitted using the computer program ESTIMATE:

Model M_1 : Recovery rates and survival rates are time specific (The Seber-Robson-Youngs model),

Model M_2 : Recovery rates are time specific, survival rates are constant through time,

Model M_3 : Recovery rates and survival rates are time invariant.

Of the three models, explicit MLE's exist only for M_1 , and numerical procedures are required in order to fit the remaining two models. Fitting all three models is automated in ESTIMATE and includes goodness-of-fit tests and likelihood ratio tests between models.

Trap dependence

In addition to M_1 , M_2 , and M_3 Brownie et al. (1985) include a model M_0 which incorporates a temporary trap response in recovery rates. This model assumes that survival and recovery rates are time specific and that recovery rates for animals in the first time period following release, f'_i , are different from recovery rates for animals released at least one time period earlier, f_i . They suggested M_0 would be useful when the tag reporting rate is different near the tagging site and would primarily affect newly tagged animals. Brownie et al. (1985) give explicit MLE's for M_0 and this is automatically fitted by ESTIMATE.

Age-dependence

In many studies the assumption of equal recovery and survival rates is unreasonable because of age-dependent differences. Brownie and Robson (1976) extended the Seber-Robson-Youngs model to allow age- and time-dependent recovery and survival rates. The age-dependent model assumes that the different age-classes are distinguishable on capture. If this is not possible then age-dependence leads to a particular form of heterogeneity. If we modify the Seber-Robson-Youngs notation by adding the superscript 0 to denote young animals and 1 to denote adults, then the form of the recovery array for the two-age study is given in Table 2.3 The cor-

Table 2.3: Recovery array for a 2-age tag-recovery experiment with 4 years of release and 5 years of recovery.

Cohort	No. released	Time first recaptured				
		$j = 1$	2	3	4	5
Released as adults						
$i = 1$	$N_1^{(1)}$	$M_{1,1}^{(1)}$	$M_{1,2}^{(1)}$	$M_{1,3}^{(1)}$	$M_{1,4}^{(1)}$	$M_{1,5}^{(1)}$
2	$N_2^{(1)}$		$M_{2,2}^{(1)}$	$M_{2,3}^{(1)}$	$M_{2,4}^{(1)}$	$M_{2,5}^{(1)}$
3	$N_3^{(1)}$			$M_{3,3}^{(1)}$	$M_{3,4}^{(1)}$	$M_{3,5}^{(1)}$
4	$N_4^{(1)}$				$M_{4,4}^{(1)}$	$M_{4,5}^{(1)}$
Released as young						
$i = 1$	$N_1^{(0)}$	$M_{1,1}^{(0)}$	$M_{1,2}^{(0)}$	$M_{1,3}^{(0)}$	$M_{1,4}^{(0)}$	$M_{1,5}^{(0)}$
2	$N_2^{(0)}$		$M_{2,2}^{(0)}$	$M_{2,3}^{(0)}$	$M_{2,4}^{(0)}$	$M_{2,5}^{(0)}$
3	$N_3^{(0)}$			$M_{3,3}^{(0)}$	$M_{3,4}^{(0)}$	$M_{3,5}^{(0)}$
4	$N_4^{(0)}$				$M_{4,4}^{(0)}$	$M_{4,5}^{(0)}$

responding probability structure is given in Table 2.4 Explicit parameter estimates are given by:

$$\hat{f}_i^{(1)} = \frac{R_i^{(1)}(C_i^{(1)} + C_i^{(0)} - M_{i,i}^{(0)})}{N_i^{(1)}(T_i^{(1)} + T_i^{(0)} - R_i^{(0)})}$$

$$\hat{f}_i^{(0)} = \frac{M_{i,i}^{(0)}}{N_i^{(0)}}$$

Table 2.4: Probability structure for the 2-age tag recovery array of Table 2.3 .

Cohort	Time first recaptured				
	$j = 1$	2	3	4	5
Released as adults					
$i = 1$	$f_1^{(1)}$	$S_1^{(1)} f_2^{(1)}$	$S_1^{(1)} S_2^{(1)} f_3^{(1)}$	$S_1^{(1)} S_2^{(1)} S_3^{(1)} f_4^{(1)}$	$S_1^{(1)} S_2^{(1)} S_3^{(1)} S_4^{(1)} f_5^{(1)}$
2		$f_2^{(1)}$	$S_2^{(1)} f_3^{(1)}$	$S_2^{(1)} S_3^{(1)} f_4^{(1)}$	$S_2^{(1)} S_3^{(1)} S_4^{(1)} f_5^{(1)}$
3			$f_3^{(1)}$	$S_3^{(1)} f_4^{(1)}$	$S_3^{(1)} S_4^{(1)} f_5^{(1)}$
4				$f_4^{(1)}$	$S_4^{(1)} f_5^{(1)}$
Released as young					
$i = 1$	$f_1^{(0)}$	$S_1^{(0)} f_2^{(1)}$	$S_1^{(0)} S_2^{(1)} f_3^{(1)}$	$S_1^{(0)} S_2^{(1)} S_3^{(1)} f_4^{(1)}$	$S_1^{(0)} S_2^{(1)} S_3^{(1)} S_4^{(1)} f_5^{(1)}$
2		$f_2^{(0)}$	$S_2^{(0)} f_3^{(1)}$	$S_2^{(0)} S_3^{(1)} f_4^{(1)}$	$S_2^{(0)} S_3^{(1)} S_4^{(1)} f_5^{(1)}$
3			$f_3^{(0)}$	$S_3^{(0)} f_4^{(1)}$	$S_3^{(0)} S_4^{(1)} f_5^{(1)}$
4				$f_4^{(0)}$	$S_4^{(0)} f_5^{(1)}$

$$\hat{S}_i^{(1)} = \frac{N_{i+1}^{(1)} R_i^{(1)} (T_i^{(1)} + T_i^{(0)} - R_i^{(0)}) - (C_i^{(1)} + C_i^{(0)} - M_{i,i}^{(0)})}{R_{i+1}^{(1)} N_i^{(1)} (T_i^{(1)} + T_i^{(0)} - R_i^{(0)})}$$

and

$$\hat{S}_i^{(1)} = \frac{N_{i+1}^{(1)} (R_i^{(0)} - M_{i,i}^{(0)})}{R_{i+1}^{(1)} N_i^{(0)}},$$

for $i=1, \dots, t$ ($f_i^{(0)}$ and $f_i^{(1)}$) and $i = 1, \dots, t - 1$ for $S_i^{(0)}$ and $S_i^{(1)}$. The respective asymptotic variances are given by

$$\begin{aligned} \text{Var}(\hat{f}_i^{(1)}) &= (f_i^{(1)})^2 \left\{ \frac{1}{E[R_i^{(1)}]} - \frac{1}{N_i^{(1)}} + \frac{1}{E[C_i^{(1)} + C_i^{(0)} - M_{i,i}^{(0)}]} \right. \\ &\quad \left. - \frac{1}{E[T_i^{(1)} + T_i^{(0)} - R_i^{(0)}]} \right\}, \\ \text{Var}(\hat{f}_i^{(0)}) &= \frac{f_i^{(0)} (1 - f_i^{(0)})}{N_i^{(0)}}, \end{aligned}$$

$$\begin{aligned} \text{Var}(\hat{S}_i^{(1)}) &= (S_i^{(1)})^2 \left\{ \frac{1}{E[R_i^{(1)}]} - \frac{1}{N_i^{(1)}} + \frac{1}{E[R_{i+1}^{(1)}]} - \frac{1}{N_{i+1}^{(1)}} \right. \\ &\quad \left. + \frac{1}{E[(T_i^{(1)} + T_i^{(0)} - R_i^{(0)}) - (C_i^{(1)} + C_i^{(0)} - M_{i,i}^{(0)})]} \right\} \end{aligned}$$

$$\left. - \frac{1}{E [T_i^{(1)} + T_i^{(0)} - R_i^{(0)}]} \right\} ,$$

and

$$Var(\hat{S}_i^{(0)}) = (S_i^{(0)})^2 \left\{ \frac{1}{E[R_i^{(0)} - M_{i,i}^{(0)}]} - \frac{1}{N_i^{(0)}} + \frac{1}{E[R_{i+1}^{(1)}]} - \frac{1}{N_{i+1}^{(1)}} \right\} .$$

Brownie et al. (1985:61) also give the estimators for products of the confounded parameters and the asymptotic covariances.

Model H_1 and a reduced parameter sequence are automatically fitted by the program BROWNIE which accompanies Brownie et al. (1985) including goodness-of-fit tests and tests between models. The goodness-of-fit tests and the tests between models follow the procedures outlined in Brownie et al. (1986).

The models fitted by BROWNIE are:

Model H_1 : Recovery rates and survival rates are time- and age-specific,

Model H_{02} : Recovery rates are time- and age-specific, survival rates are age-specific but constant through time,

Model H_{01} : Recovery rates and survival rates are age-specific but time invariant.

Model H_0 : Recovery rates and survival rates are time-specific but age invariant (i.e. model M_1 , the Seber-Robson-Youngs model).

In addition to the above set of models, Brownie et al. (1985) also generalize H_1 to allow age-dependence and temporary trap response in recovery rates, model H_2 , and models with three age classes.

Age-dependence - animals tagged only as young.

An historically important case is where animals are banded only as young. For many species it is easy to capture young animals but not older animals. The model assumes that survival rates are age-specific and to avoid being over-paramaterized also assumes that recovery and survival rates are time-invariant. Prior to the development of maximum likelihood methods for this model, analyses were carried

out using the “composite dynamic” method (Seber 1982). This method requires the assumption that sufficient time has elapsed after the experiment for all animals to have died. Burnham and Anderson (1979) examined all the assumptions of the composite dynamic method, and the underlying model, and derived a goodness-of-fit test. When applied to 45 waterfowl banding data sets they found strong ($p < 0.001$) evidence against the model in 37 cases.

Seber (1971) showed that the parameters in the life table could not be estimated without at least one constraint which is only alleviated if the number of years of recovery exceeds the number of years of tagging. If there are k years of tagging, Seber (1971) suggested the constraint $S_{k-1} = S_k$. Catchpole and Morgan (1991) give an explicit MLE. Lakhani and Newton (1983), Anderson et al. (1985), and Brownie et al. (1985) have argued strongly against studies based only on releases of young animals. Morgan and Freeman (1989) have shown that a richer class of models can be fitted by allowing time specific variation in the survival of animals in the first age class and time specific recovery rates. Barker and Buchanan (1993) independently suggested a similar approach in which in a 2-age study survival rates of animals in the first age class are time invariant but recovery rates and adult survival rates are time specific. However in their approach, only adult survival rates can be estimated. Because of the need to assume time invariance of young survival rates (or in Morgan and Freeman’s 1989 model, time invariance of survival rates for animals older than age one) Barker and Buchanan (1993) cautioned against this type of study.

2.1.6 Models allowing heterogeneous survival

Burnham and Rexstad (1993) proposed a tag-return model that allowed time-specificity of recovery rates and heterogeneous survival rates. The model assumes that individuals have different survival rates but these are constant throughout the experiment. If there is heterogeneity, animals with low survival probabilities tend to leave the population earlier than animals with high survival probabilities. Thus, heterogeneity will show up as an age-effect. Thus, in a one-age study model M_1

will systematically under-estimate the expected number of recoveries in recovery cells further from the diagonal. Burnham and Rexstad (1993) exploited this effect to develop a model which included heterogeneous survival rates. Using simulated data they concluded that detection of heterogeneous survival is at best, difficult. Successful estimation requires long-term data sets of long-lived species with large numbers of marked individuals

2.1.7 Ultrastructural models

Following Anderson and Burnham (1976) there has been considerable interest in the effect of hunting on the survival of hunted waterfowl. From the relationship

$$f_i = h_i(1 - c_i)\lambda_i$$

recovery rates are proportional to harvest rates and an obvious approach is to explore the relationship between harvest and subsequent survival by looking at the relationship between estimated recovery and survival rates using tag-return data. Early analyses interpreted a significant negative correlation between estimated recovery and survival rates as evidence of an influence of harvest in reducing rates. As noted by Anderson and Burnham (1976) this is largely an artifact introduced by the negative sampling covariance of \hat{f}_i and \hat{S}_i . To estimate the slope of the relationship between harvest rates and survival rates Anderson and Burnham (1976) used a random effects model. Anderson et al. (1982) and Burnham et al. (1984) later realized that the relationship could be directly incorporated into the probability structure of the tag-recovery model using the relationship

$$S_i = S_0(1 - \beta h_i)$$

where S_0 is the survival in the absence of hunting. Their analysis was carried out by substituting S_i , as defined above for S_i in the probability structure of the tag-recovery model. Using this approach Burnham et al. (1984) found little evidence of an effect of hunting on annual survival rates of adult mallard ducks (*Anas platyrhynchos*). Barker et al. (1991) provided a two-age extension to this model and

applied it to a grey duck (*Anas superciliosa*) data set. They found evidence that there was some influence of hunting on annual survival rates.

Burnham and Rexstad (1993) used an ultrastructural model to incorporate the effect of heterogeneity into a tag-return analysis. If heterogeneity is the only force acting on recovery and survival rates then under a beta-family of distributions they found the relationships

$$S_j = \frac{S_1 + a(j - 1)}{1 + a(j - 1)}$$

and

$$f_j = \frac{f_1}{1 + c(j - 1)}$$

where a and c are heterogeneity parameters. They incorporated these relationships directly into the M_1 model structure.

Multivariate tag-recovery models

Schwarz et al. (1988) extended the tag-return model by allowing stratification of recoveries with stratum assignment occurring after recoveries have taken place. They considered estimation under time specific survival and recovery rates with four models for stratification:

Model 1: Recovery and survival rates are stratum specific,

Model 2a: Only recovery rates are stratum specific,

Model 2b: Only survival rates are stratum specific,

Model 1: Neither survival nor recovery rates are stratum specific (model M_1 of Brownie et al. 1985).

In addition to the usual tag-recovery model assumptions Schwarz et al. (1988) also assumed that following release each animal is faithful to one, and only one, stratum. However they argued that in the absence of complete fidelity models 1 and 2a are still applicable provided animals are sampled randomly at the time of tagging and choice of stratum in year $i + 1$ is independent of stratum occupied in

year i . Schwarz et al. (1988) reported explicit MLE's for all four cases and tests between models.

The assumption of complete fidelity to the stratum following release is somewhat restrictive. If stratification occurs at the time of release as well as at the time of recovery then the model of Schwarz et al. (1993) relaxes this assumption. Their model is the tag-return analogue of the multivariate Jolly-Seber model discussed in section 1.6, where $M_{i,j}^{m,n}$ is now the number of animals released in stratum m in year i that are recovered in stratum n in year j and

$$A_i = \begin{bmatrix} \phi_i^{1,1} & \phi_i^{1,2} & \dots & \phi_i^{1,s} \\ \phi_i^{2,1} & \phi_i^{2,2} & \dots & \phi_i^{2,s} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \phi_i^{s,1} & \phi_i^{s,2} & \dots & \phi_i^{s,s} \end{bmatrix}$$

and

$$B_i = \begin{bmatrix} f_i^{1,1} & f_i^{1,2} & \dots & f_i^{1,s} \\ f_i^{2,1} & f_i^{2,2} & \dots & f_i^{2,s} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ f_i^{s,1} & f_i^{s,2} & \dots & f_i^{s,s} \end{bmatrix}$$

where $f_i^{m,n}$ is the probability the tag will be recovered in stratum n from an animal released in year i at stratum m . The probability structure for the model is given in Table 1.4 . Schwarz et al. (1993) give explicit moment estimators and these are simple matrix analogues of the expressions given by Brownie et al (1985:16) for model M_1 .

2.2 Joint Live-Recapture and Tag-Return Models

Live-recaptures in band recovery studies have traditionally been ignored, partly because of the apparent technical difficulties in simultaneously modelling the two types of data and partly because in many band recovery studies, live-recaptures during trapping have been uncommon. In some studies, live recaptures may be substantial. This is particularly true for relatively sedentary animal populations such as New Zealand waterfowl. It should be worthwhile including the additional capture data in the analysis as it may allow the fitting of additional models, and in particular, it could lead to improved efficiency of estimation.

This situation was anticipated by Jolly (1965) when he considered his solutions to the Jolly Seber model. Jolly (1965:239) noted that the statistics z_i and r_i could be obtained by operating releases and recaptures independently, using a marking method that allows easy identification in the field by relatively untrained observers. Because the “recaptures” can operate continuously through time there is potential for a large increase in the number of recaptures. The obvious extension of this is to simply augment the live recaptures with these observations as the means of “recapture” is irrelevant. All that is relevant is that the animal was known to be alive at i . Buckland (1980) includes this idea in his modified analysis, however, apart from Buckland’s paper there has been little follow-up to Jolly’s (1965) suggestion (see discussion below)

2.2.1 The Mardekian-McDonald analysis

Mardekian and McDonald (1981) proposed a method for analyzing joint band-recovery and live-recapture data that exploited the modelling approach and computer programs of Brownie et al. (1978, 1985). Following release an animal may fall into one of three mutually exclusive categories:

- (i) The animal is found dead or killed and its band is reported (terminal recovery)
- (ii) The animal returns to the banding site in a subsequent year and is captured

(iii) The animal is never seen again and its band never reported.

Note that in the case of fate (ii), the animal may be re-released and then suffer one of the fates (i) through (iii), and so forth. The full model allowing for all such recapture-recovery paths is difficult to write, but Mardekian and McDonald (1981) avoid this complication by ignoring intermediate recapture data. Thus they model the *last* known fate of each released animal and hence the live recaptures are also terminal.

Suppose we have a study with t years of banding and recovery. Using the notation of Mardekian and McDonald (1981) let $R_{i,j}$ denote the number of bands recovered from the i th release cohort in year j and $R'_{i,j}$ the number of terminal live recaptures from the i th cohort in year $j + 1$. Also, let $\pi_{i,j}$ and $\pi'_{i,j}$ be the multinomial cell probabilities for $R_{i,j}$ and $R'_{i,j}$ respectively. Then

$$\pi_{i,j} = \begin{cases} f_i & j = i \\ f_j S_i \cdots S_{j-1} & j = i + 1, \dots, t \end{cases} \quad (2.2)$$

and

$$\pi'_{i,j} = p_{j+1} S_i \cdots S_j \quad j = i, \dots, t - 1, \quad (2.3)$$

where p_j is the probability an animal is at risk of capture and is captured in year j , and is never seen again following release.

Mardekian and McDonald (1981) note that if the blanks on the diagonal of the $R'_{i,j}$ array are ignored then the terminal live-recapture probabilities are of exactly the same form as the terminal recovery probabilities but where $q_{i+1} = S_i p_{i+1}$ is equivalent to f_i . Exploiting this relationship they propose modelling the values of $R^*_{i,j} = R_{i,j} + R'_{i,j}$, the total terminal recoveries in period j , or recaptures in $j + 1$, from the i th cohort where

$$\pi^*_{i,j} = \begin{cases} f_i + q_{i+1} & j = i \\ (f_j + q_{j+1}) S_i \cdots S_{j-1} & j = i + 1, \dots, t \end{cases}, \quad (2.4)$$

and $\pi^*_{i,j}$ is the multinomial cell probability for $R^*_{i,j}$. Under this formulation the survival rates S_1, \dots, S_{t-1} are identifiable. Assuming that terminal live-recaptures

are obtained for year $t + 1$ the parameters $(f_1 + q_2), \dots, (f_t + q_{t+1})$ are also estimable but have no useful interpretation.

The primary advantage of the Mardekian-McDonald analysis is the simplicity with which it can be carried out. The estimates can be obtained in a straightforward manner utilizing the procedures and software of Brownie et al. (1985). However, as intermediate live-recaptures are ignored, the Mardekian-McDonald survival rate estimator is not fully efficient. More seriously, however, their formulation (2.3) and hence (2.4) is only correct under certain restrictive assumptions.

Mardekian-McDonald model under different types of movement

To examine the effects of different types of movement on the Mardekian-McDonald analysis we need to develop cell probabilities under a general movement form of the model. In developing these probabilities, we assume that tag recoveries can be made throughout the range of the animal population but captures at i can only be made from the at risk of capture component at time i .

Probability structure for Band-recoveries The probability structure for the band recovery component of the Mardekian-McDonald model is exactly the same as under M_1 of Brownie et al. (1985). This is true regardless of the type of movement possible (random, permanent, or Markovian) and results from ignoring the intermediate captures. Thus all possible combinations of intermediate movement and capture are permitted.

Let

μ_i = the probability an animal alive at $i + 1$ and at risk of capture at i is at risk of capture at $i + 1$,

λ_i = the probability an animal alive at $i + 1$ but not at risk of capture at i is at risk of capture at $i + 1$.

Consider the possible ways in which an animal released at i can contribute to cell probability $R_{i,i+1}$:

- (i) It survived, remained in the study area, was captured at time $i + 1$ and then was recovered. This occurs with probability $S_i \mu_i p_{i+1} f_{i+1}$
- (ii) It survived, remained in the study area, was not captured at time $i + 1$, and then was recovered. This occurs with probability $S_i \mu_i (1 - p_{i+1}) f_{i+1}$
- (iii) It survived and left the study area between i and $i + 1$ and was then recovered. This occurs with probability $S_i (1 - \mu_i) f_{i+1}$

Hence, the cell probability for $R_{i,i+1}$, denoted $\pi_{i,j,2}$, is

$$\pi_{i,i+1,2} = S_i \mu_i p_{i+1} f_{i+1} + S_i \mu_i (1 - p_{i+1}) f_{i+1} + S_i (1 - \mu_i) f_{i+1} = S_i f_{i+1} .$$

Repeating the argument for $j = i + 1, \dots$ we find

$$\pi_{i,j,2} = \begin{cases} f_i & j = i \\ f_j \prod_{h=i}^{j-1} S_h & j = i + 1, \dots, l \end{cases} \quad (2.5)$$

Note, this is simply a consequence of allowing all intermediate sample and capture paths.

Probability structure for live-recaptures As with the band recoveries, all possible sample paths between release and last recapture are permitted, with one important exception: the animals must be present in the study area at the time of capture. If we define $\alpha_{i,j}$ as the probability that an animal released at time i is at risk of capture at time j (conditional on it being alive), $\beta_{i,j}$ as the probability an animal released at time i is *not* at risk of capture at time j (conditional on it being alive) then

$$\alpha_{i,j} = \begin{cases} \mu_i & j = i + 1 \\ \alpha_{i,j-1} \mu_{j-1} + \beta_{i,j-1} \lambda_{j-1} & j = i + 2, \dots, l \end{cases} \quad (2.6)$$

and

$$\beta_{i,j} = \begin{cases} 1 - \mu_i & j = i + 1 \\ \alpha_{i,j-1} (1 - \mu_{j-1}) + \beta_{i,j-1} (1 - \lambda_{j-1}) & j = i + 2, \dots, l \end{cases} \quad (2.7)$$

The live-recapture cell probabilities $\pi_{i,j,1}$ are then given by

$$\pi_{i,j,1} = p_j \alpha_{i,j} \prod_{h=i}^{j-1} S_h, \quad (2.8)$$

Probability structure for the combined array From (2.5) and (2.8) the probability structure for the combined array $R_{i,j}^*$ is given by

$$\pi_{i,j}^* = \begin{cases} (f_i + S_i p_{i+1} \alpha_{i,i+1}) & j = i \\ (f_j + S_j p_{j+1} \alpha_{i,j+1}) \prod_{h=i}^{j-1} S_h & j = i + 1, \dots, l \end{cases} \quad (2.9)$$

Note that generally (2.9) is *not* equivalent to (2.4) because the cell probabilities given in (2.9) depend on i . The consequence is that the Markedian-McDonald model yields biased estimates of survival rate under Markovian movement. This is illustrated below for the special case of Permanent emigration.

Random emigration Under the random emigration model $\mu_i = \lambda_i = F_i$ and on expanding we find that $\alpha_{i,j} = \mu_{j-1} = F_{j-1}$ hence the cell probabilities do not depend on i . Thus, (2.9) is equivalent to (2.4) and their analysis will yield correct results.

Permanent emigration Under the permanent emigration model $\lambda_i = 0$ and expanding we find that $\alpha_{i,j} = \prod_{h=i}^{j-1} \mu_j = \prod_{h=i}^j F_j$ hence (2.9) is *not* equivalent to (2.4) and their analysis will *not* yield correct results. This is contrary to their claim (Mardekian and McDonald 1981:260).

Of interest, however, is the fact that under permanent emigration (2.8) is identical to the probability structure for model M_1 of Brownie et al. (1985), as

$$\alpha_{i,j} \prod_{h=i}^{j-1} S_h = \prod_{h=i}^{j-1} F_h S_h .$$

Furthermore (2.5) is also identical to the probability structure for M_1 , therefore we can express the joint model for the *last* encounter simply in terms of the two sets of marginal cell probabilities, with different parameters in the two factors (p_i and $\phi_i = S_i F_i$ for live recoveries and S_i and f_i for the terminal recoveries). If we factor the resulting joint likelihood we find that the MSS is simply the combined sets of MSS obtained by modelling the two parts of the model (terminal recaptures and terminal recoveries) separately using M_1 . As a consequence, the maximum

likelihood estimators of the survival, capture, and movement parameters can be obtained from the joint distribution of the $M_{i,j}$ and $R_{i,j}$'s and these exist in a relatively simple closed form:

- (i) Find \hat{p}_i and $\hat{\phi}_i$ using M_1 of Brownie et al. (1985) applied to the live recovery component of the data array (e.g. Brownie et al 1985:174).
- (ii) Find \hat{f}_i and \hat{S}_i using M_1 applied to the band recovery component of the data array.
- (iii) Find \hat{F}_i as

$$\hat{F}_i = \frac{\hat{\phi}_i}{\hat{S}_i}. \quad (2.10)$$

In this case, all information on survival and recovery rates come from the band recovery component of the data. Thus, the joint analysis provides no advantage over the usual band recovery analysis for these two parameters. Similarly, all information on capture probabilities comes from the live-recapture component of the data array, but the joint analysis based on the *last* encounter will not be as efficient with respect to the capture probability estimates as the usual Jolly-Seber analysis applied to the full live recapture data set. This loss of efficiency occurs because in the last encounter analysis information from intermediate captures is discarded.

The overall conclusion is that if migration is permanent, the Mardekian-McDonald analysis is incorrect. Moreover the joint analysis of the last encounter data provides no computational advantage over separate analyses of the live-recapture and band recovery data using the Jolly-Seber model and M_1 . Such an analysis has been suggested by Anderson and Sterling (1974). Note that in this case, \hat{F}_i can be obtained as in (2.10), and will have a smaller variance than the similar estimate from the analysis of the last encounters. As we show in later chapters, the analysis of Buckland (1980) based on Jolly's (1965) idea of augmenting the recapture data with resightings of marked animals is also invalid under permanent emigration.

2.3 Burnham's Model

Burnham (1993) proposed a model which is a natural generalization of the Jolly-Seber model and model M_1 of Brownie et al. (1985). Burnham (1993) gives alternative parameterizations of the model under the two assumptions about emigration "random" and "permanent".

The key to developing the correct probability structure for the joint analysis of the live-recapture and tag-recovery models is recognizing that the two types of events "live recapture" and "tag recovery after known death" compete with each other. "Once a recapture at occasion j ($j > i$) occurs that bird is reassigned upon release to the j^{th} release cohort and hence is no longer available to become a dead recovery from the i^{th} release cohort after occasion j ." (Burnham 1993). If we represent the joint data in the form given in Table 2.5 where

Table 2.5: Reduced m-array for a mark-recapture study carried out with t years of capture and t years of recovery

Cohort	Next encountered by capture				Next encountered by tag-recovery				
	$j = 2$	3	...	t	$j = 1$	2	...	$t - 1$	t
$i=1$	$M_{1,2,1}$	$M_{1,3,1}$...	$M_{1,t,1}$	$M_{1,1,2}$	$M_{1,2,2}$...	$M_{1,t-1,2}$	$M_{1,t,2}$
2		$M_{2,3,1}$...	$M_{2,t,1}$		$M_{2,2,2}$...	$M_{2,t-1,2}$	$M_{2,t,2}$

$t - 1$...	$M_{t-1,t,1}$...	$M_{t-1,t-1,2}$	$M_{t-1,t,2}$
t			...					-	$M_{t,t,2}$

$M_{i,j,1}$ = the number of animals last released at time i next encountered by live recapture at j ,

$M_{i,j,2}$ = the number of animals last released at time i next encountered by tag-recovery at j ,

with corresponding cell probabilities $\pi_{i,j,k}$ ($k=1,2$) then Burnham (1993) shows that

the cell probabilities are given by

$$\pi_{i,j,1} = \begin{cases} \phi_i p_{i+1} & j = i + 1 \\ \phi_{j-1} p_j \prod_{h=i}^{j-2} \phi_h (1 - p_{h+1}) & j > i + 1 \end{cases}$$

and

$$\pi_{i,j,2} = \begin{cases} f_i & j = i \\ S_i \cdots S_{j-1} \gamma_{i,j} f_j & j > i \end{cases},$$

where $\gamma_{i,j}$ is the probability that an animal released at i is alive at j and has not been captured between $i + 1$ and j inclusive.

Under permanent emigration Burnham (1990) shows

$$\gamma_{i,j} = \begin{cases} 1 & i = j \\ 1 - F_i(1 - (1 - p_{i+1})\gamma_{i+1,j}) & i = 1, \dots, j - 1 ; j = 1, \dots, t \end{cases},$$

and under random emigration

$$\gamma_{i,j} = \begin{cases} 1 & i = j \\ (1 - F_i p_{i+1}) \cdots (1 - F_{j-1} p_j) & \end{cases}$$

Burnham (1990) notes that under permanent emigration explicit MLE's do not appear to be possible but that they can be found under random emigration. Szymczak and Rexstad (1991) reported an analysis carried out based on Burnham's (1993) work.

2.4 Live-Recapture Analyses Augmented with Sightings

The problem of incorporating tag-recoveries into an analysis based on live recaptures or vice versa is a specific example of the more general situation envisaged by Jolly (1965). In discussing his solutions for the Jolly-Seber model, Jolly(1965) remarked that recaptures "enter into the estimates in two distinct ways, first...as the proportion of previously marked animals in n_i, \dots , and, secondly, as the ratio of future recaptures". In particular, it is the ratio of future recaptures that is

important for the estimation of survival rate. This led Jolly to suggest that two methods of observation could operate simultaneously, one involving the captures at time i , and the second involving observations of marked animals obtained over a wide area which is carried out continuously because, as Jolly remarked, the exact time an animal is recaptured (meaning observed) is of no importance. Estimation would then be carried out by including the additional observations of animals in the Jolly-Seber model statistics z_i and r_i . The problem was also briefly discussed by Schwarz et al. (1993). They suggested that the experiment could be improved by incorporating ancillary resightings of animals between releases, although they were specifically interested in using this information to help estimate movement probabilities.

In subsequent chapters we consider the problem of incorporating auxiliary sightings (live or dead) into a mark-recapture. As pointed out by Jolly (1965) such an approach could lead to improved precision. We also show that analyses of this type can expand the range of models that can be fitted to a data set.

Chapter 3

Single-Stratum Mark-Recapture Models with Ancillary Observations

3.1 Background

Mark-recapture data in the form suitable for the Jolly-Seber model can be an inefficient means of obtaining information on animal population parameters. In the example given in Table 3.1 only 8% of animals were ever recaptured following release. Because we cannot tell whether the remaining 92% were not recaptured

Table 3.1: Live-recapture reduced m-array for brown trout *Salmo trutta* captured and tagged in Lake Brunner 1987-1990

Year released	No. released	Year next captured			Never seen again
		88	89	90	
87	353	25	25	9	294
88	924		70	27	827
89	1316			64	1252

because they had died, or instead were alive but not caught, these animals provide

no direct information on the survival and capture processes. Clearly, an “efficient” study will be one in which the proportion of animals unaccounted for is small.

The only factors that the experimenter can influence in order to reduce the proportion of animals that are never recaptured are the efficiency of the capture process, and the length of the study. In reality, capture probabilities can be difficult to increase, and the benefits of a lengthy study period will be low for short-lived animals, and for long-lived animals dependent on how urgently the estimates are required. An alternative approach to obtaining information on the animals never recaptured would be to utilize a separate sampling scheme as envisaged by Jolly (1965). The efficiency of this approach would clearly depend on how effective the alternative sampling scheme was in obtaining information on animals that would otherwise be unaccounted for.

The joint capture-recapture and band-recovery study considered in detail by Burnham (1990, 1993) is in fact a special case of the situation discussed by Jolly (1965) but where the animals are removed from the population on “observation”. However the unified theory developed by Burnham (1990) for joint capture-recapture and band-recovery studies is appropriate for the more general situation envisaged by Jolly (1965). In this chapter we utilize this theory to develop a general model for the situation considered by Jolly (1965) with t capture occasions for a single age class.

3.2 The Experimental Situation, Notation, and Assumptions

The model is expressed in terms of two “capture” methods. The first is actual physical capture at time i ($i=1,\dots,t$), which we refer to as capture at i . There are t distinct times at which capture is carried out and it is assumed that capture occurs instantaneously at these times. However, we do not require that the capture times be regularly spaced. Capture may occur if the animals are present in the “at risk of capture” component of the population. By this we mean that the population

comprises “at risk of capture” and “not at risk of capture” individuals allowing for the common situation where the physical capture process targets a specific subset of the population. For example in waterfowl banding studies it is only birds that are associated with the banding site that are at risk of capture. It is important that a mark-recapture model be general enough to allow for this possibility, and in particular, to accommodate any movement between these components of the population between capture times.

The second type of “capture” is where animals are observed (resighted) at some time in the interval $i, i + 1$, denoted observation at time i . Note that the interval begins at i and ends just before $i + 1$, so that an animal seen exactly at i is classified as having been observed in the interval $i, i + 1$. We assume that observations of marked animals are made throughout the range of the population of interest (i.e. both the “at risk of capture” component, and the “not at risk of capture” component are observed). By observation we mean any method of obtaining ancillary observations, and may include some other type of capture.

3.2.1 Notation

Statistics

$M_{i,j,1,1}$ = the number of marked animals last released following capture at time i that are next encountered by capture at time j .

$M_{i,j,1,2}$ = the number of marked animals last released following capture at time i that are next encountered by observation at time j (i.e. resighted in $j, j + 1$).

$M_{i,j,2,1}$ = the number of marked animals last encountered by observation at time i that are next encountered by capture at time j .

$M_{i,j,2,2}$ = the number of marked animals last encountered by observation at time i that are next encountered by observation at time j .

$R_{i,1}$ = the total number of marked animals released following capture at time i that are subsequently encountered by either method.

$R_{i,2}$ = the total number of marked animals released following observation at time i that are subsequently encountered by either method.

C_i = the total number of marked animals captured at time i (i.e. last released by either method).

O_i = the total number of marked animals observed at time i (i.e. last released by either method).

$L_{i,1}$ = the number of animals removed from the population following capture at time i (i.e. not released on capture).

$L_{i,2}$ = the number of marked animals removed from the population following observation at time i (i.e. not released on observation).

Z_i = the number of marked animals *last* released before i , not captured at i , but subsequently caught or observed (includes animals observed in $i, i + 1$).

r_i = the number of marked animals at i that are subsequently encountered after sampling time i (i.e. includes animals observed in $i, i + 1$, but not those captured at i). NB $r_i = Z_i + R_{i,1}$.

T_i = the number of marked animals at i that are observed, or captured, at or after i (i.e. includes those captured at i). NB $T_i = Z_i + C_i$.

N_i = the number of marked animals released at i following capture (i.e. excludes losses on capture at i).

n_i = the number of marked animals released at i following observation (i.e. excludes losses on observation at i).

Parameters of interest

S_i = the probability that a marked animal survives from time i until time $i + 1$, given that it is alive at time i .

p_i = the probability that a marked animal is captured at time i given that it is alive and at risk of capture at time i .

f_i = the probability a marked animal is observed in the interval $(i, i + 1)$ given that it is alive at time i .

θ_i = the probability that a marked animal alive at time i is not observed in the interval $(i, i + 1)$ given that it is alive at $i + 1$.

F_i = the probability a marked animal that is alive at time $i + 1$ and was at risk of capture at time i is at risk of capture at time $i + 1$.

η_i = the probability a marked animal is released at i , given that it is captured at i (i.e. not lost on capture at i).

ρ_i = the probability a marked animal is released at i given that it is observed at i (i.e. not lost on observation at i).

Working parameters

$\pi_{i,j,m,n}$ = the multinomial cell probability for $M_{i,j,m,n}$ conditional on release at i .

$\alpha_{i,1}$ = the probability a member of a release cohort at time i is removed from that cohort by capture at time $i + 1$.

$\alpha_{i,2}$ = the probability a member of a release cohort at time i is removed from that cohort by observation in the interval $i, i + 1$. NB $\alpha_{i,2} = f_i$.

β_i = the probability a member of a release cohort at time i is still a member of that release cohort at time $i + 1$ (i.e. it has not died or been observed in $i, i + 1$ and has not been captured at $i + 1$).

$\gamma_{i,j,1}$ = the probability a marked animal last captured and released at time i and alive at j is not captured before time j but is at risk of capture at time j .

$\gamma_{i,j,2}$ = the probability a marked animal last captured and released at time i and alive at j is not captured at or before time j .

$\lambda_{i,1}$ = the probability an animal last released following capture at i is ever captured or observed again.

$\lambda_{i,2}$ = the probability an animal last released following observation at i is ever captured or observed again.

$\tau_{i,1}$ = the probability a member of T_i is captured at i .

$\tau_{i,2}$ = the probability a member of r_i is observed at i .

3.2.2 Assumptions

- (i) At time i all marked animals have the same p_i and S_i in common (the homogeneity assumption).
- (ii) Every animal captured in the i th sample has the same probability η_i of being released on capture.
- (iii) Marked animals do not lose their marks and all marks are correctly reported when encountered.
- (iv) Captures are made instantaneously at time i and each release is made immediately after the sample.

We also assume:

- (v) At time i all animals have F_i , θ_i , and f_i in common (the “homogeneity” assumption).

- (vi) Observations are made throughout the animals range, but capture only occurs in that portion of their range where they are at risk of capture.

Note that the homogeneity assumption applies only to marked animals and so far we have made no assumptions about the relationship between marked and unmarked animals. If the goal of the experiment is to estimate the size of the animal population then we need to assume that marked and unmarked animals have the same capture probabilities at i , p_i . Following recent trends (Lebreton et al. 1992) our emphasis will be placed on the use of mark-recapture experiments to estimate survival probabilities. For the experiment to provide useful inference regarding the dynamics of the animal population we need to assume that survival probabilities at i , S_i , are the same for marked and unmarked animals.

3.2.3 Data structure

The set of individual capture histories for each animal encountered in the study form the raw data for any mark-recapture study. The capture history for a particular animal indicates the status of that animal at each sampling period. Because of the observations of animals in the interval $i, i + 1$ we need a modified capture history such as that used by Pollock et al. (1990) to record the data obtained from the experiment. We have further modified their capture history format to allow for animals removed on observation (Table 3.2).

Although any analysis must be based on these capture histories, we adopt the approach advocated by Burnham (1993) of modelling the sufficient statistics obtained by first summarizing the data based on the outcome of each paired release and subsequent encounter. This summary is produced as follows.

When an animal is released following the first occasion on which it was marked (at time i , say) it may fall into one of $2t$ mutually exclusive classes ($M_{i,i+1,1,1}, \dots, M_{i,t,1,1}, M_{i,i,1,2}, \dots, M_{i,t,1,2}, N_i - R_{i,1}$) with the final class (i.e. $N_i - R_{i,1}$) representing those animals released at i , that are never captured or observed again. Once an animal is encountered at time j (i.e. becomes one of the $M_{i,j,1,1}$ or $M_{i,j,1,2}$'s), the animal is transferred to a new release cohort depending on how it was encountered. If the

Table 3.2: Capture history codes -adapted from Pollock et al. (1990).

Code	Definition
0	Not captured in sample
1	Captured and released in sample
2	captured and not released in sample
3	Not captured in sample, observed after sample and before next sample, released on observation
4	Not captured in sample, observed after sample and before next sample, not released on observation
5	Captured and released in sample and observed after sample and before next sample, released on observation
6	Captured and released in sample and observed after sample and before next sample, not released on observation

animal is next encountered by capture at j it is transferred to the release cohort of animals that were last encountered by capture at time j (denoted $C_{j,1}$). If the animal is next encountered by observation in the interval $j, j + 1$ it is transferred to the release cohort of animals that were last encountered by observation at time j (denoted $C_{j,2}$). Note

- (i) Multiple observations of animals in an interval are ignored. We just make use of the fact that the animal was seen at some time in that interval.
- (ii) All animals first enter the study as a member of a $C_{i,1}$ cohort
- (iii) Members of $C_{i,1}$ may transfer to $C_{j,1}$ ($j = i + 1, \dots, t$) or $C_{j,2}$ ($j = i, \dots, t - 1$)
- (iv) Members of $C_{i,2}$ may transfer to $C_{j,1}$ ($j = i + 1, \dots, t$) or $C_{j,2}$ ($j = i + 1, \dots, t - 1$)

Thus animals that are captured at i and then seen in the interval $i, i + 1$ become members of $C_{i,1}$, contribute to $M_{i,i,1,2}$, and then are transferred to $C_{i,2}$. As already pointed out, however, multiple observations of animals in $i, i + 1$ are ignored.

Using the capture-history codes of Table 3.2 consider a fictitious animal with capture history 05013. This animal first entered the study at time 2, hence was initially released as a member of $C_{2,1}$. Following this release the animal was next encountered by an observation at least once at some point between times 2 and 3. Thus, the animal contributed to $M_{2,2,1,2}$ then was “re-released” as a member of release cohort $C_{2,2}$. Our animal was next encountered by capture at time 4, hence it contributed to $M_{2,4,2,1}$, then was re-released as a member of $C_{4,1}$. The final encounter of this animal was an observation some time between times 5 and 6 hence it makes a contribution to $M_{4,5,1,2}$. The contributions that this animal makes to the $M_{i,j,k,l}$ (i.e. the now extended reduced m-array) is illustrated in Table 3.3. Note that an animal may contribute to several of the $M_{i,j,k,l}$'s, but only one per release cohort. This emphasizes the point that we are conditioning on each release event.

Table 3.3: Contributions to the reduced m-array by an animal with capture history 05013 in a study with $t = 5$.

	Next encountered by capture				Next encountered by observation				
	$j = 2$	3	4	5	$j = 1$	2	3	4	5
A. Released following capture									
1									
2						1			
3									
4									1
5									
B. Released following observation									
1									
2			1						
3									
4									

The general form of a mark-recapture data set with ancillary observations is given in Table 3.4. A numerical example is given in Table 3.5 with the various

Table 3.4: Reduced m-array for a mark-recapture study carried out with t years of capture and ancillary observations of marked animals obtained during the interval $1, t + 1$.

Cohort	No. released	Next encountered by capture				Next encountered by observation				
		$j = 2$	3	...	t	$j = 1$	2	...	$t - 1$	t
$C_{i,1}$ - last released following capture										
$i=1$	N_1	$M_{1,2,1,1}$	$M_{1,3,1,1}$...	$M_{1,t,1,1}$	$M_{1,1,1,2}$	$M_{1,2,1,2}$...	$M_{1,t-1,1,2}$	$M_{1,t,1,2}$
2	N_2		$M_{2,3,1,1}$...	$M_{2,t,1,1}$		$M_{2,2,1,2}$...	$M_{2,t-1,1,2}$	$M_{2,t,1,2}$

$t - 1$	N_{t-1}			...	$M_{t-1,t,1,1}$...	$M_{t-1,t-1,1,2}$	$M_{t-1,t,1,2}$
t	N_t			...					$M_{t,t,1,2}$	
$C_{i,2}$ - last released following observation										
$i=1$	n_1	$M_{1,2,2,1}$	$M_{1,3,2,1}$...	$M_{1,t,2,1}$		$M_{1,2,2,2}$...	$M_{1,t-1,2,2}$	$M_{1,t,2,2}$
2	n_2		$M_{2,3,2,1}$...	$M_{2,t,2,1}$...	$M_{2,t-1,2,2}$	$M_{2,t,2,2}$

$t - 1$	n_{t-1}			...	$M_{t-1,t,2,1}$...		$M_{t-1,t,2,2}$

summary statistics for this data set given in Table 3.6.

Table 3.5: Reduced m-array for a hypothetical $t = 4$ mark- recapture study with ancillary observations of animals in the interval $i, i + 1$.

Cohort	No. released	Next encountered			Next encountered			
		by capture			by observation			
		$j = 2$	3	4	$j = 1$	2	3	4
A. Last released following capture								
$i = 1$	1000	51	16	13	108	48	16	12
2	1000		50	19		94	56	18
3	1000			48			101	54
4	1000							107
B. Last released following observation								
$i = 1$	108	12	2	3		8	4	1
2	150		13	5			12	5
3	189			9				11

Table 3.6: Summary statistics for the hypothetical reduced m-array.

Year	N_i	n_i	$R_{i,1}$	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	$L_{i,2}$
1	1000	108	264	30		108			264	0
2	1000	150	237	35	63	150	123	186	360	0
3	1000	189	203	20	81	189	164	245	367	0
4	1000		107		97	208	101	198	208	0

3.2.4 Random emigration model

To simplify our discussion we first consider the form of the model under random emigration (Burnham 1993) as this leads to closed-form maximum likelihood solutions facilitating comparison with published mark-recapture models. Under random

emigration, we assume that those animals not at risk of capture at time i , that are alive at $i + 1$, have the same probability of being at risk of capture at time $i + 1$ as those animals at risk of capture at time i that are alive at $i + 1$. This probability is F_i .

For members of a $C_{i,1}$ cohort, the probability structure of the model under random emigration is given by

$$\pi_{i,j,1,k} = \begin{cases} \alpha_{i,1} & j = i + 1, k = 1 \\ \alpha_{i,2} & j = i, k = 2 \\ \alpha_{j-1,1} \prod_{h=i}^{j-2} \beta_h & j = i + 2, \dots, t, k = 1 \\ \alpha_{j,2} \prod_{h=i}^{j-1} \beta_h & j = i + 1, \dots, t, k = 2 \end{cases} \quad (3.1)$$

and for members of a $C_{i,2}$ cohort by

$$\pi_{i,j,2,k} = \begin{cases} \delta_i \alpha_{i,1} & j = i + 1, k = 1 \\ \delta_i \alpha_{j-1,1} \prod_{h=i}^{j-2} \beta_h & j = i + 2, \dots, t, k = 1 \\ \delta_i \alpha_{j,2} \prod_{h=i}^{j-1} \beta_h & j = i + 1, \dots, t, k = 2 \end{cases} \quad (3.2)$$

where

$$\alpha_{i,k} = \begin{cases} S_i \theta_i F_i p_{i+1} & k = 1 \\ f_i & k = 2 \end{cases} \quad (3.3)$$

$$\beta_i = S_i \theta_i (1 - F_i p_{i+1}), \quad (3.4)$$

and

$$\delta_i = \frac{1 - \theta_i}{\theta_i f_i p_i}. \quad (3.5)$$

The probability structure for a $t = 4$ study is illustrated in Tables 3.2.4 and 3.2.4. In particular, notice that the probability that animals in cohort $C_{i,2}$ survive from i to $i + 1$ is not S_i . Rather, we need the probability that an animal survives from year i to year $i + 1$ *conditional* on being observed in $i, i + 1$ and released following observation. Because we have seen these these animals after i , and hence know that they are alive at some time after i , we expect this survival probability

Table 3.7: Probability structure for animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$, and random movement into and out of the area where they are at risk of capture. In this parameterization $p_i^* = F_{i-1}p_i$ and $q_i^* = 1 - p_i^*$.

A. Last released following capture

Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	$S_1\theta_1p_2^*$	$S_2\theta_2p_3^*S_1\theta_1q_2^*$...	$S_{t-1}\theta_{t-1}p_t^* \prod_{h=1}^{t-2} S_h\theta_hq_{h+1}^*$
2	-	$S_2\theta_2p_3^*$...	$S_{t-1}\theta_{t-1}p_t^* \prod_{h=2}^{t-2} S_h\theta_hq_{h+1}^*$
.
.
.
$t - 1$	-	-	...	$S_{t-1}\theta_{t-1}p_t^*$

Cohort	Next encountered by observation				
	$j = 1$	2	...	$t - 1$	t
$i = 1$	f_1	$f_2S_1\theta_1q_2^*$...	$f_{t-1} \prod_{h=1}^{t-2} S_h\theta_hq_{h+1}^*$	$f_t \prod_{h=1}^{t-1} S_h\theta_hq_{h+1}^*$
2	-	f_2	...	$f_{t-1} \prod_{h=2}^{t-2} S_h\theta_hq_{h+1}^*$	$f_t \prod_{h=2}^{t-1} S_h\theta_hq_{h+1}^*$
.
.
.
$t - 1$	-	-	...	f_{t-1}	$f_tS_{t-1}\theta_{t-1}q_t^*$
t	-	-	...	-	f_t

Table 3.8: Probability structure for animals last released following observation in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$, and random movement into and out of the area where they are at risk of capture. In this parameterization $p_i^* = F_{i-1}p_i$ and $q_i^* = 1 - p_i^*$, and $\delta_i = \frac{1-\theta_i}{\theta_i f_i \rho_i}$.

B. Last released following observation				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i=1$	$\delta_1 \theta_1 S_1 p_2^*$	$\delta_1 \theta_1 S_2 \theta_2 p_3^* S_1 q_2^*$...	$\delta_1 \theta_1 S_{t-1} \theta_{t-1} p_t^* S_1 \prod_{h=2}^{t-2} S_h \theta_h q_{h+1}^*$
2	-	$\delta_2 \theta_2 S_2 p_3^*$...	$\delta_2 \theta_2 S_{t-1} p_t^* S_2 \prod_{h=3}^{t-2} S_h \theta_h q_{h+1}^*$
.
.
$t-1$	-	-	...	$\delta_{t-1} \theta_{t-1} S_{t-1} p_t^*$
Next encountered by observation				
Cohort	$j = 2$...	$t-1$	t
	$i = 1$	$\delta_1 \theta_1 f_2 S_1 q_2^*$...	$\delta_1 \theta_1 f_{t-1} S_1 q_2^*$ $\times \prod_{h=2}^{t-2} S_h \theta_h q_{h+1}^*$
2	-	...	$\delta_2 \theta_2 f_{t-1} S_2 q_3^*$ $\times \prod_{h=3}^{t-2} S_h \theta_h q_{h+1}^*$	$\delta_2 \theta_2 f_t S_2 q_3^*$ $\times \prod_{h=3}^{t-1} S_h \theta_h q_{h+1}^*$
.
.
$t-1$	-	...	-	$\delta_{t-1} \theta_{t-1} f_t S_{t-1} q_t^*$

to be higher than S_i . From the definitions of f_i , θ_i , ρ_i , and S_i and using the result

$$\begin{aligned}
& Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1) \\
&= Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1 | \text{released}) Pr(\text{released}) \\
&\quad + Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1 | \text{not released}) Pr(\text{not released}) \\
&= Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1 | \text{released}) Pr(\text{released}) + 0,
\end{aligned}$$

we obtain

$$\begin{aligned}
& Pr(\text{survives from } i \text{ to } i + 1 | \text{seen in } i, i + 1 \text{ and released}) \\
&= \frac{Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1 \text{ and released})}{Pr(\text{seen in } i, i + 1 \text{ and released})} \\
&= \frac{Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1 | \text{released}) Pr(\text{released})}{Pr(\text{released} | \text{seen in } i, i + 1) Pr(\text{seen in } i, i + 1)} \\
&= \frac{Pr(\text{survives from } i \text{ to } i + 1 \text{ and seen in } i, i + 1)}{Pr(\text{released} | \text{seen in } i, i + 1) Pr(\text{seen in } i, i + 1)} \\
&= \frac{(1 - \theta_i) S_i}{f_i \rho_i} \tag{3.6}
\end{aligned}$$

Because we ignore subsequent observations in the interval $i, i + 1$, the cohort survival rate from i to $i + 1$, β_i , for animals released following observation at i , should not include the θ_i term, and furthermore the survival rate should be adjusted as in equation (3.6). The parameter δ_i is used to adjust β_i as defined in equation (3.4) so that it is correct for members of $C_{i,2}$.

To illustrate computation of the multinomial cell probabilities for the reduced m-array, consider the cell probability for $M_{1,3,1,1}$. We know that following release at time 1 the animals that contributed to $M_{1,3,1,1}$ survived from time 1 to 2, an event which happened with probability S_1 . Given that they were alive at 2 we know they were not observed between 1 and 2, they remained in the population at risk of capture between 1 and 2 and were not captured at 2. The joint probability of these events is $\theta_1(1 - F_1 p_2)$. We know the animals then survived from time 2 to 3 with probability S_2 , they were not observed between 2 and 3 with probability θ_2 and they remained in the population at risk of capture with probability F_2 . Given

that they were alive at 3, we know they were captured with probability p_3 . Thus,

$$\begin{aligned}\pi_{1,3,1,1} &= S_1\theta_1(1 - F_1p_2)S_2\theta_2F_2p_3 \\ &= \alpha_{2,1}\beta_1.\end{aligned}$$

The cell probability for $M_{1,3,2,2}$ is computed in an identical manner with the exception that the survival probability from 1 to 2 is now conditional on the fact that the animals were observed and released following observation. Hence

$$\begin{aligned}\pi_{1,3,2,1} &= \frac{1 - \theta_1}{f_1\rho_1}S_1(1 - F_1p_2)S_2\theta_2F_2p_3 \\ &= \alpha_{2,1}\frac{1 - \theta_1}{\theta_1f_1\rho_1}\beta_1 \\ &= \delta_1\alpha_{2,1}\beta_1.\end{aligned}$$

3.2.5 The likelihood function under random emigration

Using the peeling and pooling method described by Burnham (1990) we can express the likelihood in the form $\mathcal{L} = Pr(\text{Data}|\text{MSS})Pr(\text{MSS})$ where MSS denotes a set of jointly minimal sufficient statistics. As shown below we can factor the likelihood to obtain the result that a MSS is the set of $R_{i,1}$ ($i = 1, \dots, t$), $R_{i,2}$ ($i=1, \dots, t-1$), C_i ($i=2, \dots, t$), and O_i ($i = 1, \dots, t - 1$) which has dimension $4t - 3$, with $4t - 3$ free parameters in the model. The distribution of this MSS, i.e. $Pr(\text{MSS})$, can be expressed as the product of independent binomial terms conditional on the releases, N_i and n_i , and the following functions of the MSS:

$$T_i = Z_i + C_i$$

and

$$\tau_i = Z_i + R_{i,1}$$

where

$$Z_i = \begin{cases} 0 & i = 1 \\ Z_{i-1} + R_{i-1,1} + R_{i-1,2} - C_i - O_{i-1} & i = 2, \dots, t \end{cases} \quad (3.7)$$

The set of “residual” terms, $Pr(\text{Data}|\text{MSS})$, are conditionally independent multi-hypergeometric random variables. This set of terms involves the partial column

totals $M_{i,j,p,k}$ where

$$M_{i,j,p,k} = \begin{cases} \sum_{h=1}^i M_{h,j,1,1} + \sum_{h=1}^{i-1} M_{h,j,2,1} & k = 1 \\ \sum_{h=1}^i M_{h,j,1,2} + M_{h,j,2,1} & k = 2 \end{cases}$$

Derivation of the factorization $\mathcal{L} = Pr(\text{Data}|\text{MSS})Pr(\text{MSS})$ is based on repeated application of the following theorem:

Theorem 3.1 (Multinomial factorization theorem) Let (X_1, \dots, X_k) be multinomial with parameters N, p_1, \dots, p_k . Then

$$Pr(X_1, \dots, X_k) = Pr(X_1)Pr(X_2, \dots, X_k|N - X_1)$$

where

$$Pr(X_1) = \binom{N}{X_1} p_1^{X_1} (1 - p_1)^{N - X_1}$$

and

$$Pr(X_2, \dots, X_k|N - X_1) = \frac{(N - X_1)!}{\prod_{i=2}^k X_i!} \prod_{i=2}^k \left(\frac{p_i}{1 - p_1} \right)^{X_i}$$

Proof From Larsen and Marx (1986) Theorem 9.2.1, the marginal distribution of X_i is binomial. Now,

$$\begin{aligned} Pr(X_1, \dots, X_k) &= Pr(X_1)Pr(X_2, \dots, X_k|X_1) \\ &= Pr(X_1) \frac{Pr(X_1, \dots, X_k)}{Pr(X_1)} \\ &= \frac{N!}{X_1!(N - X_1)!} p_1^{X_1} (1 - p_1)^{N - X_1} \\ &\quad \times \frac{\frac{N!}{\prod_{i=1}^k X_i!} \prod_{i=1}^k \left(\frac{p_i}{1 - p_1} \right)^{X_i}}{\frac{N!}{X_1!(N - X_1)!} p_1^{X_1} (1 - p_1)^{N - X_1}} \\ &= \frac{N!}{X_1!(N - X_1)!} p_1^{X_1} (1 - p_1)^{N - X_1} \end{aligned}$$

$$\begin{aligned}
& \times \frac{(N - X_1)!}{\prod_{i=2}^k X_i!} \prod_{i=2}^k \left(\frac{p_i}{1 - p_1} \right)^{X_i} \\
& = Pr(X_1) Pr(X_2, \dots, X_K | N - X_1)
\end{aligned}$$

Now, we can write the likelihood as

$$\begin{aligned}
Pr(\text{Data}) &= \prod_{i=1}^t \left(\frac{N_i!}{(N_i - R_{i,1})! \prod_{j=i+1}^t M_{i,j,1,1}! \prod_{j=i}^t M_{i,j,1,2}!} \right) \\
&\quad \times \prod_{j=i+1}^t \pi_{i,j,1,1}^{M_{i,j,1,1}} \prod_{j=i}^t \pi_{i,j,1,2}^{M_{i,j,1,2}} (1 - \lambda_{i,1})^{N_i - R_{i,1}} \\
&\quad \times \prod_{i=1}^{t-1} \left(\frac{n_i!}{(n_i - R_{i,2})! \prod_{j=i+1}^t M_{i,j,2,1}! \prod_{j=i+1}^t M_{i,j,2,2}!} \right) \\
&\quad \times \prod_{j=i+1}^t \pi_{i,j,2,1}^{M_{i,j,2,1}} \prod_{j=i+1}^t \pi_{i,j,2,2}^{M_{i,j,2,2}} (1 - \lambda_{i,2})^{n_i - R_{i,2}}
\end{aligned} \tag{3.8}$$

where

$$\lambda_{i,k} = \begin{cases} \sum_{j=i+1}^t \pi_{i,j,1,1} + \sum_{j=i}^t \pi_{i,j,1,2} & k = 1 \\ \sum_{j=i+1}^t \pi_{i,j,2,1} + \sum_{j=i+1}^t \pi_{i,j,2,2} & k = 2 \end{cases}$$

We can also write

$$\begin{aligned}
\lambda_{i,1} &= (\alpha_{i,1} + \alpha_{i,2}) + (\alpha_{i+1,1} + \alpha_{i+1,2})\beta_i + \dots + (\alpha_{t-1,1} + \alpha_{t-1,2})\beta_i \cdots \beta_{t-2} \\
&\quad + \alpha_{t,2}\beta_i \cdots \beta_{t-1} \\
&= (\alpha_{i,1} + \alpha_{i,2}) + \beta_i \lambda_{i+1,1}
\end{aligned} \tag{3.9}$$

and

$$\lambda_{i,2} = \delta_i (\lambda_{i,1} - \alpha_{i,2}) . \tag{3.10}$$

Factoring out the marginal distributions of $R_{i,1}$ and $R_{i,2}$ (strictly $R_{i,1}|N_i$ and

$R_{i,2}|n_i$ from (3.8) we obtain

$$\begin{aligned} \Pr(\text{Data}) &= \prod_{i=1}^t \Pr(R_{i,1}|N_i) \prod_{i=1}^{t-1} \Pr(M_{i,i+1,1,1}, \dots, M_{i,t,1,1}, M_{i,i+1,2}, \dots, M_{i,t,1,2}|R_{i,1}) \\ &\quad \times \prod_{i=1}^{t-1} \Pr(R_{i,2}|n_i) \Pr(M_{i,i+1,1,2}, \dots, M_{i,t,1,2}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2}|R_{i,2}). \end{aligned}$$

Now, the marginal distributions of the $R_{i,k}$'s are binomial, conditional on the numbers released in each cohort:

$$R_{i,1} | N_i \sim B(N_i, \lambda_{i,1})$$

$$R_{i,2} | n_i \sim B(n_i, \lambda_{i,2}),$$

and the distributions of

$$(M_{i,i+1,1,1}, \dots, M_{i,t,1,1}, M_{i,i+1,1,2}, \dots, M_{i,t,1,2}|R_{i,1})$$

and

$$(M_{i,i+1,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2}|R_{i,2})$$

are multinomial, conditional on the $R_{i,k}$'s, with multinomial cell probabilities $\frac{\pi_{i,j,1,k}}{\lambda_{i,1}}$ and $\frac{\pi_{i,j,2,k}}{\lambda_{i,2}}$ respectively. Hence

$$\begin{aligned} \Pr(\text{Data}) &= \prod_{i=1}^t \binom{N_i}{R_{i,1}} \lambda_{i,1}^{R_{i,1}} (1 - \lambda_{i,1})^{(N_i - R_{i,1})} \\ &\quad \times \prod_{i=1}^{t-1} \left\{ \binom{R_{i,1}}{[M_{i,j,1,1}]_{j=i+1}^t, [M_{i,j,1,2}]_{j=i}^t} \prod_{j=i+1}^t \left(\frac{\pi_{i,j,1,1}}{\lambda_{i,1}} \right)^{M_{i,j,1,1}} \right. \\ &\quad \left. \times \prod_{j=i}^t \left(\frac{\pi_{i,j,1,2}}{\lambda_{i,1}} \right)^{M_{i,j,1,2}} \right\} \\ &\quad \times \prod_{i=1}^{t-1} \left\{ \binom{n_i}{R_{i,2}} \lambda_{i,2}^{R_{i,2}} (1 - \lambda_{i,2})^{(n_i - R_{i,2})} \right. \\ &\quad \times \binom{R_{i,2}}{[M_{i,j,2,1}]_{j=i+1}^t, [M_{i,j,2,2}]_{j=i+1}^t} \prod_{j=i+1}^t \left(\frac{\pi_{i,j,2,1}}{\lambda_{i,2}} \right)^{M_{i,j,2,1}} \\ &\quad \left. \times \prod_{j=i+1}^t \left(\frac{\pi_{i,j,2,2}}{\lambda_{i,2}} \right)^{M_{i,j,2,2}} \right\} \end{aligned} \quad (3.11)$$

where

$$\binom{x}{[y_i]_{i=a}^b}$$

is used to denote

$$\frac{x!}{\prod_{i=a}^b y_i!}.$$

The next step is to factor $\Pr(M_{1,2,1,1}, \dots, M_{1,t,1,1}, M_{1,1,1,2}, \dots, M_{1,t,1,2} | R_{1,1})$ obtaining

$$\begin{aligned} \Pr(M_{1,2,1,1}, \dots, M_{1,t,1,1}, M_{1,1,1,2}, \dots, M_{1,t,1,2} | R_{1,1}) = \\ \Pr(M_{1,1,1,2} | R_{1,1}) \times \Pr(M_{1,2,1,1} | R_{1,1} - M_{1,1,1,2}) \\ \times \Pr(M_{1,3,1,1}, \dots, M_{1,t,1,1}, M_{1,2,1,2}, \dots, M_{1,t,1,2} | R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1}) \end{aligned} \quad (3.12)$$

where

$$\Pr(M_{1,1,1,2} | R_{1,1}) = \binom{R_{1,1}}{M_{1,1,1,2}} \left(\frac{\alpha_{1,2}}{\lambda_{1,1}} \right)^{M_{1,1,1,2}} \left(1 - \frac{\alpha_{1,2}}{\lambda_{1,1}} \right)^{R_{1,1} - M_{1,1,1,2}}, \quad (3.13)$$

and

$$\Pr(M_{1,2,1,1} | R_{1,1} - M_{1,1,1,2}) = \quad (3.14)$$

$$\binom{R_{1,1} - M_{1,1,1,2}}{M_{1,2,1,1}} \left(\frac{\alpha_{1,1}}{\lambda_{1,1} - \alpha_{1,2}} \right)^{M_{1,2,1,1}} \left(1 - \frac{\alpha_{1,1}}{\lambda_{1,1} - \alpha_{1,2}} \right)^{R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1}} \quad (3.15)$$

$$(3.16)$$

The distribution of $(M_{1,3,1,1}, \dots, M_{1,t,1,1}, M_{1,2,1,2}, \dots, M_{1,t,1,2} | R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1})$ is multinomial and making use of relationship (3.9) we find the j, k 'th cell probability is given by

$$\begin{aligned} \frac{\pi_{1,j,1,k}}{\lambda_{1,1} - \alpha_{1,1} - \alpha_{1,2}} &= \frac{\beta_1 \pi_{2,j,1,k}}{\beta_1 \lambda_{2,1}} \\ &= \frac{\pi_{2,j,1,k}}{\lambda_{2,1}}. \end{aligned}$$

Similarly, we factor $\Pr(M_{1,2,2,1}, \dots, M_{1,t,2,1}, M_{1,2,2,2}, \dots, M_{1,t,2,2} | R_{1,2})$ obtaining

$$\begin{aligned} \Pr(M_{1,2,2,1}, \dots, M_{1,t,2,1}, M_{1,2,2,2}, \dots, M_{1,t,2,2} | R_{1,2}) = \\ \Pr(M_{1,2,2,1} | R_{1,2}) \Pr(M_{1,3,2,1}, \dots, M_{1,t,2,1}, M_{1,2,2,2}, \dots, M_{1,t,2,2} | R_{1,2} - M_{1,2,2,1}). \end{aligned} \quad (3.17)$$

Using the relationship (3.10), we find

$$\Pr(M_{1,2,2,1}|R_{1,2}) = \binom{R_{1,2}}{M_{1,2,2,1}} \left(\frac{\alpha_{1,1}}{\lambda_{1,1} - \alpha_{1,2}} \right)^{M_{1,2,2,1}} \left(1 - \frac{\alpha_{1,1}}{\lambda_{1,1} - \alpha_{1,2}} \right)^{R_{1,2} - M_{1,2,2,1}}, \quad (3.18)$$

and the binomial success parameter $\frac{\alpha_{1,1}}{\lambda_{1,1} - \alpha_{1,2}}$ is the same as in (3.14). Thus, we can “pool” $(M_{1,2,1,1}|R_{1,2} - M_{1,1,1,2})$ with $(M_{1,2,2,1}|R_{1,2})$. Noting that $M_{1,2,1,1} + M_{1,2,2,1} = C_1$, $M_{1,1,1,2} = O_1$, and $R_{1,1} - O_1 + R_{1,2} = T_2$ we obtain the result

$$\begin{aligned} & \Pr(M_{1,2,1,1}|R_{1,1} - M_{1,1,1,2}) \Pr(M_{1,2,2,1}|R_{1,2}) = \\ & \frac{\binom{R_{1,1} - M_{1,1,1,2}}{M_{1,2,1,1}} \binom{R_{1,2}}{M_{1,2,2,1}}}{\binom{T_2}{C_2}} \\ & \times \binom{T_2}{C_2} \left(\frac{\alpha_{1,1}}{\lambda_1 - \alpha_{1,2}} \right)^{C_2} \left(1 - \frac{\alpha_{1,1}}{\lambda_1 - \alpha_{1,2}} \right)^{T_2 - Z_2}. \end{aligned}$$

Now, using the relationship (3.9) and (3.10) we find that the j, k 'th cell probability for the conditional multinomial $(M_{1,3,2,1}, \dots, M_{1,t,2,1}, M_{1,2,2,2}, \dots, M_{1,t,2,2}|R_{1,2} - M_{1,2,2,1})$ is given by

$$\frac{\pi_{2,j,1,k}}{\lambda_{2,1}}.$$

But, $\frac{\pi_{2,j,1,k}}{\lambda_{2,1}}$ is also the j, k th cell probability for the conditional multinomials

$$(M_{1,3,1,1}, \dots, M_{1,t,1,1}, M_{1,2,1,2}, \dots, M_{1,t,1,2}|R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1})$$

and

$$(M_{2,3,1,1}, \dots, M_{2,t,1,1}, M_{2,2,1,2}, \dots, M_{2,t,1,2}|R_{2,1})$$

thus we are able to “pool” the corresponding cell counts. Now,

$$M_{1,j,1,k} + M_{1,2,2,k} + M_{2,j,1,k} = M_{2,j,p,k}$$

and

$$R_{1,1} - M_{1,1,1,2} - C_1 + R_{1,2} + R_{2,1} = r_2$$

hence the result

$$\begin{aligned}
& \Pr(M_{1,3,1,1}, \dots, M_{1,t,1,1}, M_{1,2,1,2}, \dots, M_{1,t,1,2} | R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1}) \\
& \quad \times \Pr(M_{1,3,2,1}, \dots, M_{1,t,2,1}, M_{1,2,2,2}, \dots, M_{1,t,2,2} | R_{1,2} - M_{1,2,2,1}) \\
& \quad \quad \times M_{2,3,1,1}, \dots, M_{2,t,1,1}, M_{2,3,1,2}, \dots, M_{2,t,1,2} | R_{2,1}) \\
= & \frac{\binom{R_{1,1} - M_{1,1,1,2} - M_{1,2,1,1}}{[M_{1,j,1,1}]_{j=3}^t, [M_{1,j,1,2}]_{j=2}^t} \binom{R_{1,2} - M_{1,2,2,1}}{[M_{2,j,2,1}]_{j=3}^t, [M_{2,j,2,2}]_{j=2}^t}}{\binom{r_2}{[M_{2,j,p,1}]_{j=3}^t, [M_{2,j,p,2}]_{j=2}^t}} \\
& \times \binom{R_{2,1}}{[M_{2,j,1,1}]_{j=3}^t, [M_{2,j,1,2}]_{j=2}^t} \times \Pr(M_{2,3,p,1}, \dots, M_{2,t,p,1}, M_{2,2,p,2}, \dots, M_{2,t,p,2} | r_2),
\end{aligned}$$

where

$$\begin{aligned}
& \Pr(M_{2,3,p,1}, \dots, M_{2,t,p,1}, M_{2,2,p,2}, \dots, M_{2,t,p,2} | r_2) = \\
& \quad \binom{r_2}{[M_{2,j,p,1}]_{j=3}^t, [M_{2,j,p,2}]_{j=2}^t} \prod_{j=3}^t \frac{\pi_{2,j,1,1}}{\lambda_{2,1}} \prod_{j=2}^t \frac{\pi_{2,j,1,2}}{\lambda_{2,1}}.
\end{aligned}$$

To complete the derivation of $\Pr(\text{MSS})$ we make repeated use of the following factorizations:

$$\begin{aligned}
& \Pr(M_{i,i+1,p,1}, \dots, M_{i,t,p,1}, M_{i,i,p,2}, \dots, M_{i,t,p,2} | r_i) = \\
& \quad \Pr(M_{i,i,p,2} | r_i) \times \Pr(M_{i,i+1,p,1} | r_i - M_{i,i,p,2}) \\
& \quad \times \Pr(M_{i,i+2,p,1}, \dots, M_{i,t,p,1}, M_{i,i+1,p,2}, \dots, M_{i,t,p,2} | r_i - M_{i,i,p,2} - M_{i,i+1,p,1}),
\end{aligned}$$

and

$$\begin{aligned}
& \Pr(M_{i,i+1,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2} | R_{i,2}) = \\
& \quad \Pr(M_{i,i+1,2,1} | R_{i,2}) \Pr(M_{i,i+2,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2} | R_{i,2} - M_{i,i+1,2,1})
\end{aligned}$$

where

$$\begin{aligned}
\Pr(M_{i,i,p,2} | r_i) &= \Pr(O_i | r_i) \\
&= \binom{r_i}{O_i} \left(\frac{\alpha_{i,2}}{\lambda_{i,1}} \right)^{O_i} \left(1 - \frac{\alpha_{i,2}}{\lambda_{i,1}} \right)^{r_i - O_i}, \tag{3.19}
\end{aligned}$$

$$\Pr(M_{i,i+1,1,1} | r_i - O_i) = \binom{r_i - O_i}{M_{i,i+1,p,1}} \left(\frac{\alpha_{i,1}}{\lambda_{i,1} - \alpha_{i,2}} \right)^{M_{i,i+1,p,1}} \left(1 - \frac{\alpha_{i,1}}{\lambda_{i,1} - \alpha_{i,2}} \right)^{r_i - O_i - M_{i,i+1,p,1}} \quad (3.20)$$

$$\Pr(M_{i,i+1,2,1} | R_{i,2}) = \binom{R_{i,2}}{M_{i,i+1,2,1}} \left(\frac{\alpha_{i,1}}{\lambda_i - \alpha_{i,2}} \right)^{M_{i,i+1,2,1}} \left(1 - \frac{\alpha_{i,1}}{\lambda_i - \alpha_{i,2}} \right)^{R_{i,2} - M_{i,i+1,2,1}}, \quad (3.21)$$

$(M_{i,i+2,1,1}, \dots, M_{i,t,1,1}, M_{i,i+1,1,2}, \dots, M_{i,t,1,2} | R_{i,1} - M_{i,i,1,2} - M_{i,i+1,1,1})$ is multinomial with i, j, k 'th cell probability given by

$$\frac{\pi_{i,j,1,k}}{\lambda_{i,1} - \alpha_{i,1} - \alpha_{i,2}} = \frac{\pi_{i+1,j,1,k}}{\lambda_{i+1,1}}$$

and $(M_{i,i+2,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2} | R_{i,2} - M_{i,i+1,2,1})$ is multinomial with i, j, k 'th cell probability also given by

$$\frac{\pi_{i+1,j,1,k}}{\lambda_{i+1,1}}$$

Now, $(M_{i,i+1,p,1} | r_i - O_i)$ and $(M_{i,i+1,2,1} | R_{i,2})$ have the same binomial success parameter so can be "pooled" forming $(C_{i+1} | T_{i+1})$ because $r_i - O_i + R_{i,2} = T_{i+1}$. Similarly, the multinomial cell probabilities for $(M_{i,i+2,1,1}, \dots, M_{i,t,1,1}, M_{i,i+1,1,2}, \dots, M_{i,t,1,2} | r_i - O_i - M_{i,i+1,1,1})$ and $(M_{i,i+2,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2} | R_{i,2} - M_{i,i+1,2,1})$ are the same as the cell probabilities for the conditional multinomial

$$(M_{i+1,i+2,1,1}, \dots, M_{i+1,t,1,1}, M_{i+1,i+1,1,2}, \dots, M_{i+1,t,1,2} | R_{i+1,1})$$

hence corresponding cell counts can be pooled to form

$$(M_{i+1,i+2,p,1}, \dots, M_{i+1,t,p,1}, M_{i+1,i+1,p,2}, \dots, M_{i+1,t,p,2} | r_{i+1}),$$

since

$$M_{i+1,t,p,k} = M_{i,t,p,k} + M_{i,t,2,k} + M_{i+1,t,1,k}$$

and making use of (3.7)

$$\begin{aligned} r_{i+1} &= r_i - O_i - C_{i+1} + R_{i,2} + R_{i+1,1} \\ &= Z_i + R_{i,1} - O_i - C_{i+1} + R_{i,2} + R_{i+1,1} \\ &= Z_{i+1} + R_{i+1,1} \end{aligned}$$

Noting that $r_1 = R_{1,1}$, $O_1 = M_{1,1,1,2}$, and $M_{1,j,p,k} = M_{1,j,1,k}$ we begin with cohort 1, and iterate the “peeling” and “pooling” (factorization) cycles up to and including cohorts $C_{t-1,1}$ and $C_{t-1,2}$, and then $C_{t,1}$. At each cycle we

1. “peel” off a

$$\Pr(M_{i,i,p,2}|r_i) = \binom{r_i}{O_i} \left(\frac{\alpha_{i,2}}{\lambda_{i,1}}\right)^{O_i} \left(1 - \frac{\alpha_{i,2}}{\lambda_{i,1}}\right)^{r_i - O_i},$$

term,

2. “peel” then “pool” to form a

$$\begin{aligned} & \Pr(M_{i,i+1,1,1}|r_i - O_i) \times \Pr(M_{i,i+1,2,1}|R_{i,2}) = \\ & \frac{\binom{r_i - O_i}{M_{i,i+1,1,1}} \binom{R_{i,2}}{M_{i,i+1,2,1}}}{\binom{T_{i+1}}{C_{i+1}}} \\ & \times \binom{T_{i+1}}{C_{i+1}} \left(\frac{\alpha_{i,1}}{\lambda_i - \alpha_{i,2}}\right)^{C_{i+1}} \left(1 - \frac{\alpha_{i,1}}{\lambda_i - \alpha_{i,2}}\right)^{T_{i+1} - Z_{i+1}}. \end{aligned}$$

term

3. then “pool” the residual terms to form a

$$\begin{aligned} & \Pr(M_{i,i+2,1,1}, \dots, M_{i,t,1,1}, M_{i,i+1,1,2}, \dots, M_{i,t,1,2}|r_i - O_i - M_{i,i+1,1,1}) \\ & \times \Pr(M_{i,i+2,2,1}, \dots, M_{i,t,2,1}, M_{i,i+1,2,2}, \dots, M_{i,t,2,2}|R_{1,2} - M_{1,2,2,1}) \\ & \times M_{i+1,i+2,1,1}, \dots, M_{i+1,t,1,1}, M_{i+1,i+2,1,2}, \dots, M_{i+1,t,1,2}|R_{2,1} \\ & = \frac{\binom{r_i - O_i - M_{i,i+1,1,1}}{[M_{i,j,1,1}]_{j=i+2}^t, [M_{i,j,1,2}]_{j=i+1}^t} \binom{R_{i,2} - M_{i,i+1,2,1}}{[M_{i+1,j,2,1}]_{j=i+2}^t, [M_{i+1,j,2,2}]_{j=i+1}^t}}{\binom{r_{i+1}}{[M_{i+1,j,p,1}]_{j=i+2}^t, [M_{i+1,j,p,2}]_{j=i+1}^t}} \\ & \times \binom{R_{i+1,1}}{[M_{i+1,j,1,1}]_{j=i+2}^t, [M_{i+1,j,1,2}]_{j=i+1}^t} \end{aligned}$$

$$\times \binom{r_{i+1}}{[M_{i+1,j,p,1}]_{j=i+2}^t, [M_{i+1,j,p,2}]_{j=i+1}^t} \prod_{j=i+2}^t \frac{\pi_{i+1,j,1,1}}{\lambda_{i+1,1}} \prod_{j=i+1}^t \frac{\pi_{i+1,j,1,2}}{\lambda_{i+1,1}} \quad (3.22)$$

term.

After cycle t , the residual term given by (3.22) has the value 1 hence $\Pr(\text{Data}) = \mathcal{L}$ reduces to

$$\begin{aligned} \mathcal{L} &= \prod_{i=1}^t \left\{ \binom{N_i}{R_{i,1}} (\lambda_{i,1})^{R_{i,1}} (1 - \lambda_{i,1})^{(N_i - R_{i,1})} \right\} \\ &\quad \prod_{i=1}^{t-1} \left\{ \binom{n_i}{R_{i,2}} (\lambda_{i,2})^{R_{i,2}} (1 - \lambda_{i,2})^{(n_i - R_{i,2})} \right\} \\ &\quad \times \prod_{i=2}^t \left\{ \binom{T_i}{C_i} (\tau_{i,1})^{C_i} (1 - \tau_{i,1})^{Z_i} \right\} \\ &\quad \prod_{i=1}^{t-1} \left\{ \binom{r_i}{O_i} (\tau_{i,2})^{O_i} (1 - \tau_{i,2})^{r_i - O_i} \right\} \\ &\quad \times \prod_{i=2}^t \frac{\binom{r_{i-1} - O_{i-1}}{C_i - M_{i-1,i,2,1}} \binom{R_{i-1,2}}{M_{i-1,1,2,1}}}{\binom{T_i}{C_i}} \\ &\quad \times \left\{ \prod_{i=1}^{t-2} \frac{\binom{r_i - O_i - M_{i,i+1,p,1}}{[M_{i,j,p,1}]_{j=i+2}^t [M_{i,j,p,2}]_{j=i+1}^t} \binom{R_{i+1}(1)}{[M_{i+1,j,1,1}]_{j=i+2}^t [M_{i+1,j,1,2}]_{j=i+1}^t}}{\binom{r_{i+1}}{[M_{i+1,j,p,1}]_{j=i+2}^t [M_{i+1,j,p,2}]_{j=i+1}^t}} \right. \\ &\quad \left. \times \frac{\binom{R_{i,2} - M_{i,i+1,2,1}}{[M_{i,j,2,1}]_{j=i+2}^t [M_{i,j,2,2}]_{j=i+1}^t}}{1} \right\}, \quad (3.23) \end{aligned}$$

where

$$\tau_{i+1,1} = \frac{\alpha_{i,1}}{\lambda_{i,1} - \alpha_{i,2}} \quad i = 2, \dots, t$$

and

$$\tau_{i,2} = \frac{\alpha_{i,2}}{\lambda_{i,1}} \quad i = 1, \dots, t - 1$$

Thus, we have the result that the distribution of the MSS $R_{i,1}$ ($i = 1, \dots, t$), $R_{i,2}$, C_i ($i=2, \dots, t$, and O_i ($i = 1, \dots, t - 1$) can be expressed as the product of the conditionally independent binomial random variables:

$$R_{i,1} | N_i \sim B(N_i, \lambda_{i,1}) \quad i = 1, \dots, t$$

$$R_{i,2} | n_i \sim B(n_i, \lambda_{i,2}) \quad i = 1, \dots, t - 1$$

$$C_i | T_i \sim B(T_i, \tau_{i,1}) \quad i = 2, \dots, t$$

$$O_i | r_i \sim B(r_i, \tau_{i,2}) \quad i = 1, \dots, t - 1.$$

The remaining “residual” term in the distribution of the data (i.e. $\Pr(\text{data}|\text{MSS})$) is the product of conditionally independent hypergeometric distributions. To see that these residual terms are of the form of multi-hypergeometric random variables, note that each component takes the form

$$\frac{\prod_{i=1}^I \binom{a_i}{b_{i,1}, \dots, b_{i,J}}}{\binom{a_{\cdot}}{b_{\cdot,1}, \dots, b_{\cdot,J}}} \quad (3.24)$$

where $a_{\cdot} = \sum_{i=1}^I a_i$ and $b_{\cdot,j} = \sum_{i=1}^I b_{i,j}$. The a_i partition the sufficient statistic a_{\cdot} , and the mutually exclusive set $b_{i,1}, \dots, b_{i,k}$, conditional on a_i , are multinomial random variables with cell probabilities π_1, \dots, π_k . Recall that these terms result from the pooling of observations that had the same conditional cell-probabilities hence these cell probabilities are common for all i . We will return to these when we consider goodness-of-fit tests for this model.

3.2.6 Parameter estimation

The parameters of interest S_i , θ_i , f_i , and the confounded pair $F_i p_{i+1} = p_{i+1}^*$ are one-to-one functions of the $\lambda_{i,1}$, $\lambda_{i,2}$, $\tau_{i,1}$, and $\tau_{i,2}$:

$$f_i = \begin{cases} \tau_{i,2} \lambda_{i,1} & i = 1, \dots, t-1 \\ \lambda_{t,1} & i = t \end{cases}$$

$$p_i^* = \frac{\lambda_{i,1} \tau_{i,1}}{1 + (\lambda_{i,1} - 1) \tau_{i,1}}$$

$$\theta_i = \frac{1 - \tau_{i,2}}{1 + \tau_{i,2}(\lambda_{i,2} - 1)}$$

and

$$S_i = (1 + \tau_{i,2}(\lambda_{i,2} - 1)) \frac{\lambda_{i,1}}{\lambda_{i+1,1}} \{1 + \tau_{i+1,1}(\lambda_{i,1} - 1)\} .$$

Note also, that δ_i is only defined with respect to marked animals. Since we condition on the releases, the probability ρ_i which appears in δ_i is taken to be exactly n_i/O_i , and is known without error (i.e. for all marked animals resighted in $(i, i+1)$ we know whether or not they were released).

Substituting the MLE's

$$\hat{\lambda}_{i,1} = \frac{R_{i,1}}{N_i}$$

$$\hat{\lambda}_{i,2} = \frac{R_{i,2}}{n_i}$$

$$\hat{\tau}_{i,1} = \frac{C_i}{T_i}$$

and

$$\hat{\tau}_{i,2} = \frac{O_i}{r_i}$$

and solving for \hat{f}_i , \hat{p}_i^* , $\hat{\theta}_i$, and \hat{S}_i , leads to the MLE's

$$\hat{f}_i = \begin{cases} \frac{R_{i,1}}{N_i} & i = t \\ \frac{O_i R_{i,1}}{N_i r_i} & i = 1, \dots, t-1 \end{cases} \quad (3.25)$$

$$\hat{p}_i^* = \frac{C_i}{\frac{N_i Z_i}{R_{i,1}} + C_i} \quad i = 2, \dots, t \quad (3.26)$$

$$\hat{\theta}_i = \frac{r_i - O_i}{T_{i+1}} \quad i = 1, \dots, t - 1 \quad (3.27)$$

and

$$\hat{S}_i = \frac{R_{i,1}}{N_i r_i} \left\{ \frac{N_{i+1} Z_{i+1}}{R_{i+1,1}} + C_{i+1} \right\} \quad i = 1, \dots, t - 1. \quad (3.28)$$

Note that \hat{p}_i^* and \hat{S}_i are the Jolly-Seber estimators but with $R_{i,1}$ and Z_i augmented by the inclusion of observed animals.

For example, from Table 3.6 we obtain

$$\begin{aligned} \hat{f}_1 &= \frac{O_1 R_{1,1}}{N_1 r_1} \\ &= \frac{108 \times 264}{1000 \times 264} \\ &= 0.1080 \end{aligned}$$

$$\begin{aligned} \hat{p}_2^* &= \frac{C_2}{\frac{N_2 Z_2}{R_{2,1}} + C_2} \\ &= \frac{63}{\frac{1000 \times 123}{237} + 63} \\ &= 0.1082 \end{aligned}$$

$$\begin{aligned} \hat{\theta}_1 &= \frac{n_1 (r_1 - O_1)}{r_1 n_1 + O_1 (R_{1,2} - n_1)} \\ &= \frac{108 \times (264 - 108)}{264 \times 108 + 108 \times (30 - 108)} \\ &= 0.8387 \end{aligned}$$

and

$$\begin{aligned} \hat{S}_1 &= \frac{R_{1,1}}{N_1 r_1} \left\{ \frac{N_2 Z_2}{R_{2,1}} + C_2 \right\} \\ &= \frac{264}{1000 \times 264} \left(\frac{1000 \times 123}{237} + 63 \right) \\ &= 0.5820 \end{aligned}$$

Estimates of the remaining parameters and their standard errors (see following section) are given in Table 3.9

Table 3.9: Parameter estimates and associated standard errors for the hypothetical mark-recapture data.

Year	\hat{p}_i^*	$se(\hat{p}_i^*)$	$\hat{\theta}_i$	$se(\hat{\theta}_i)$	\hat{f}_i	$se(\hat{f}_i)$	\hat{S}_i	$se(\hat{S}_i)$
1			.8387	.0270	.1080	.0098	.5820	.0527
2	.1082	.0159	.8571	.0224	.0988	.0083	.5852	.0550
3	.0911	.0124	.8990	.0214	.1045	.0084	.5758	.0735
4	.0932	.0143			.1070	.0098		

3.2.7 Asymptotic variances and covariances

Using the delta-method (Seber 1982) asymptotic variances and covariances can be readily obtained. We make use of the following partial derivatives (all other partial derivatives are zero):

$$\frac{\partial f_i}{\partial \lambda_{i,1}} = \begin{cases} \frac{f_i}{\lambda_{i,1}} & (i = 1, \dots, t-1) \\ 1 & i = t \end{cases}$$

$$\frac{\partial f_i}{\partial \tau_{i,2}} = \begin{cases} \frac{f_i}{\tau_{i,2}} & (i = 1, \dots, t-1) \\ 0 & i = t \end{cases}$$

$$\frac{\partial S_i}{\partial \lambda_{i,1}} = \frac{S_i}{\lambda_{i,1}},$$

$$\frac{\partial S_i}{\partial \lambda_{i+1,1}} = \frac{-S_i(1 - p_{i+1}^*)}{\lambda_{i+1,1}}$$

$$\frac{\partial S_i}{\partial \lambda_{i,2}} = \frac{S_i(1 - \theta_i)}{\lambda_{i,2}}$$

$$\frac{\partial S_i}{\partial \tau_{i+1,1}} = \frac{-S_i p_{i+1}^*(1 - \lambda_{i+1,1})}{\tau_{i+1,1} \lambda_{i+1,1}}$$

$$\frac{\partial S_i}{\partial \tau_{i,2}} = \frac{S_i \theta_i (\lambda_{i,2} - 1)}{1 - \tau_{i,2}}$$

$$\frac{\partial \theta_i}{\partial \lambda_{i,2}} = \frac{-\theta_i(1 - \theta_i)}{\lambda_{i,2}}$$

$$\frac{\partial \theta_i}{\partial \tau_{i,2}} = \frac{-\theta_i(1 - \theta_i)}{\tau_{i,2}(1 - \tau_{i,2})}$$

$$\frac{\partial p_i^*}{\partial \lambda_{i,1}} = \frac{p_i^*(1 - p_i^*)}{\lambda_{i,1}}$$

$$\frac{\partial p_i^*}{\partial \tau_{i,1}} = \frac{p_i^*(1 - p_i^*)}{\tau_{i,1}(1 - \tau_{i,1})}$$

Following Pollock et al. (1990) we use the notation $Var(\hat{f}_i)$ to denote $Var(f_i|f_i)$, and similarly for the other parameters. The variances and non-zero covariances are obtained as follows:

For $i = 1, \dots, t - 1$

$$\begin{aligned} Var(\hat{f}_i) &= \left(\frac{\partial f_i}{\partial \lambda_{i,1}} \right)^2 Var(\hat{\lambda}_{i,1}|N_i) + \left(\frac{\partial f_i}{\partial \tau_{i,2}} \right)^2 Var(\hat{\tau}_{i,2}|r_i) \\ &= f_i^2 \left(\frac{1 - \lambda_{i,1}}{\lambda_{i,1}N_i} + \frac{1 - \tau_{i,2}}{\tau_{i,2}r_i} \right) \\ &= f_i^2 \left(\frac{1}{E[R_{i,1}]} - \frac{1}{N_i} + \frac{1}{E[O_i]} - \frac{1}{r_i} \right) \end{aligned}$$

$$\begin{aligned} Var(f_i) &= Var(\hat{\lambda}_{t,1}|N_t) \\ &= \frac{E[R_{t,1}](N_t - E[R_{t,1}])}{N_t^3} \\ &= f_t^2 \left(\frac{1}{E[R_{t,1}]} - \frac{1}{N_t} \right) \end{aligned}$$

$$\begin{aligned} Var(\hat{S}_i) &= \left(\frac{\partial S_i}{\partial \lambda_{i,1}} \right)^2 Var(\hat{\lambda}_{i,1}|N_i) + \left(\frac{\partial S_i}{\partial \lambda_{i+1,1}} \right)^2 Var(\hat{\lambda}_{i+1,1}|N_{i+1}) + \left(\frac{\partial S_i}{\partial \lambda_{i,2}} \right)^2 \\ &\quad \times Var(\hat{\lambda}_{i,2}|n_i) + \left(\frac{\partial S_i}{\partial \tau_{i+1,1}} \right)^2 Var(\hat{\tau}_{i+1,1}|T_{i+1}) \\ &\quad + \left(\frac{\partial S_i}{\partial \tau_{i,2}} \right)^2 Var(\hat{\tau}_{i,2}|r_i) \\ &= S_i^2 \left\{ \frac{1}{E[R_{i,1}]} - \frac{1}{N_i} + (1 - p_{i+1}^*)^2 \left(\frac{1}{E[R_{i+1,1}]} - \frac{1}{N_{i+1}} \right) \right. \\ &\quad + p_{i+1}^*(1 - p_{i+1}^*) \frac{(N_{i+1} - R_{i+1,1})^2}{N_{i+1}R_{i+1,1}T_{i+1}} + (1 - \theta_i)^2 \left(\frac{1}{E[R_{i,2}]} - \frac{1}{n_i} \right) \\ &\quad \left. + \left[\frac{\theta_i(O_i - E[R_{i,2}])}{n_i} \right]^2 \left(\frac{1}{r_i - E[O_i]} - \frac{1}{r_i} \right) \right\} \end{aligned}$$

$$\begin{aligned} Var(\hat{\theta}_i) &= \left(\frac{\partial \theta_i}{\partial \lambda_{i,2}} \right)^2 Var(\lambda_{i,2}|n_i) + \left(\frac{\partial \theta_i}{\partial \tau_{i,2}} \right)^2 Var(\tau_{i,2}|n_i) \\ &= \theta_i^2(1 - \theta_i)^2 \left(\frac{1}{\tau_{i,2}(1 - \tau_{i,2})r_i} + \frac{1 - \lambda_{i,2}}{\lambda_{i,2}n_i} \right) \\ &= [\theta_i(1 - \theta_i)]^2 \left(\frac{1}{E[O_i]} + \frac{1}{(r_i - E[O_i])} + \frac{1}{E[R_{i,2}]} - \frac{1}{n_i} \right) \end{aligned}$$

$$\begin{aligned}
\text{Var}(\hat{p}_i^*) &= \left(\frac{\partial p_i^*}{\partial \lambda_{i,1}} \right)^2 \text{Var}(\hat{\lambda}_{i,1}|N_i) + \left(\frac{\partial p_i^*}{\partial \tau_{i,1}} \right)^2 \text{Var}(\hat{\tau}_{i,1}|T_i) \\
&= \left[\frac{p_i^*(1-p_i^*)}{\lambda_{i,1}} \right]^2 \frac{\lambda_{i,1}(1-\lambda_{i,1})}{N_i} + [p_i^*(1-p_i^*)]^2 \frac{1}{\tau_{i,1}(1-\tau_{i,1})T_i} \\
&= [p_i^*(1-p_i^*)]^2 \left(\frac{1}{R_{i,1}} - \frac{1}{N_i} + \frac{1}{C_i} + \frac{1}{Z_i} \right)
\end{aligned}$$

$$\begin{aligned}
\text{Cov}(\hat{f}_i, \hat{S}_i) &= \left(\frac{\partial f_i}{\partial \lambda_{i,1}} \right) \left(\frac{\partial S_i}{\partial \lambda_{i,1}} \right) \text{Var}(\hat{\lambda}_{i,1}|N_i) + \left(\frac{\partial f_i}{\partial \tau_{i,2}} \right) \left(\frac{\partial S_i}{\partial \tau_{i,2}} \right) \text{Var}(\hat{\tau}_{i,2}|r_i) \\
&= f_i S_i \left(\frac{1-\lambda_{i,1}}{\lambda_{i,1}N_i} + \frac{f_i S_i \theta_i (\lambda_{i,2}-1)}{r_i} \right) \\
&= f_i S_i \left(\frac{1}{E[R_{i,1}]} - \frac{1}{N_i} + \frac{\theta_i (E[R_{i,2}]-n_i)}{n_i r_i} \right)
\end{aligned}$$

$$\begin{aligned}
\text{Cov}(\hat{f}_i, \hat{p}_i^*) &= \left(\frac{\partial f_i}{\partial \lambda_{i,1}} \right) \left(\frac{\partial p_i^*}{\partial \lambda_{i,1}} \right) \text{Var}(\hat{\lambda}_{i,1}|N_i) \\
&= f_i p_i^*(1-p_i^*) \left(\frac{1-\lambda_{i,1}}{\lambda_{i,1}N_i} \right) \\
&= f_i p_i^*(1-p_i^*) \left(\frac{1}{E[R_{i,1}]} - \frac{1}{N_i} \right)
\end{aligned}$$

$$\begin{aligned}
\text{Cov}(\hat{f}_{i+1}, \hat{S}_i) &= \left(\frac{\partial f_{i+1}}{\partial \lambda_{i+1,1}} \right) \left(\frac{\partial S_i}{\partial \lambda_{i+1,1}} \right) \text{Var}(\hat{\lambda}_{i+1,1}|N_{i+1}) \\
&= -f_{i+1} S_i (1-p_{i+1}^*) \left(\frac{1-\lambda_{i+1,1}}{\lambda_{i+1,1}N_{i+1}} \right) \\
&= -f_{i+1} S_i (1-p_{i+1}^*) \left(\frac{1}{E[R_{i+1,1}]} - \frac{1}{N_{i+1}} \right)
\end{aligned}$$

$$\begin{aligned}
\text{Cov}(\hat{S}_i, \hat{S}_{i+1}) &= \left(\frac{\partial S_i}{\partial \lambda_{i+1,1}} \right) \left(\frac{\partial S_{i+1}}{\partial \lambda_{i+1,1}} \right) \text{Var}(\hat{\lambda}_{i+1,1}|N_{i+1}) \\
&= -S_i S_{i+1} (1-p_{i+1}^*) \left(\frac{1-\lambda_{i+1,1}}{\lambda_{i+1,1}N_{i+1}} \right) \\
&= -S_i S_{i+1} (1-p_{i+1}^*) \left(\frac{1}{E[R_{i+1,1}]} - \frac{1}{N_{i+1}} \right)
\end{aligned}$$

$$\text{Cov}(\hat{S}_i, \hat{\theta}_i) = \left(\frac{\partial S_i}{\partial \lambda_{i,2}} \right) \left(\frac{\partial \theta_i}{\partial \lambda_{i,2}} \right) \text{Var}(\hat{\lambda}_{i,2}|n_i) + \left(\frac{\partial S_i}{\partial \tau_{i,2}} \right) \left(\frac{\partial \theta_i}{\partial \tau_{i,2}} \right) \text{Var}(\hat{\tau}_{i,2}|r_i)$$

$$\begin{aligned}
&= -S_i \theta_i (1 - \theta_i) \left(\frac{(1 - \theta_i)(1 - \lambda_{i,2})}{\lambda_{i,2} n_i} + \frac{\theta_i (\lambda_{i,2} - 1)}{(1 - \tau_{i,2}) r_i} \right) \\
&= -S_i \theta_i (1 - \theta_i)^2 \left(\frac{1}{E[R_{i,2}]} - \frac{1}{n_i} + \frac{\theta_i}{(1 - \theta_i) O_i} \frac{(E[R_{i,2}] - O_i)}{r_i - E[O_i]} \right)
\end{aligned}$$

$$\begin{aligned}
Cov(\hat{S}_i, \hat{p}_{i+1}) &= \left(\frac{\partial S_i}{\partial \lambda_{i+1,1}} \right) \left(\frac{\partial p_{i+1}}{\partial \lambda_{i+1,1}} \right) Var(\hat{\lambda}_{i+1,1} | N_{i+1}) + \left(\frac{\partial S_i}{\partial \tau_{i+1,1}} \right) \left(\frac{\partial p_{i+1}}{\partial \tau_{i+1,1}} \right) \\
&\quad \times Var(\hat{\tau}_{i+1,1} | T_{i+1}) \\
&= -S_i (1 - p_{i+1}^*)^2 p_{i+1}^* \left(\frac{1 - \lambda_{i+1,1}}{\lambda_{i+1,1} N_{i+1}} \right) - S_i [p_{i+1}^*]^2 (1 - p_{i+1}^*) \\
&\quad \times \left(\frac{1 - \lambda_{i+1,1}}{\lambda_{i+1,1} \tau_{i+1,1} T_{i+1}} \right) \\
&= -S_i (1 - p_{i+1}^*)^2 p_{i+1}^* \left(\frac{1}{E[R_{i+1,1}]} - \frac{1}{N_{i+1}} + \frac{p_{i+1}^*}{1 - p_{i+1}^*} \right) \\
&\quad \times \frac{N_{i+1} - E[R_{i+1,1}]}{E[R_{i+1,1}] E[C_{i+1}]}
\end{aligned}$$

$$\begin{aligned}
Cov(\hat{S}_i, \hat{p}_i) &= \left(\frac{\partial S_i}{\partial \lambda_{i,1}} \right) \left(\frac{\partial p_i}{\partial \lambda_{i,1}} \right) Var(\hat{\lambda}_{i,1} | N_i) \\
&= S_i p_i^* (1 - p_i^*) \left(\frac{1 - \lambda_{i,1}}{\lambda_{i,1} N_i} \right) \\
&= S_i p_i (1 - p_i^*) \left(\frac{1}{E[R_{i,1}]} - \frac{1}{N_i} \right)
\end{aligned}$$

In the above expressions all the expectations are with respect to the appropriate binomial indices. Estimates of the above variances and covariances can be obtained by substituting observed values for expected values and parameter estimates for the parameters.

Replacing parameters by their estimates and expected values by observed values, we obtain for our hypothetical example (Table 3.6),

$$\begin{aligned}
Var(\hat{p}_2^*) &= [\hat{p}_2^* (1 - \hat{p}_2^*)]^2 \left(\frac{1}{R_{i,1}} - \frac{1}{N_i} + \frac{1}{C_i} + \frac{1}{Z_i} \right) \\
&= [0.1082 \times 0.8918]^2 \left(\frac{1}{237} - \frac{1}{1000} + \frac{1}{63} + \frac{1}{123} \right) \\
&= 0.0002535
\end{aligned}$$

$$\begin{aligned}
V\hat{ar}(\hat{\theta}_1) &= [\hat{\theta}_1(1 - \hat{\theta}_1)]^2 \left(\frac{r_1}{O_1(r_1 - O_1)} + \frac{1}{R_{1,2}} - \frac{1}{n_1} \right) \\
&= [0.8387 \times 0.1613]^2 \left(\frac{264}{108 \times (264 - 108)} + \frac{1}{30} - \frac{1}{108} \right) \\
&= 0.0007274
\end{aligned} \tag{3.29}$$

$$\begin{aligned}
V\hat{ar}(\hat{f}_1) &= \hat{f}_1^2 \left(\frac{1}{R_{1,1}} - \frac{1}{N_1} + \frac{1}{O_1} - \frac{1}{r_1} \right) \\
&= 0.1080^2 \left(\frac{1}{264} - \frac{1}{1000} + \frac{1}{108} - \frac{1}{264} \right) \\
&= 0.0000963
\end{aligned} \tag{3.30}$$

and

$$\begin{aligned}
V\hat{ar}(\hat{S}_1) &= \hat{S}_1^2 \left\{ \frac{1}{R_{1,1}} - \frac{1}{N_1} + (1 - \hat{p}_2^*)^2 \left(\frac{1}{R_{2,1}} - \frac{1}{N_2} \right) \right. \\
&\quad + \hat{p}_2^*(1 - \hat{p}_2^*) \frac{(N_2 - R_{2,1})^2}{N_2 R_{2,1} T_2} + (1 - \hat{\theta}_1)^2 \left(\frac{1}{R_{1,2}} - \frac{1}{n_1} \right) \\
&\quad \left. + \frac{\hat{\theta}_1^2 (n_1 - R_{1,2})}{n_1} \left(\frac{1}{r_1 - E[O_1]} - \frac{1}{r_1} \right) \right\} \\
&= 0.5820 \left\{ \frac{1}{264} - \frac{1}{1000} + 0.8918^2 \left(\frac{1}{237} - \frac{1}{1000} \right) \right. \\
&\quad + 0.1082 \times 0.8918 \frac{(1000 - 237)^2}{1000 \times 237 \times 186} + 0.1613^2 \left(\frac{1}{30} - \frac{1}{108} \right) \\
&\quad \left. + \frac{0.8387^2 (108 - 30)}{108} \left(\frac{1}{264 - 108} - \frac{1}{264} \right) \right\} \\
&= 0.0028
\end{aligned}$$

Standard errors ($se(\hat{p}_i^*) = \sqrt{V\hat{ar}(\hat{p}_i^*)}$ etc) for the remaining parameter estimates are given in Table 3.9.

3.2.8 Goodness-of-fit tests under random emigration

From (3.23) we obtained the result that the distribution of the MSS could be factored into a component depending on the parameters and a “residual” component which takes the form of independent multi-hypergeometric distributions conditional on sufficient statistics. Following Pollock et al. (1985) (see also Robson 1969, Brownie and Robson 1983) we can utilize this component to develop goodness-of-fit tests.

We exploit the fact that in each multi-hypergeometric term the $b_{i,j}$, ($j=1,\dots,J$) of expression (3.24) are multinomial with cell probabilities in common for all i . This allows us to form an $I \times J$ contingency table corresponding to each component of the residual distribution.

From (3.23) the residual component comprises two parts:

$$\prod_{i=2}^t \frac{\begin{pmatrix} r_{i-1} - O_{i-1} \\ C_i - M_{i-1,i,2,1} \end{pmatrix} \begin{pmatrix} R_{i-1,2} \\ M_{i-1,i,2,1} \end{pmatrix}}{\begin{pmatrix} T_i \\ C_i \end{pmatrix}} \quad (3.31)$$

and

$$\prod_{i=1}^{t-2} \frac{\begin{pmatrix} r_i - O_i - M_{i,i+1,p,1} \\ [M_{i,j,p,1}]_{j=i+2}^t [M_{i,j,p,2}]_{j=i+1}^t \end{pmatrix} \begin{pmatrix} R_{i+1,1} \\ [M_{i+1,j,1,1}]_{j=i+2}^t [M_{i+1,j,1,2}]_{j=i+1}^t \end{pmatrix}}{\begin{pmatrix} r_{i+1} \\ [M_{i+1,j,p,1}]_{j=i+2}^t [M_{i+1,j,p,2}]_{j=i+1}^t \end{pmatrix}} \times \frac{\begin{pmatrix} R_{i,2} - M_{i,i+1,2,1} \\ [M_{i,j,2,1}]_{j=i+2}^t [M_{i,j,2,2}]_{j=i+1}^t \end{pmatrix}}{1} \quad (3.32)$$

In the first component (3.31), the sufficient statistic T_i , the total number of marked animals at i that are captured or seen at i , or at any time after i , is partitioned into $r_{i-1} - O_{i-1}$ and $R_{i-1,2}$. This provides a partitioning of T_i according to whether the animals were observed at $i - 1$ or not. The term $C_i - M_{i-1,i,2,1}$ represents those members of T_i not observed at $i - 1$ that were captured at i , and the term $M_{i-1,i,2,1}$ represents those members of T_i observed at $i - 1$ that were captured at i . Thus from this component we can form $(t-1) 2 \times 2$ contingency tables which test whether the event "member of T_i and captured at i " is independent of the event "member of T_i and observed at $i - 1$ ". Thus the component (3.31) leads to a test of whether observation has a short-term (i.e. one sampling period) effect on the probability that the animal is captured. Note that this effect may occur through influences on any of the p_i , S_{i-1} , or F_{i-1} . This test may be particularly

important in a study where “observation” involves physically handling the animals. The general form of these contingency tables is illustrated in Table 3.10.

Table 3.10: Example of a 2×2 contingency table for the component 1 goodness-of-fit test

	Member of T_i captured at i	Member of T_i not captured at i	
Observed at $i - 1$	$M_{i-1,i,2,1}$	$R_{i-1,2} - M_{i-1,i,2,1}$	$R_{i-1,2}$
Not observed at $i - 1$	$C_i - M_{i-1,i,2,1}$	$r_{i-1} - O_{i-1} - C_i + M_{i-1,i,2,1}$	$r_{i-1} - O_{i-1}$
	C_i	Z_i	T_i

To illustrate using a numerical example we partition T_2 from the data in Table 3.5 giving

$$r_1 - O_1 = 264 - 108 = 156$$

$$R_{1,2} = 30$$

$$C_2 - M_{1,2,2,1} = 63 - 12 = 51$$

$$M_{1,2,2,1} = 12$$

and hence the contingency table

	Member of T_2 captured at 2	Member of T_2 not captured at 2	
Observed at 1	12	18	30
Not observed at 1	51	105	156
	63	123	186

The null hypothesis of independence of the events “observed at time 1” and “captured at time 2” for members of T_2 cannot be rejected $\chi_1^2 = 0.60$, $p = 0.44$, so there is no evidence of a one-period effect of observation on the probability of capture at time 2.

In the component (3.32) the sufficient statistic r_{i+1} is partitioned into $r_i - O_i - M_{i,i+1,p,1}$, $R_{i+1,1}$, and $R_{i,2} - M_{i,i+1,2,1}$. These represent a partitioning of r_{i+1} firstly according to whether the animals were captured at $i + 1$, and secondly for those animals not captured at $i + 1$, according to whether they were observed at i . Note, if a member of r_{i+1} was not captured at i we know that it was marked at or before i . The second partitioning of r_{i+1} is by release/observation category. Thus, from component (3.32) we form $(t - 3) 2(t - i - 1) \times 3$ contingency tables, which test whether membership in one of the capture/observation cells $M_{i,i+2,p,1}, \dots, M_{i,t,p,1}$, $M_{i,i+1,p,2}, \dots, M_{i,t,p,2}$ is independent of the events “captured at $i + 1$ ”, “not captured at $i + 1$ and not observed at i ”, and “not captured at $i + 1$ and observed at i ”. Therefore this test will be sensitive to a “capture” effect (short- or long-term) on the probability that the animal is captured or seen again and an “observation” effect (short- or long-term) on the probability the animal is captured or seen again. A particularly important “capture” effect occurs when the random emigration assumption is violated (see section 3.6), therefore this component tests, among other things, the random emigration assumption. An example showing the general form of a component 2 contingency table is provided in Table 3.11.

A numerical example using the data from Table 3.5 gives the partitioning of r_2

$$R_{1,1} - O_1 - M_{1,2,p,1} = 264 - 108 - 51 = 105$$

$$R_{1,2} - M_{1,2,2,1} = 30 - 12 = 18$$

$$R_{2,1} = 237$$

with the corresponding contingency table

Table 3.11: Example of a contingency table for the component 2 goodness-of-fit test at time i .

	Member of r_{i+1} not observed at i not captured at $i + 1$	Member of r_{i+1} observed at i not captured at $i + 1$	Member of r_{i+1} captured at $i + 1$	
Member of $M_{i+1,i+2,p,1}$	$M_{i,i+2,p,1}$	$M_{i,i+2,2,1}$	$M_{i+1,i+2,1,1}$	$M_{i+1,i+2,p,1}$
.	.	.	.	
.	.	.	.	
.	.	.	.	
Member of $M_{i+1,t,p,1}$	$M_{i,t,p,1}$	$M_{i,t,2,1}$	$M_{i+1,t,1,1}$	$M_{i+1,i+2,p,1}$
Member of $M_{i+1,i+1,p,2}$	$M_{i,i+1,p,2}$	$M_{i,i+1,2,2}$	$M_{i+1,i+1,1,2}$	$M_{i+1,i+1,p,2}$
.	.	.	.	
.	.	.	.	
.	.	.	.	
Member of $M_{i+1,t,p,2}$	$M_{i,t,p,2}$	$M_{i,t,2,2}$	$M_{i+1,t,1,2}$	$M_{i+1,i+2,p,2}$
	$R_{i,1} - O_i - M_{i,i+1,p,1}$	$R_{i,2} - M_{i,i+1,2,1}$	$R_{i+1,1}$	r_{i+1}

	Member of r_2 not observed at 1 not captured at 2	Member of r_2 observed at 1 not captured at 2	Member of r_2 captured at 1	
Member of $M_{2,3,p,1}$	16	2	50	68
Member of $M_{2,4,p,1}$	13	3	19	35
Member of $M_{2,2,p,2}$	48	8	94	150
Member of $M_{2,3,p,2}$	16	4	56	76
Member of $M_{2,4,p,2}$	12	1	18	31
	105	18	237	360

Because several of the cells have expected values less than 5, and one has an expected value less than 2, the chi-squared approximation may not be good. This is likely to be a commonly encountered problem. Under these circumstances two approaches may be used. The first is to compute the probability of the observed, or a more extreme, result exactly using the hypergeometric distribution. In most cases this approach is likely to be computationally intensive, although there are algorithms for $r \times c$ tables (Mehta and Patel 1983). The alternative approach is to pool cells, and use the large sample chi-square approximation on the pooled data.

Because in the multi-hypergeometric term we are conditioning on the marginal totals $R_{i,1} - O_i - M_{i,i+1,p,1}$, $R_{i,2} - M_{i,i+1,2,1}$, and $R_{i+1,1}$ an obvious pooling rule is to maintain these marginal values and instead pool the elements $M_{i,j,p,k}$ across some j . Alternatively, or in addition, we can pool columns of the contingency table e.g. data for members of $R_{i,1} - O_i - M_{i,i+1,p,1}$ with data for members of $R_{i,2} - M_{i,i+1,2,1}$ (see section 3.6). A pooled contingency table from the above example, with pooling across some j

	Member of r_2 not observed at 1, not captured at 2	Member of r_2 observed at 1 not captured at 2	Member of r_2 captured at 2	
Captured at or after 3	29	5	69	103
Not captured, observed at 2	48	8	94	150
Not captured, observed after 2	28	5	74	107
	105	18	237	360

and provides no evidence that the probability an animal was captured at time 3 or later was influenced by whether it was captured at 2 or observed at 1 ($\chi_2^4 = 1.27$, $p = 0.867$).

Even in the “exact” hypergeometric case, it may still be preferable to pool if several of the cell expected values are small. The power of the hypothesis tests under pooling will tend to be more powerful than in the unpooled case. However, it is important to note that pooling changes the hypothesis being tested.

3.3 Permanent emigration

In the permanent emigration model we allow animals to leave the at risk of capture component of the population between i and $i + 1$, but these animals can never return. As in the random emigration model the probability an animal at risk of capture at i and alive at $i + 1$ is at risk of capture at $i + 1$ is given by F_i . However, in the permanent emigration model the probability an animal not at risk of capture at i and alive at $i + 1$ is at risk of capture at $i + 1$ is zero.

Because emigration is permanent, the probability an animal released at i and alive at j , is at risk of capture at j but was not captured between i and j is given

by

$$\gamma_{i,j,1} = F_{j-1} \prod_{h=i}^{j-2} F_h (1 - p_{h+1}) . \quad (3.33)$$

i.e. because emigration is permanent, such an animal must be at risk of capture at each of $i, i + 1, \dots, j$. In contrast, all animals are at risk of being observed, regardless of whether or not they are at risk of capture. For animals released at i there are $j - i + 1$ possible pathways by which they can be not recaptured between i and j , complicating computation of $\gamma_{i,j,2}$. This can be computed recursively as follows:

Let $a_{i,j}$ denote the probability an animal alive and at risk of capture at i , and alive at j , is at risk of capture at j , but is not captured between i and j . Similarly, let $b_{i,j}$ denote the probability an animal alive and at risk of capture at i , and alive at j , is not at risk of capture at j and is not captured between i and j . Then

$$a_{i,j} = \begin{cases} F_{j-1} & j = i + 1 \\ a_{i,j-1}(1 - p_{j-1})F_{j-1} & j = i + 2, \dots, t \end{cases} \quad (3.34)$$

and

$$b_{i,j} = \begin{cases} (1 - F_{j-1}) & j = i + 1 \\ a_{i,j-1}(1 - p_{j-1})(1 - F_{j-1}) + b_{i,j-1} & j = i + 2, \dots, t \end{cases} , \quad (3.35)$$

then

$$\gamma_{i,j,2} = a_{i,j}(1 - p_j) + b_{i,j} \quad (3.36)$$

Utilizing (3.33) the probability structure for the model under permanent emigration for animals last released following capture is given as follows. Let

$$\alpha_{i,1} = S_i F_i \theta_i p_{i+1}$$

$$\alpha_{i,2} = f_i$$

and

$$\beta_i = S_i \theta_i .$$

then

$$\pi_{i,j,1,k} = \begin{cases} \alpha_{i,1} & (j = i + 1, k = 1) \\ \alpha_{i,2} & (j = i, k = 2) \\ \alpha_{j-1,1} \gamma_{i,j,1} \prod_{h=i}^{j-2} \beta_h & (j = i + 2, \dots, t, k = 1) \\ \alpha_{j,2} \gamma_{i,j,2} \prod_{h=i}^{j-1} \beta_h & (j = i + 1, \dots, t, k = 2) \end{cases} \quad (3.37)$$

For animals released following observation, the situation is more complicated, as the subscript i in $\gamma_{i,j,k}$ indexes the last capture occasion. The consequence is that the m-array data summary used under random emigration is not sufficient under permanent emigration. One remedy is to partition the n_i and the $M_{i,j,2,k}$'s according to last capture occasion. The second is to model the capture histories directly.

Let h denote a specific capture history. Derivation of $Pr(h)$ involves partitioning $Pr(h|\text{first release})$ into three parts (K.P. Burnham pers. comm):

$Pr(\text{last encounter}|\text{first release}) \times$

$Pr(\text{encounter history between first and last encounter}|\text{first release and last encounter})$
 $\times Pr(\text{never encountered again after last encounter}|\text{last encounter}) .$

For an animal first released at i and last encountered at j , the first term is

$$Pr(\text{last encounter}|\text{first release}) = \begin{cases} S_i \cdots S_{j-1} f_j & \text{if last encountered by observation} \\ S_i \cdots S_{j-1} p_j & \text{if last encountered by capture} \end{cases} .$$

The encounter history between the first and last encounters can be broken into two parts, one part for the recaptures and one part for the resightings. The component for the recaptures will involve the product of $F_h p_{h+1}$ and $F_h (1 - p_{h+1})$ terms ($h \leq t - 1$), and for an animal which was last recaptured and released at k but not captured at j ($k < j$), there will be an additional $\gamma_{k,j,2}$ term. The component for resightings will simply involve the product of θ_h and $(1 - \theta_h)$ terms.

For example, for the fictitious animal with capture history $h = 05013$ discussed in section 3.2.3 the information we have available is:

- (i) The animal was captured at time 2, released, and resighted between 2 and 3 and released.

- (ii) The animal was captured and released at time 4, but not resighted between times 4 and 5.
- (iii) The animal was resighted between times 5 and 6 and was released on resighting.

Note that because the animal was recaptured at time 4 we know it must have been at risk of capture at time 3 even though it was not captured. However, because all encounters after time 4 were resightings we do not know whether it was at risk of capture at time 5.

From the above information

$$Pr(\text{last encounter}|\text{first release}) = S_2S_3S_4f_5 .$$

To compute

$Pr(\text{encounter history between first and last encounter}|\text{first release and last encounter})$

we note that following release at time 2, and before the last encounter by resighting between times 5 and 6, the animal was recaptured at time 4, and resighted between times 2 and 3. Therefore, the recapture at time 4 will contribute an $F_2(1 - p_3)F_3p_4$ term, and the resightings a $(1 - \theta_2)\theta_3\theta_4$ term. Also, the last recapture was at time 4 and it was resighted between times 5 and 6, therefore we will need a $\gamma_{4,5,2}$ term, leading to

$$\begin{aligned} Pr(\text{encounter history between first and last encounter}|\text{first release and last encounter}) \\ = F_2(1 - p_3)F_3p_4(1 - \theta_2)\theta_3\theta_4\gamma_{4,5,2} . \end{aligned}$$

In this example, computation is simplified because the animal was observed during interval $5 = t$, and

$$Pr(\text{never encountered again after last encounter}|\text{last encounter}) = 1 ,$$

hence

$$\begin{aligned} Pr(h = 05013|\text{first release at 2}) = \\ F_2S_2(1 - \theta_2)(1 - p_3)S_3\theta_3F_3p_4S_4\theta_4f_5 * \{F_4(1 - p_5) + (1 - F_4)\} \\ = p_2F_2S_2(1 - \theta_2)(1 - p_3)S_3\theta_3F_3p_4S_4\theta_4f_5\gamma_{4,5,2} . \end{aligned}$$

If capture and observation are possible for periods following the last occasion on which the animal was captured or observed, an additional term for the probability that an animal last encountered at j is never encountered again must be computed. This term is most easily obtained as $1 - Pr(\text{animal is encountered again} | \text{last release at } j)$ and is obtained by partitioning the compound event

$$(\text{animal is encountered again} | \text{last release at } j)$$

into the set of disjoint events

$$(\text{animal is encountered at } h | \text{last release at } j)$$

for each $h > j$ (K.P. Burnham, pers. comm.).

Once $Pr(h | \text{first release})$ is determined for each animal the likelihood function is then

$$\mathcal{L} = \prod_h \{Pr(h | \text{first release})\}^{X_h}$$

where X_h is the number of animals sharing capture history h .

Because the observation component of the model is expressed in terms of the $\gamma_{i,j,2}$'s the likelihood does not factor as in (3.23) and closed-form maximum likelihood estimates do not appear to exist (see comments by Burnham 1993). Thus numerical procedures must be used to compute the maximum-likelihood estimates. Because emigration is permanent the pathways involved in $\gamma_{i,t,2}$ are one of three possible types: one pathway where animals were at risk of capture at t , but not captured, another where the animals were at risk of capture at $t - 1$ but not at t , and a remaining set where the animals left the at risk of capture component of the population before $t - 1$. Thus $\gamma_{i,t,2}$ has the form

$$\begin{aligned} \kappa_1 F_{t-1}(1 - p_t) + \kappa_1(1 - F_{t-1}) + \kappa_2 \\ = \kappa_1(1 - F_{t-1}p_t) + \kappa_2 \end{aligned} \tag{3.38}$$

where neither κ_1 nor κ_2 include terms involving F_{t-1} or p_{t-1} . Thus F_{t-1} only appears in the product $F_{t-1}p_t$ and these parameters cannot be separately esti-

mated. However, unlike the random emigration model we can obtain estimates of F_i , ($i=1, \dots, t-2$).

Finally, we note that under permanent emigration if all animals are released on observation, the $\gamma_{i,j,2}$ are identical to the $\gamma_{i,j}$ of Burnham (1993).

3.4 Stationary Markov Movement

A third type of movement that we can allow between the at risk of capture and not at risk of capture population components is where the movement process follows a Markov chain. In this model, in addition to allowing animals to move from the at risk of capture component of the population to the not at risk of capture component between i and $i+1$, we also allow movement in the reverse direction. Under the stationary Markov movement model the movement probabilities depend on the population component occupied at $i-1$, but not the component occupied before $i-1$. Because of the additional movement probabilities we adopt a different notation. If component 1 is the at risk of capture component and component 2 the not at risk of capture component, and Ψ_i the transition matrix governing the movement of animals between the two components at i then $\psi_{i,m,n}$ is the probability an animal located in component m ($m=1,2$) at time i is located in component n ($n=1,2$) at time $i+1$, given that it is alive at $i+1$ (NB $\psi_{i,m,2} = 1 - \psi_{i,m,1}$). As usual, we assume that at time i all animals share Ψ_i .

Because of the two-way movement, $\gamma_{i,j,1}$ no longer has an explicit form. If component 1 is the at risk of capture segment of the population, and component 2 the not at risk of capture segment, the $\gamma_{i,j,k}$'s are defined recursively as follows: Let

$$a_{i,j} = \begin{cases} \psi_{j-1,1,1} & j = i+1 \\ a_{i,j-1}(1-p_{j-1})\psi_{j-1,1,1} + b_{i,j-1}\psi_{j-1,2,1} & j = i+2, \dots, t \end{cases} \quad (3.39)$$

and

$$b_{i,j} = \begin{cases} (1 - \psi_{j-1,1,1}) & j = i+1 \\ a_{i,j-1}(1-p_{j-1})\psi_{j-1,1,2} + b_{i,j-1}\psi_{j-1,2,2} & j = i+2, \dots, t \end{cases}, \quad (3.40)$$

then

$$\gamma_{i,j,k} = \begin{cases} a_{i,j} & k = 1 \\ a_{i,j}(1 - p_j) + b_{i,j} & k = 2 \end{cases} \quad (3.41)$$

Let

$$\alpha_{i,k} = \begin{cases} S_i \theta_i p_{i+1} & k = 1 \\ f_i & k = 2 \end{cases} \quad (3.42)$$

and

$$\beta_i = S_i \theta_i, \quad (3.43)$$

then following capture at time i the probability structure for the capture/observation array for animals last released following capture is given by

$$\pi_{i,j,1,k} = \begin{cases} \alpha_{i,k} \gamma_{i,j,k} & (j = i + 1, k = 1) \\ \alpha_{i,k} & (j = i, k = 2) \\ \alpha_{j-1,k} \gamma_{i,j,k} \prod_{h=i}^{j-2} \beta_h & (j = i + 2, \dots, t, k = 1) \\ \alpha_{j,k} \gamma_{i,j,k} \prod_{h=i}^{j-1} \beta_h & (j = i + 1, \dots, t, k = 2) \end{cases} \quad (3.44)$$

As with the permanent emigration model, the m -array summary is not sufficient for the Markov emigration model, and the n_i and $M_{i,j,2,k}$'s must be partitioned according to last capture occasion.

To model the capture histories for each animal directly, we use the same approach as outlined for the permanent emigration model but with $\gamma_{i,j,2}$ defined as above under Markov emigration. Also, we need to use $\gamma_{i,j,1}$ in the computation of

$Pr(\text{encounter history between first and last encounter} | \text{first release and last encounter})$

and

$Pr(\text{never encountered again after last encounter} | \text{last encounter})$.

This is done by inserting a $\gamma_{i,j,1}$ term between adjacent recaptures as a substitute for the F_h and $F_h(1 - p_{h+1})$ terms which appear in

$Pr(\text{encounter history between first and last encounter} | \text{first release and last encounter})$

under permanent emigration. Thus, for the animal with capture history 05013 under Markov emigration

$$\begin{aligned} Pr(\text{encounter history between first and last encounter} | \text{first release and last encounter}) \\ = \gamma_{2,4,1} p_4 (1 - \theta_2) \theta_3 \theta_4 \gamma_{4,5,2} . \end{aligned}$$

Without constraints, the model is almost certainly over-paramaterized and in particular we need constraints on the $\psi_{i,j,k}$'s. If we make the constraint $\psi_{i,1,1} = \psi_{i,2,1} = F_i \forall i$ then we obtain the random emigration model, and $\gamma_{i,j,1} = F_{j-1} \prod_{h=i}^{j-2} (1 - F_h p_{h+1})$ and $\gamma_{i,j,2} = \prod_{h=i}^{j-1} (1 - F_h p_{h+1})$. To obtain the permanent emigration model we make the constraint $\psi_{i,2,1} = 0 \forall i$, leading to $\gamma_{i,j,1}$ as given by (3.36) with $\psi_{i,1,1} = F_i$.

Another set of constraints that we can make is to assume a stationary Markov movement model where $\psi_{1,1,1} = \psi_{2,1,1} = \dots = \psi_{t-1,1,1}$ and $\psi_{1,2,1} = \psi_{2,3,1} = \dots = \psi_{t-1,2,1}$ (i.e. movement probabilities constant through time). Because the $\pi_{i,j,k}$ are expressed in terms of $\gamma_{i,j,k}$'s MLE's do not appear to exist in closed-form. However, using numerical procedures the parameters $p_2, \dots, p_t, \theta_1, \dots, \theta_{t-1}, f_1, \dots, f_t, S_1, \dots, S_{t-1}, \psi_{1,1,1}$, and $\psi_{1,2,1}$ all appear to be estimable.

3.5 Losses On Capture

Because we are conditioning on the releases the model already allows for losses on capture and losses on observation. If the η_i and ρ_i 's are of particular interest then we can readily determine explicit maximum likelihood estimates of the parameters η_i and ρ_i . If for the random emigration model we now partition the data so that

$M_{i,j,k,l,1}$ = the number of animals last encountered and released by method k at time i that are next encountered by method l at time j and released

$M_{i,j,k,l,2}$ = the number of animals last encountered and released by method k at time i that are next encountered by method l at time j and removed from the population

$\pi_{i,j,k,j,m}$ = the multinomial cell probability for $M_{i,j,k,l,m}$ conditional on the releases

then

$$\pi_{i,j,k,l,1} = \begin{cases} \pi_{i,j,k,1}\eta_i & l = 1 \\ \pi_{i,j,k,2}\rho_i & l = 2 \end{cases} \quad (3.45)$$

and

$$\pi_{i,j,k,l,2} = \begin{cases} \pi_{i,j,k,1}(1 - \eta_i) & l = 1 \\ \pi_{i,j,k,2}(1 - \rho_i) & l = 2 \end{cases}, \quad (3.46)$$

where $\pi_{i,j,k,1}$ and $\pi_{i,j,k,2}$ are given by (3.1) and (3.2).

Note that an animal may be observed more than once in $i, i + 1$ but can only be removed from the population on the last occasion on which it was observed. The removal of the animal from the population is the important information. Thus where there are multiple sightings and releases between sampling occasions i and $i + 1$ we ignore the earlier sightings and subsequent releases in $i, i + 1$ and just make use of the last, terminal, sighting. Thus, $\hat{\rho}_i$ will tend to overestimate the probability an animal is released each time it is observed in $i, i + 1$. If this latter probability is of particular interest, then if

- (i) ρ_i^* is the probability an animal is released each time it is observed in $i, i + 1$,
- (ii) y_i denotes the total number of animals released on observation in $i, i + 1$,
- (iii) x_i denotes the total number of observations of animals including repeat observation in $i, i + 1$
- (iv) each observation and release pair is independent

then y_i is a binomial (x_i, ρ_i^*) random variable and

$$\hat{\rho}_i^* = \frac{y_i}{x_i}$$

the maximum likelihood estimator of ρ_i^* .

If we factor the likelihood obtained using (3.45) and (3.46) we find that a minimal sufficient statistic (MSS) includes $C_{i,1}$ and $C_{i,2}$ ($i = 2, \dots, t$), $O_{i,1}$ and $O_{i,2}$ ($i=1, \dots, t$), which are in fact jointly minimal sufficient for η_i and ρ_i , where

$$C_{j,k} = \sum_{i=1}^{j-1} M_{i,j,1,1,k} + M_{i,j,2,1,k}$$

and

$$O_{j,k} = \sum_{i=1}^j M_{i,j,1,2,k} + M_{i,j,2,2,k}$$

Also,

$$E[C_{i,k}] = \begin{cases} \alpha_{i-1,1} \xi_{i-1,1} \eta_i & k = 1 \\ \alpha_{i-1,1} \xi_{i-1,1} (1 - \eta_i) & k = 2 \end{cases}$$

and

$$E[O_{i,k}] = \begin{cases} \alpha_{i,2} \xi_{i,2} \rho_i & k = 1, \\ \alpha_{i,2} \xi_{i,2} (1 - \rho_i) & k = 2 \end{cases},$$

where

$$\xi_{i,1} = (N_i + n_i \delta_i) \gamma_{i,i+1,1} + (N_{i-1} + n_{i-1} \delta_{i-1}) \gamma_{i-1,i+1,1} \beta_{i-1} + \dots + (N_1 + n_1 \delta_1) \gamma_{1,i+1,1} \beta_1 \dots \beta_{i-1}$$

and

$$\xi_{i,2} = N_i + (N_{i-1} + n_{i-1} \delta_{i-1}) \gamma_{i-1,i,1} \beta_{i-1} + \dots + (N_1 + n_1 \delta_1) \gamma_{1,i,1} \beta_1 \dots \beta_{i-1}.$$

Using the method of equating the MSS (or linear functions of the MSS) to its expected value (Davidson and Soloman, 1974, see also Brownie et al. 1985) we obtain the MLE's

$$\hat{\eta}_i = \frac{C_{i,1}}{C_{i,1} + C_{i,2}} \quad (3.47)$$

and

$$\hat{\rho}_i = \frac{O_{i,1}}{O_{i,1} + O_{i,2}}. \quad (3.48)$$

Estimators for all remaining parameters in the model are identical to those already discussed. Note that using similar arguments, the above results will hold under both permanent and Markov emigration.

3.6 Comparison with Jolly's Solution

Jolly (1965) did not propose an explicit model for the situation where ancillary observations are obtained. The model that we have proposed is an extension of the Jolly-Seber model, and in the special case of random emigration yields the estimator suggested by Jolly (1965). In the case of permanent emigration Jolly's estimator is not the MLE and is biased, as shown below. This is despite the fact that for the Jolly-Seber model with permanent emigration (but no ancillary observations), Jolly's estimator is the MLE.

Jolly's estimator is based on the approximation (in our notation):

$$\frac{Z_i}{M_i - C_i} \sim \frac{R_{i,1}}{N_i} \quad (3.49)$$

i.e. the proportion of animals marked before i and not captured at i that are ever seen or captured again should equal, on average, the proportion of animals captured at i that are ever seen again. When there are ancillary observations, C_i and $R_{i,1}$ have components due to captured animals and observed animals.

The ancillary data provide observations on animals that would not otherwise have been obtained. We can partition the statistics Z_i and $R_{i,1}$ into a component obtained under the ordinary Jolly-Seber model and a component provided by the ancillary observations as follows.

$Z_i^{(1)}$ = those members of Z_i that were captured after i ($i=2, \dots, t-1$).

$Z_i^{(2)}$ = those members of Z_i that were not captured after i but that were observed after i (including those observed in $i, i+1$) ($i=2, \dots, t$).

$R_{i,1}^{(1)}$ = those members of $R_{i,1}$ captured after i ($i=1, \dots, t-1$)

$R_{i,1}^{(2)}$ = those members of $R_{i,1}$ not captured after i but observed after i (including those observed in $i, i+1$) ($i=2, \dots, t$)

Since, $Z_i^{(1)}$, $R_{i,1}^{(1)}$ and C_i are the data we would obtain under the usual Jolly-Seber model (i.e. without ancillary observations) then from Jolly (1965) we know

that the approximation

$$\frac{Z_i^{(1)}}{M_i - C_i} \sim \frac{R_{i,1}^{(1)}}{N_i}$$

holds. Therefore the approximation (3.49) will be valid if and only if

$$\frac{Z_i^{(2)}}{M_i - C_i} \sim \frac{R_{i,1}^{(2)}}{N_i}$$

Now, $Z_i^{(1)}$ and $Z_i^{(2)}$ are mutually exclusive, as are $R_{i,1}^{(1)}$ and $R_{i,1}^{(2)}$. Hence the above approximation will be valid if and only if $\Pr(\text{seen again and not captured at } i+1, \dots, \text{not captured at } t \mid \text{not captured at } i) = \Pr(\text{seen again and not captured at } i+1, \dots, \text{not captured at } t \mid \text{captured at } i)$. To be captured at i the animals have to be at risk of capture hence these two probabilities will not be equal under permanent emigration. This is because an animal not captured at i is more likely to be not caught at $i+1$ (or after $i+1$) than one which was captured at i . Note that under random emigration, an animals "at risk of capture" status at i has no influence on it's "at risk of capture" status at j ($j \neq i$) hence these probabilities will be equal under random emigration.

In section (3.2.8) we considered a test based on a partitioning of $r_{i+1} = Z_{i+1} + R_{i+1,1}$ into $R_{i,1} - O_i - M_{i,i+1,p,1}$, $R_{i+1,1}$, and $R_{i,2} - M_{i,i+1,2,1}$. An alternative is to partition r_i into $Z_i^{(1)} + R_{i,1}^{(1)}$ and $Z_i^{(2)} + R_{i,1}^{(2)}$ as discussed above leading to $t-2$ conditional independent contingency tables forming alternative component 2 goodness-of-fit tests that test the random emigration assumption. This contingency table is obtained from the contingency table 3.11 by pooling $R_{i,1} - O_i - M_{i,i+1,p,1}$ with $R_{i,2} - M_{i,i+1,2,1}$ and the elements of $M_{i,j,p,k}$ across all j .

An example of one of these contingency tables is illustrated in Table 3.12, where $r_i^{(1)}$ denotes those members of r_i captured after i , and $r_i^{(2)}$ those members of r_i observed in the interval $i, i+1$ or later.

Table 3.12: Example of a 2×2 contingency table for the alternative component 2 goodness-of-fit test. This contingency table tests the random emigration assumption. Note observed after i includes observed in the interval $i, i + 1$.

	Member of r_i captured after i	Member of r_i not captured but observed after i	
Captured at i	$R_{i,1}^{(1)}$	$R_{i,1}^{(2)}$	$R_{i,1}$
Not captured at i	$Z_i^{(1)}$	$Z_i^{(2)}$	Z_i
	$r_i^{(1)}$	$r_i^{(2)}$	r_i

Chapter 4

Multi-Strata Mark-Recapture Models with Ancillary Observations

4.1 Background

The assumption made in the models considered in Chapter 3 that all members of the population share the same parameters in common is unrealistic in many mark-recapture experiments. A more reasonable assumption may be that the population can be divided into homogeneous sub-units, or strata, which share parameters in common. If animals belong to the strata throughout their lives, and if stratum membership can be determined at capture, then the models of Chapter 3 can be simply applied to each stratum separately. In this chapter we consider the case where stratum membership can be determined at capture, and where movement of animals among strata between captures is unidirectional and deterministic.

4.2 The Age-Dependence Model

All animal populations can be stratified according to age, although allocation of animals to age class on capture may be difficult. It seems likely that parameters

will differ between age groups and this appears to be the case for many waterfowl species (Seber, 1983:528). The extension of the Jolly-Seber model to allow for age-dependence is described by Pollock (1981), Stokes (1984), and Pollock et al. (1990), and models for age dependent tag-recovery are described by Brownie et al. (1985).

4.2.1 Assumptions, notation and data structure

We assume that on capture at time i , unmarked animals can be classified as belonging to age class ν , $\nu = 0, \dots, l$, i.e. unmarked animals can be placed into one of $l + 1$ distinct age classes. Note that animals which belong to age class l are in fact those animals which are of age l or older.

In addition to the assumptions listed in section 3.2.2 we assume

- (i) The interval between captures is the same as the length of time for which animals remain in age class ν .
- (ii) Members of each age class have the same capture, survival, movement, and observation probabilities at time i .
- (iii) Animals of age $l, l + 1, \dots$ share capture, survival, movement, and observation probabilities at i .

We use superscripts to denote age class membership. For example, $M_{i,j,m,n}^{(\nu)}$ is the number of animals last released following encounter by method m ($m=1,2$) at time i as members of age class ν ($\nu = 0, \dots, l$) that are next encountered by method n at time j . Similarly, $S_i^{(\nu)}$ is the probability that a member of age class ν survives from time i until time $i + 1$, given that it is alive at time i .

For estimation, we require that some statistics are indexed according to the $\nu + 2$ age classes that we can in fact identify for marked animals - animals of exactly age ν ($\nu = 0, \dots, l$), and those animals in age class l at i that were in age class l at $i - 1$ (denoted age class $l + 1$). Note that this is simply a “book-keeping” device, parameters for animals of exactly age l are assumed to equal those for older animals. For these statistics, the terminology “of age ν ” refers to those marked animals that

are exactly age ν ($\nu = 1, \dots, l$), or at least age $l + 1$ if $\nu = l + 1$. The statistics affected are:

$C_i^{(\nu)}$ = the total number of marked animals of age ν captured at time i

$Z_i^{(\nu)}$ = the total number of marked animals of age ν but not captured at i , subsequently caught or observed (includes animals observed in i , $i + 1$).

$T_i^{(\nu)}$ = the total number of animals already marked and of age ν at i that are observed or captured, at or after i .

When an animal is released as a member of age class ν following the first occasion on which it was marked, at time i , it may fall into one of $2t$ mutually exclusive classes ($M_{i,i+1,1,1}^{(\nu)}, \dots, M_{i,t,1,1}^{(\nu)}, M_{i,i,1,2}^{(\nu)}, \dots, M_{i,t,1,2}^{(\nu)}, M_{i,2t,1,1}^{(\nu)}$). As in the single age class model the final class represents those animals released at i that were never captured or observed again. If the animal is next encountered by capture at j , $j - i$ time periods following its last release it contributes to $M_{i,j,1,1}^{(\nu)}$. However, we now know it is a member of age class ω , where $\omega = \nu + j - i$ if $\nu + j - i < l$, or $\omega = l$ otherwise. Hence the animal is transferred to the release cohort that were last encountered by capture at time j as members of age class ω , denoted $C_{j,1}^{(\omega)}$. Similarly all animals next encountered by observation in the interval $j, j + 1$, as members of age class ω are transferred to the release cohort of animals that were last encountered by observation at time j as members of age class ω , denoted $C_{j,2}^{(\omega)}$.

Consider our fictitious animal from Chapter 3 with capture history 05013. Suppose there are 3 distinguishable age classes 0, 1, and 2 and that our animal was a member of age class 0 on first capture. Our animal was initially released as a member of $C_{2,1}^{(0)}$. Following this release the animal was next encountered by an observation at least once at some point between times 2 and 3, at which time it is still a member of age class 0. Thus, the animal contributed to $M_{2,2,1,2}^{(0)}$ then was "re-released" as a member of release cohort $C_{2,2}^{(0)}$. Our animal was next encountered by capture at time 4, as a member of age class 2, hence it contributed to $M_{2,4,2,1}^{(0)}$, then was re-released as a member of $C_{4,1}^{(2)}$. The final encounter of this animal was

an observation some time between times 5 and 6 hence it makes a contribution to $M_{4,5,1,2}^{(2)}$. Although we know that this animal was exactly of age 3 at the time of this last observation, we will only use the information that the animal was in age class 2 or older at the time of this final observation.

4.2.2 Random emigration model

As in the single age class case we begin by examining the random emigration model in detail.

Let

$$\omega = \begin{cases} \nu + 1 & \nu = 0, \dots, l - 1 \\ l, & \nu = l \end{cases} \quad (4.1)$$

$$\alpha_{i,k}^{(\nu)} = \begin{cases} S_i^{(\nu)} \theta_i^{(\nu)} F_i^{(\nu)} p_{i+1}^{(\omega)} & k = 1 \\ f_i^{(\nu)} & k = 2 \end{cases} \quad (4.2)$$

$$\beta_i^{(\nu)} = S_i^{(\nu)} \theta_i^{(\nu)} (1 - F_i^{(\nu)} p_{i+1}^{(\omega)})$$

and

$$\delta_i^{(\nu)} = \frac{1 - \theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}} \quad (4.3)$$

For animals last released following capture at time i in age class l the probability structure for the reduced m-array is given by

$$\pi_{i,j,1,k}^{(l)} = \begin{cases} \alpha_{i,1}^{(l)} & j = i + 1, k = 1 \\ \alpha_{i,2}^{(l)} & j = i, k = 2 \\ \alpha_{j-1,1}^{(l)} \prod_{h=i}^{j-2} \beta_h^{(l)} & j = i + 2, \dots, t, k = 1 \\ \alpha_{j,2}^{(l)} \prod_{h=i}^{j-1} \beta_h^{(l)} & j = i + 1, \dots, t, k = 2 \end{cases} \quad (4.4)$$

and for those last released following observation at time i as members of age class l

$$\pi_{i,j,2,k}^{(l)} = \begin{cases} \delta_i^{(l)} \alpha_{i,1}^{(l)} & j = i + 1, k = 1 \\ \delta_i^{(l)} \alpha_{j-1,1}^{(l)} \prod_{h=i}^{j-2} \beta_h^{(l)} & j = i + 2, \dots, t, k = 1 \\ \delta_i^{(l)} \alpha_{j,2}^{(l)} \prod_{h=i}^{j-1} \beta_h^{(l)} & j = i + 2, \dots, t, k = 2 \end{cases} \quad (4.5)$$

For animals last released following capture at time i as members of age class ν ($\nu = 0, \dots, l - 1$), the probability structure for the capture/observation array is given by

$$\pi_{i,j,1,k}^{(\nu)} = \begin{cases} \alpha_{i,1}^{(\nu)} & j = i + 1, k = 1 \\ \alpha_{i,2}^{(\nu)} & j = i, k = 2 \\ \alpha_{j-1,1}^{(\nu+j-i-1)} \prod_{h=i}^{j-2} \beta_h^{(\nu+h-i)} & j = i + 2, \dots, t, k = 1 \\ \alpha_{j,2}^{(\nu+j-i)} \prod_{h=i}^{j-1} \beta_h^{(\nu+h-i)} & j = i + 1, \dots, t, k = 2 \end{cases} \quad (4.6)$$

and for those last released following observation at time i as members of age class ν by

$$\bar{\pi}_{i,j,2,k}^{(\nu)} = \begin{cases} \delta_i^{(\nu)} \alpha_{i,1}^{(\nu)} & j = i + 1, k = 1 \\ \delta_i^{(\nu)} \alpha_{j-1,1}^{(\nu+j-i)} \prod_{h=i}^{j-2} \beta_h^{(h-i)} & j = i + 2, \dots, t, k = 1 \\ \delta_i^{(\nu)} \alpha_{j,2}^{(\nu+j-i)} \prod_{h=i}^{j-1} \beta_h^{(\nu+h-i)} & j = i + 1, \dots, t, k = 2 \end{cases} \quad (4.7)$$

Using $M_{1,3,1,1}^{(0)}$ as an example, we know the animals that contributed to $M_{1,3,1,1}^{(0)}$ survived from time 1 to 2 as members of age class 0, an event which happened with probability $S_1^{(0)}$. Given that they were alive at 2 we know they were not observed between 1 and 2, they remained in the population at risk of capture between 1 and 2 and were not captured at 2 when they were now members of age class 1. The joint probability of these events is $\theta_1^{(0)}(1 - F_1^{(0)}p_2^{(1)})$. We know the animals then survived from time 2 to 3 as members of age class 1, with probability $S_2^{(1)}$, they were not observed between 2 and 3 with probability $\theta_2^{(1)}$ and they remained in the population at risk of capture with probability $F_2^{(1)}$. Given that they were alive at 3, we then know they were captured as members of age class 2, which happened with probability $p_3^{(2)}$. Thus,

$$\pi_{1,3,1,1}^{(0)} = S_1^{(0)}\theta_1^{(0)}(1 - F_1^{(0)}p_2^{(1)})S_2^{(1)}\theta_2^{(1)}F_2^{(1)}p_3^{(2)} \quad (4.8)$$

$$= \alpha_{2,1}^{(1)}\beta_1^{(0)}. \quad (4.9)$$

The cell probability for $M_{1,3,2,2}^{(0)}$ is computed in an identical manner with the exception that the survival probability from 1 to 2 is now conditional on the fact that

the animals were observed. Hence

$$\begin{aligned}
 \pi_{1,3,2,1}^{(0)} &= \frac{1 - \theta_1^{(0)}}{f_1^{(0)} \rho_1^{(0)}} S_1^{(0)} (1 - F_1^{(0)} p_2^{(1)}) S_2^{(1)} \theta_2^{(1)} F_2^{(1)} p_3^{(2)} \\
 &= \alpha_{2,1}^{(1)} \frac{1 - \theta_1^{(0)}}{\theta_1^{(0)} f_1^{(0)} \rho_1^{(0)}} \beta_1^{(0)} \\
 &= \delta_1^{(0)} \alpha_{2,1}^{(1)} \beta_1^{(0)}.
 \end{aligned}$$

The probability structure for a $t = 4$ study with two age classes (i.e. $l=1$) is illustrated in Tables 4.1 through 4.4.

Note that no estimate of $p_i^{(0)}$ is possible, irrespective of the constraints on movement, as this parameter does not appear in the model - only animals of age 1 or older can be recaptured. To estimate $p_i^{(0)}$ we require additional information which can only be obtained by modifying the study. For example we could capture animals between anniversary dates as in the model of Stokes (1984), or we could use the robust design (Pollock et al. 1990).

Table 4.1: Probability structure under random emigration for age-class 0 animals last released following capture in a 2-age mark-recapture study with t years of capture and ancillary observations of marked animals obtained during the interval $(1, t + 1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$.

A. Last released following capture				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	$S_1^{(0)} \theta_1^{(0)} p_2^{*(0)}$	$S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$
		$\times S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$...	$\times S_1^{(0)} \theta_1^{(0)} q_2^{*(0)} \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$S_2^{(0)} \theta_2^{(0)} p_3^{*(0)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$
				$\times S_2^{(0)} \theta_2^{(0)} q_3^{*(0)} \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$S_{t-1}^{(0)} \theta_{t-1}^{(0)} p_t^{*(0)}$
Next encountered by observation				
Cohort	$j = 1$	2	...	t
	$t - 1$			
$i = 1$	$f_1^{(0)}$	$f_2^{(1)} S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$...	$f_{t-1}^{(1)} S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$
				$\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
				$\times \prod_{h=2}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$f_2^{(0)}$...	$f_{t-1}^{(1)} S_2^{(0)} \theta_2^{(0)} q_3^{*(0)}$
				$\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$f_{t-1}^{(0)}$
				$f_t^{(1)} S_{t-1}^{(0)} \theta_{t-1}^{(0)} q_t^{*(0)}$
t	-	-	...	$f_t^{(0)}$

Table 4.2: Probability structure under random emigration for age class 0 animals last released following observation in a 2-age mark-recapture study with t years of capture, and ancillary observations of marked animals obtained during the interval $(1, t + 1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1 - \theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} p_i^{(\nu)}}$.

B. Last released following observation				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} p_2^{*(0)}$	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} q_2^{*(0)}$ $\times S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} q_1^{*(0)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$\delta_2^{(0)} \theta_2^{(0)} S_2^{(0)} p_3^{*(0)}$...	$\delta_2^{(0)} \theta_2^{(0)} S_2^{(0)} q_2^{*(0)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
.
.
$t - 1$	-	-	...	$\delta_{t-1}^{(0)} \theta_{t-1}^{(0)} S_{t-1}^{(0)} p_t^{*(0)}$
Next encountered by observation				
Cohort	$j = 2$...	$t - 1$	t
	$\delta_1^{(0)} \theta_1^{(0)} f_2^{(1)} S_1^{(0)} q_2^{*(0)}$...	$\delta_1^{(0)} \theta_1^{(0)} f_{t-1}^{(1)} S_1^{(0)} q_2^{*(0)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_1^{(0)} \theta_1^{(0)} f_t^{(1)} S_1^{(0)} q_2^{*(0)}$ $\times \prod_{h=2}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	...	$\delta_2^{(0)} \theta_2^{(0)} f_{t-1}^{(1)} S_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_2^{(0)} \theta_2^{(0)} f_t^{(1)} S_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
.
.
$t - 1$	-	...	-	$\delta_{t-1}^{(0)} \theta_{t-1}^{(0)} f_t^{(1)} S_{t-1}^{(0)} q_t^{*(0)}$

Table 4.3: Probability structure under random emigration for age-class 1 animals last released following capture in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$.

Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$.

A. Last released following capture		Next encountered by capture			
Cohort	$j = 2$	3	...	t	
$i = 1$	$S_1^{(1)} \theta_1^{(1)} p_2^{*(1)}$	$S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$	
		$\times S_1^{(1)} \theta_1^{(1)} q_2^{*(1)}$...	$\times S_1^{(1)} \theta_1^{(1)} q_2^{*(1)} \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	
2	-	$S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$	
				$\times S_2^{(1)} \theta_2^{(1)} q_3^{*(1)} \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	
	
	
	
$t - 1$	-	-	...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$	
		Next encountered by observation			
	$j = 1$	2	...	$t - 1$	t
$i = 1$	$f_1^{(1)}$	$f_2^{(1)} S_1^{(1)} \theta_1^{(1)} q_2^{*(1)}$...	$f_{t-1}^{(1)} S_1^{(1)} \theta_1^{(1)} q_2^{*(1)}$	$f_t^{(1)} S_1^{(1)} \theta_1^{(1)} q_2^{*(1)}$
				$\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\times \prod_{h=2}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$f_2^{(1)}$...	$f_{t-1}^{(1)} S_2^{(1)} \theta_2^{(1)} q_3^{*(1)}$	$f_t^{(1)} S_2^{(1)} \theta_2^{(1)} q_3^{*(1)}$
				$\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$f_{t-1}^{(1)}$	$f_t^{(1)} S_{t-1}^{(1)} \theta_{t-1}^{(1)} q_t^{*(1)}$
t	-	-	...	-	$f_t^{(1)}$

Table 4.4: Probability structure under random emigration for age class 1 animals last released following observation in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1 - \theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} p_i^{(\nu)}}$.

B. Last released following observation				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	$\delta_1^{(1)} \theta_1^{(1)} S_1^{(1)} p_2^{*(1)}$	$\delta_1^{(1)} \theta_1^{(1)} S_1^{(1)} q_2^{*(1)}$ $\times S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$\delta_1^{(1)} \theta_1^{(1)} S_1^{(1)} q_1^{*(1)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$\delta_2^{(1)} \theta_2^{(1)} S_2^{(1)} p_3^{*(1)}$...	$\delta_2^{(1)} \theta_2^{(1)} S_2^{(1)} q_2^{*(1)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
.
.
$t - 1$	-	-	...	$\delta_{t-1}^{(1)} \theta_{t-1}^{(1)} S_{t-1}^{(1)} p_t^{*(1)}$
Next encountered by observation				
Cohort	$j = 2$...	$t - 1$	t
	$\delta_1^{(1)} \theta_1^{(1)} f_2^{(1)} S_1^{(1)} q_2^{*(1)}$...	$\delta_1^{(1)} \theta_1^{(1)} f_{t-1}^{(1)} S_1^{(1)} q_2^{*(1)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_1^{(1)} \theta_1^{(1)} f_t^{(1)} S_1^{(1)} q_2^{*(1)}$ $\times \prod_{h=2}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	...	$\delta_2^{(1)} \theta_2^{(1)} f_{t-1}^{(1)} S_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_2^{(1)} \theta_2^{(1)} f_t^{(1)} S_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
.
.
$t - 1$	-	...	-	$\delta_{t-1}^{(1)} \theta_{t-1}^{(1)} f_t S_{t-1}^{(1)} q_t^{*(1)}$

4.2.3 Distribution of the MSS

Factoring the likelihood (see below) we find a set of jointly minimal sufficient statistics (MSS) is the set of $R_{i,1}^{(\nu)}$ ($i = 1, \dots, t, \nu = 0, \dots, l$), $R_{i,2}^{(\nu)}$ ($i=1, \dots, t-1, \nu = 0, \dots, l$), $C_i^{(\nu)}$ ($i=2, \dots, t, \nu = 1, \dots, l+1$), $O_i^{(\nu)}$ ($i = 1, \dots, t-1, \nu = 0, \dots, l$), which has dimension $(l+1)(4t-3)$, with $(l+1)(4t-3)$ free parameters in the model.

As in the single-stratum model we can re-express the likelihood in terms of products of conditionally independent binomial distributions and conditionally independent multiple hypergeometric distributions (i.e. $Pr(\text{MSS})$ and $Pr(\text{Data}|\text{MSS})$ respectively).

Let

$$\lambda_{i,1}^{(\nu)} = \begin{cases} \alpha_{i,2}^{(\nu)} & i = t \\ (\alpha_{i,1}^{(\nu)} + \alpha_{i,2}^{(\nu)}) + \beta_i^{(\nu)} \lambda_{i+1,1}^{(\omega)} & i = 1, \dots, t-1 \end{cases},$$

$$\lambda_{i,2}^{(\nu)} = \delta_i^{(\nu)} (\lambda_{i,1}^{(\nu)} - \alpha_{i,2}^{(\nu)}),$$

$$\tau_{i+1,1}^{(\nu+1)} = \frac{\alpha_{i,1}^{(\nu)}}{\lambda_{i,1}^{(\nu)} - \alpha_{i,2}^{(\nu)}},$$

$$\tau_{i,2}^{(\nu)} = \frac{\alpha_{i,2}^{(\nu)}}{\lambda_{i,1}^{(\nu)}},$$

and define the statistics

$$Z_i^{(1)} = R_{i-1,1}^{(0)} + R_{i-1,2}^{(0)} - C_i^{(1)} - O_{i-1}^{(0)} \quad i = 2, \dots, t$$

$$Z_i^{(\nu)} = Z_{i-1}^{(\nu-1)} + R_{i-1,1}^{(\nu-1)} + R_{i-1,2}^{(\nu-1)} - C_i^{(\nu)} - O_{i-1}^{(\nu-1)} \quad i = 2, \dots, t; \nu = 2, \dots, l$$

$$Z_i^{(l+1)} = Z_{i-1}^{(l+1)} + Z_{i-1}^{(l)} + R_{i-1,1}^{(l)} + R_{i-1,2}^{(l)} - C_i^{(l+1)} - O_{i-1}^{(l)} \quad i = 2, \dots, t$$

$$T_i^{(\nu)} = Z_i^{(\nu)} + C_i^{(\nu)} \quad i = 2, \dots, t; \nu = 1, \dots, l+1.$$

and

$$r_i^{(\nu)} = \begin{cases} R_{i,1}^{(0)} & \nu = 0 \\ Z_i^{(\nu)} + R_{i,1}^{(\nu)} & \nu = 1, \dots, l-1 \\ Z_i^{(l)} + Z_i^{(l+1)} + R_{i,1}^{(l)} & \nu = l \end{cases}.$$

Also, $M_{i,j,p,1}^{(\nu)}$ and $M_{i,j,p,2}^{(\nu)}$ are the partial capture and observation totals given by

$$M_{i+1,j,p,1}^{(\nu)} = \begin{cases} M_{i+1,j,1,1}^{(0)} & \nu = 0 \\ M_{i+1,j,1,1}^{(\nu)} + M_{i,j,p,1}^{(\nu-1)} + M_{i,j,2,1}^{(\nu-1)} & \nu = 1, \dots, l-1 \\ M_{i+1,j,1,1}^{(l)} + \sum_{k=l-1}^l M_{i,j,p,1}^{(k)} + M_{i,j,2,1}^{(k)} & \nu = l \end{cases}$$

and

$$M_{i+1,j,p,2}^{(\nu)} = \begin{cases} M_{i+1,j,1,2}^{(0)} & \nu = 0 \\ M_{i+1,j,1,2}^{(\nu)} + M_{i,j,p,2}^{(\nu-1)} + M_{i,j,2,2}^{(\nu-1)} & \nu = 1, \dots, l-1 \\ M_{i+1,j,1,2}^{(l)} + \sum_{k=l-1}^l M_{i,j,p,2}^{(k)} + M_{i,j,2,2}^{(k)} & \nu = l \end{cases}$$

We first factor out the marginal distributions of the $R_{i,k}^{(\nu)}$'s. Starting with the first release cohorts in each age class we then factor the remaining components of the likelihood as follows:

$$\begin{aligned} & Pr(M_{1,2,1,1}^{(\nu)}, \dots, M_{1,t,1,1}^{(\nu)}, M_{1,1,1,2}^{(\nu)}, \dots, M_{1,t,1,2}^{(\nu)} | R_{1,1}^{(\nu)}) = \\ & Pr(M_{1,1,1,2}^{(\nu)} | R_{1,1}^{(\nu)}) Pr(M_{1,2,1,1}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)}) \\ & \times Pr(M_{1,3,1,1}^{(\nu)}, \dots, M_{1,t,1,1}^{(\nu)}, M_{1,2,1,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} - M_{1,2,1,1}^{(\nu)}) \end{aligned}$$

and

$$\begin{aligned} & Pr(M_{1,2,2,1}^{(\nu)}, \dots, M_{1,t,2,1}^{(\nu)}, M_{1,2,2,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,2}^{(\nu)}) = \\ & Pr(M_{1,2,2,1}^{(\nu)} | R_{1,2}^{(\nu)}) \\ & \times Pr(M_{1,3,2,1}^{(\nu)}, \dots, M_{1,t,2,1}^{(\nu)}, M_{1,2,2,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,2}^{(\nu)} - M_{1,2,2,1}^{(\nu)}) \end{aligned}$$

where

$$(M_{1,1,1,2}^{(\nu)} | R_{1,1}^{(\nu)}) \sim B(R_{1,1}^{(\nu)}, \tau_{1,2}^{(\nu)}) \quad \nu = 0, \dots, l.$$

Now,

$$(M_{1,2,1,1}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)}) \sim B(R_{1,1}^{(\nu)}, \tau_{2,1}^{(\nu+1)}) \quad \nu = 0, \dots, l$$

and

$$(M_{1,2,2,1}^{(\nu)} | R_{1,2}^{(\nu)}) \sim B(R_{1,2}^{(\nu)}, \tau_{2,1}^{(\nu+1)}) \quad \nu = 0, \dots, l,$$

thus, we can pool

$$(M_{1,2,1,1}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)})$$

with

$$(M_{1,2,2,1}^{(\nu)} | R_{1,2}^{(\nu)})$$

to form

$$(C_2^{(\nu+1)} | T_2^{(\nu+1)}) \quad \nu = 1, \dots, l+1,$$

leading to the result

$$\begin{aligned} & Pr(M_{1,2,1,1}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)}) Pr(M_{1,2,2,1}^{(\nu)} | R_{1,2}^{(\nu)}) = \\ & \frac{\begin{pmatrix} R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} \\ M_{1,2,1,1}^{(\nu)} \end{pmatrix} \begin{pmatrix} R_{1,2}^{(\nu)} \\ M_{1,2,2,1}^{(\nu)} \end{pmatrix}}{\begin{pmatrix} T_2^{(\nu+1)} \\ C_2^{(\nu+1)} \end{pmatrix}} \\ & \times \begin{pmatrix} T_2^{(\nu+1)} \\ C_2^{(\nu+1)} \end{pmatrix} (\tau_{2,1}^{(\nu+1)})^{C_2^{(\nu+1)}} (1 - \tau_{2,1}^{(\nu+1)})^{Z_2^{(\nu+1)}}. \end{aligned}$$

Also,

$$(M_{1,3,1,1}^{(\nu)}, \dots, M_{1,t,1,1}^{(\nu)}, M_{1,2,1,2}^{(\nu)}, \dots, M_{1,t,1,2}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} - M_{1,2,1,1}^{(\nu)})$$

and

$$(M_{1,3,2,1}^{(\nu)}, \dots, M_{1,t,2,1}^{(\nu)}, M_{1,2,2,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,2}^{(\nu)} - M_{1,2,2,1}^{(\nu)})$$

are multinomial with conditional cell probabilities

$$\frac{\pi_{1,j,1,k}^{(\nu)}}{\lambda_{1,1}^{(\nu)} - \alpha_{1,1}^{(\nu)} - \alpha_{1,2}^{(\nu)}} = \frac{\pi_{1,j,2,k}^{(\nu)}}{\delta_1^{(\nu)} (\lambda_{1,1}^{(\nu)} - \alpha_{1,1}^{(\nu)} - \alpha_{1,2}^{(\nu)})} = \frac{\pi_{2,j,1,k}^{(\omega)}}{\lambda_{2,j,1,k}^{(\omega)}}, \quad (4.10)$$

where ω is defined as in (4.1). Hence for $(\nu = 0, \dots, l-2)$ we pool

$$(M_{1,3,1,1}^{(\nu)}, \dots, M_{1,t,1,1}^{(\nu)}, M_{1,2,1,2}^{(\nu)}, \dots, M_{1,t,1,2}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} - M_{1,2,1,1}^{(\nu)})$$

with

$$(M_{1,3,2,1}^{(\nu)}, \dots, M_{1,t,2,1}^{(\nu)}, M_{1,2,2,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,2}^{(\nu)} - M_{1,2,2,1}^{(\nu)})$$

and

$$(M_{2,3,1,1}^{(\nu+1)}, \dots, M_{2,t,1,1}^{(\nu+1)}, M_{2,2,1,2}^{(\nu+1)}, \dots, M_{2,t,1,2}^{(\nu+1)} | R_{2,1}^{(\nu+1)})$$

giving

$$\begin{aligned} & Pr(M_{1,3,1,1}^{(\nu)}, \dots, M_{1,t,1,1}^{(\nu)}, M_{1,2,1,2}^{(\nu)}, \dots, M_{1,t,1,2}^{(\nu)} | R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} - M_{1,2,1,1}^{(\nu)}) \\ & \quad \times (M_{1,3,2,1}^{(\nu)}, \dots, M_{1,t,2,1}^{(\nu)}, M_{1,2,2,2}^{(\nu)}, \dots, M_{1,t,2,2}^{(\nu)} | R_{1,2}^{(\nu)} - M_{1,2,2,1}^{(\nu)}) \\ & \quad \times Pr(M_{2,3,1,1}^{(\nu+1)}, M_{2,t,1,1}^{(\nu+1)}, M_{2,2,1,2}^{(\nu+1)}, \dots, M_{2,t,1,2}^{(\nu+1)} | R_{2,1}^{(\nu+1)}) \\ & = \frac{\binom{R_{1,1}^{(\nu)} - M_{1,1,1,2}^{(\nu)} - M_{1,2,1,1}^{(\nu)}}{[M_{1,j,1,1}^{(\nu)}]_{j=3}^t, [M_{1,j,1,2}^{(\nu)}]_{j=2}^t} \binom{R_{1,2}^{(\nu)} - M_{1,2,2,1}^{(\nu)}}{[M_{1,j,2,1}^{(\nu)}]_{j=3}^t, [M_{1,j,2,2}^{(\nu)}]_{j=2}^t}}{\binom{r_2^{(\nu+1)}}{[M_{2,j,p,1}^{(\nu+1)}]_{j=3}^t, [M_{1,j,p,2}^{(\nu+1)}]_{j=2}^t}} \\ & \quad \times \binom{R_{2,1}^{(\nu+1)}}{[M_{2,j,1,1}^{(\nu+1)}]_{j=3}^t, [M_{2,j,1,2}^{(\nu+1)}]_{j=2}^t}} \\ & \quad \times \binom{r_2^{(\nu+1)}}{[M_{2,j,p,1}^{(\nu+1)}]_{j=3}^t, [M_{1,j,p,2}^{(\nu+1)}]_{j=2}^t}} \prod_{j=3}^t \frac{\pi_{2,j,1,1}^{(\nu+1)}}{\lambda_{2,1}^{(\nu+1)}} \prod_{j=2}^t \frac{\pi_{2,j,1,2}^{(\nu+1)}}{\lambda_{2,1}^{(\nu+1)}} \quad \nu = 0, \dots, l-2. \end{aligned}$$

Similarly, since the conditional multinomial cell probabilities given by (4.10) are identical for age classes $l-1$ and l we also pool

$$(M_{1,3,1,1}^{(l)}, \dots, M_{1,t,1,1}^{(l)}, M_{1,2,1,2}^{(l)}, \dots, M_{1,t,1,2}^{(l)} | R_{1,1}^{(l)} - M_{1,1,1,2}^{(l)} - M_{1,2,1,1}^{(l)})$$

with

$$\begin{aligned} & (M_{1,3,2,1}^{(l)}, \dots, M_{1,t,2,1}^{(l)}, M_{1,2,2,2}^{(l)}, \dots, M_{1,t,2,2}^{(l)} | R_{1,2}^{(l)} - M_{1,2,2,1}^{(l)}) \\ & (M_{1,3,1,1}^{(l-1)}, \dots, M_{1,t,1,1}^{(l-1)}, M_{1,2,1,2}^{(l-1)}, \dots, M_{1,t,1,2}^{(l-1)} | R_{1,1}^{(l-1)} - M_{1,1,1,2}^{(l-1)} - M_{1,2,1,1}^{(l-1)}) \\ & (M_{1,3,2,1}^{(l-1)}, \dots, M_{1,t,2,1}^{(l-1)}, M_{1,2,2,2}^{(l-1)}, \dots, M_{1,t,2,2}^{(l-1)} | R_{1,2}^{(l-1)} - M_{1,2,2,1}^{(l-1)}) \end{aligned}$$

and

$$(M_{2,3,1,1}^{(l)}, \dots, M_{2,t,1,1}^{(l)}, M_{2,2,1,2}^{(l)}, \dots, M_{2,t,1,2}^{(l)} | R_{2,1}^{(l)}) \quad \bullet$$

to give

$$Pr(M_{1,3,1,1}^{(l)}, \dots, M_{1,t,1,1}^{(l)}, M_{1,2,1,2}^{(l)}, \dots, M_{1,t,1,2}^{(l)} | R_{1,1}^{(l)} - M_{1,1,1,2}^{(l)} - M_{1,2,1,1}^{(l)})$$

$$\begin{aligned}
& \times Pr(M_{1,3,2,1}^{(l)}, \dots, M_{1,t,2,1}^{(l)}, M_{1,2,2,2}^{(l)}, \dots, M_{1,t,2,2}^{(l)} | R_{1,2}^{(l)} - M_{1,2,2,1}^{(l)}) \\
& \times (M_{1,3,1,1}^{(l-1)}, \dots, M_{1,t,1,1}^{(l-1)}, M_{1,2,1,2}^{(l-1)}, \dots, M_{1,t,1,2}^{(l-1)} | R_{1,1}^{(l-1)} - M_{1,1,1,2} - M_{1,2,1,1}^{(l-1)}) \\
& \times Pr(M_{1,3,2,1}^{(l-1)}, \dots, M_{1,t,2,1}^{(l-1)}, M_{1,2,2,2}^{(l-1)}, \dots, M_{1,t,2,2}^{(l-1)} | R_{1,2}^{(l-1)} - M_{1,2,2,1}^{(l-1)}) \\
& \times Pr(M_{2,3,1,1}^{(l)}, \dots, M_{2,t,1,1}^{(l)}, M_{2,2,1,2}^{(l)}, \dots, M_{2,t,1,2}^{(l)} | R_{2,1}^{(l)}) \\
& = \frac{\binom{R_{1,1}^{(l)} - M_{1,1,1,2} - M_{1,2,1,1}^{(l)}}{[M_{1,j,1,1}^{(l)}]_{j=3}^t, [M_{1,j,1,2}^{(l)}]_{j=2}^t} \binom{R_{1,2}^{(l)} - M_{1,2,2,1}^{(l)}}{[M_{1,j,2,1}^{(l)}]_{j=3}^t, [M_{1,j,2,2}^{(l)}]_{j=2}^t}}{\binom{r_2^{(l)}}{[M_{2,j,p,1}^{(l)}]_{j=3}^t, [M_{1,j,p,2}^{(l)}]_{j=2}^t}} \\
& \times \binom{R_{1,1}^{(l-1)} - M_{1,1,1,2} - M_{1,2,1,1}^{(l-1)}}{[M_{1,j,1,1}^{(l-1)}]_{j=3}^t, [M_{1,j,1,2}^{(l-1)}]_{j=2}^t} \binom{R_{1,2}^{(l-1)} - M_{1,2,2,1}^{(l-1)}}{[M_{1,j,2,1}^{(l-1)}]_{j=3}^t, [M_{1,j,2,2}^{(l-1)}]_{j=2}^t} \\
& \quad \times \binom{R_{2,1}^{(l)}}{[M_{2,j,1,1}^{(l)}]_{j=3}^t, [M_{2,j,1,2}^{(l)}]_{j=2}^t} \\
& \quad \binom{r_2^{(l)}}{[M_{2,j,p,1}^{(l)}]_{j=3}^t, [M_{1,j,p,2}^{(l)}]_{j=2}^t} \prod_{j=3}^t \frac{\pi_{2,j,1,1}^{(l)}}{\lambda_{2,1}^{(l)}} \prod_{j=2}^t \frac{\pi_{2,j,1,2}^{(l)}}{\lambda_{2,1}^{(l)}}.
\end{aligned}$$

As we did in the single age class case we begin with cohorts $C_{1,1}^{(\nu)}$ and $C_{1,2}^{(\nu)}$ ($\nu = 0, \dots, l$), and repeat the “peeling” and “pooling” cycles through each release time. We make use of the relationships

$$O_i^{(\nu)} = M_{i,i,p,2}^{(\nu)} \quad \nu = 0, \dots, l$$

and

$$C_{i+1}^{(\nu+1)} = M_{i,i+1,p,1}^{(\nu)} + M_{i,i+1,2,1}^{(\nu)} \quad \nu = 0, \dots, l$$

and the factorizations

$$\begin{aligned}
& Pr(M_{i,i+1,p,1}^{(\nu)}, \dots, M_{i,t,p,1}^{(\nu)}, M_{i,i,p,2}^{(\nu)}, \dots, M_{i,t,p,2}^{(\nu)} | r_i^{(\nu)}) = \\
& Pr(M_{i,i,p,2}^{(\nu)} | r_i^{(\nu)}) Pr(M_{i,i+1,p,1}^{(\nu)} | r_i^{(\nu)} - M_{i,i,p,2}^{(\nu)}) \\
& \times Pr(M_{i,i+2,p,1}^{(\nu)}, \dots, M_{i,t,p,1}^{(\nu)}, M_{i,i+1,p,2}^{(\nu)}, \dots, M_{i,t,p,2}^{(\nu)} | r_i^{(\nu)} - M_{i,i,p,2} - M_{i,i+1,p,1}^{(\nu)})
\end{aligned}$$

and

$$\begin{aligned} Pr(M_{i,i+1,2,1}^{(\nu)}, \dots, M_{i,t,2,1}^{(\nu)}, M_{i,i+1,2,2}^{(\nu)}, \dots, M_{i,t,2,2}^{(\nu)} | R_{i,2}^{(\nu)}) = \\ Pr(M_{i,i+1,2,1}^{(\nu)} | R_{i,2}^{(\nu)}) \\ \times Pr(M_{i,i+2,2,1}^{(\nu)}, \dots, M_{i,t,2,1}^{(\nu)}, M_{i,i+1,2,2}^{(\nu)}, \dots, M_{i,t,2,2}^{(\nu)} | R_{i,2}^{(\nu)} - M_{i,i+1,2,1}^{(\nu)}) \end{aligned}$$

At each cycle we "peel" off

$$\begin{pmatrix} r_i^{(\nu)} \\ O_i^{(\nu)} \end{pmatrix} (\tau_{i,2}^{(\nu)})^{O_i^{(\nu)}} (1 - \tau_{i,2}^{(\nu)})^{r_i^{(\nu)} - O_i^{(\nu)}}$$

and

$$\frac{\begin{pmatrix} r_i^{(\nu)} - O_i^{(\nu)} \\ M_{i,i+1,p,1}^{(\nu)} \end{pmatrix} \begin{pmatrix} R_{i,2}^{(\nu)} \\ M_{i,i+1,2,1}^{(\nu)} \end{pmatrix}}{\begin{pmatrix} T_{i+1}^{(\nu+1)} \\ C_{i+1}^{(\nu+1)} \end{pmatrix}} \begin{pmatrix} T_{i+1}^{(\nu+1)} \\ C_{i+1}^{(\nu+1)} \end{pmatrix} (\tau_{i+1,1}^{(\nu+1)})^{C_{i+1}^{(\nu+1)}} (1 - \tau_{i+1,1}^{(\nu+1)})^{T_{i+1}^{(\nu+1)}} Z_{i+1}^{(\nu+1)}$$

terms, and noting that

$$\begin{aligned} \begin{pmatrix} r_{t-1}^{(\nu)} - M_{t-1,t-1,p,2}^{(\nu)} - M_{t-1,t,p,1}^{(\nu)} \\ M_{t-1,t,p,2}^{(\nu)} \end{pmatrix} &= \begin{pmatrix} R_{t-1,2}^{(\nu)} - M_{t-1,t,2,1}^{(\nu)} \\ M_{t-1,t,2,2}^{(\nu)} \end{pmatrix} \\ &= \begin{pmatrix} R_{t,1}^{(\nu)} \\ M_{t,t,1,2}^{(\nu)} \end{pmatrix} \frac{\pi_{t,t,1,2}^{(\nu)}}{\lambda_{t,1}^{(\nu)}} = 1, \end{aligned}$$

we obtain

$$\begin{aligned} Pr(\text{Data}) &= \prod_{\nu=0}^l \left\{ \prod_{i=1}^t \left\{ \begin{pmatrix} N_i^{(\nu)} \\ R_{i,1}^{(\nu)} \end{pmatrix} (\lambda_{i,1}^{(\nu)})^{R_{i,1}^{(\nu)}} (1 - \lambda_{i,1}^{(\nu)})^{(N_i^{(\nu)} - R_{i,1}^{(\nu)})} \right\} \right. \\ &\quad \times \prod_{i=1}^{t-1} \left\{ \begin{pmatrix} n_i^{(\nu)} \\ R_{i,2}^{(\nu)} \end{pmatrix} (\lambda_{i,2}^{(\nu)})^{R_{i,2}^{(\nu)}} (1 - \lambda_{i,2}^{(\nu)})^{(n_i^{(\nu)} - R_{i,2}^{(\nu)})} \right\} \\ &\quad \times \prod_{i=2}^t \left\{ \begin{pmatrix} T_i^{(\nu+1)} \\ C_i^{(\nu+1)} \end{pmatrix} (\tau_{i,1}^{(\nu+1)})^{C_i^{(\nu+1)}} (1 - \tau_{i,1}^{(\nu+1)})^{T_i^{(\nu+1)} - C_i^{(\nu+1)}} \right\} \\ &\quad \left. \times \prod_{i=1}^{t-1} \left\{ \begin{pmatrix} r_i^{(\nu)} \\ O_i^{(\nu)} \end{pmatrix} (\tau_{i,2}^{(\nu)})^{O_i^{(\nu)}} (1 - \tau_{i,2}^{(\nu)})^{r_i^{(\nu)} - O_i^{(\nu)}} \right\} \right\} \end{aligned}$$

$$\begin{aligned}
& \times \prod_{\nu=0}^l \prod_{i=1}^{t-1} \frac{\begin{pmatrix} r_i^{(\nu)} - O_i^{(\nu)} \\ M_{i,i+1,p,1}^{(\nu)} \end{pmatrix} \begin{pmatrix} R_{i,2}^{(\nu)} \\ M_{i,i+1,2,1}^{(\nu)} \end{pmatrix}}{\begin{pmatrix} T_{i+1}^{(\nu+1)} \\ C_{i+1}^{(\nu+1)} \end{pmatrix}} \\
& \times \prod_{i=1}^{t-2} \left\{ \frac{\begin{pmatrix} r_i^{(l)} - O_i^{(l)} - M_{i,i+1,p,1}^{(l)} \\ [M_{i,j,p,1}^{(l)}]_{j=i+2}^t [M_{i,j,p,2}^{(l)}]_{j=i+1}^t \end{pmatrix} \begin{pmatrix} R_{i+1,1}^{(l)} \\ [M_{i+1,j,1,1}^{(l)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(l)}]_{j=i+1}^t \end{pmatrix}}{\begin{pmatrix} r_{i+1}^{(l)} \\ [M_{i+1,j,p,1}^{(l)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(l)}]_{j=i+1}^t \end{pmatrix}} \right. \\
& \quad \times \frac{\begin{pmatrix} R_{i,2}^{(l)} - M_{i,i+1,2,1}^{(l)} \\ [M_{i,j,2,1}^{(l)}]_{j=i+2}^t [M_{i,j,2,2}^{(l)}]_{j=i+1}^t \end{pmatrix} \begin{pmatrix} r_i^{(l-1)} - M_{i,i,p,2}^{(l-1)} - M_{i,i+1,p,1}^{(l-1)} \\ [M_{i,j,p,1}^{(l-1)}]_{j=i+2}^t [M_{i,j,p,2}^{(l-1)}]_{j=i+1}^t \end{pmatrix}}{1} \\
& \quad \times \frac{\begin{pmatrix} R_{i,2}^{(l-1)} - M_{i,i+1,2,1}^{(l-1)} \\ [M_{i,j,2,1}^{(l-1)}]_{j=i+2}^t [M_{i,j,2,2}^{(l-1)}]_{j=i+1}^t \end{pmatrix}}{1} \\
& \quad \times \left. \prod_{\nu=0}^{l-2} \frac{\begin{pmatrix} r_i^{(\nu)} - O_i^{(\nu)} - M_{i,i+1,p,1}^{(\nu)} \\ [M_{i,j,p,1}^{(\nu)}]_{j=i+2}^t [M_{i,j,p,2}^{(\nu)}]_{j=i+1}^t \end{pmatrix} \begin{pmatrix} R_{i+1,1}^{(\nu+1)} \\ [M_{i+1,j,1,1}^{(\nu+1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(\nu+1)}]_{j=i+1}^t \end{pmatrix}}{\begin{pmatrix} r_{i+1}^{(\nu+1)} \\ [M_{i+1,j,p,1}^{(\nu+1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(\nu+1)}]_{j=i+1}^t \end{pmatrix}} \right. \\
& \quad \left. \times \frac{\begin{pmatrix} R_{i,2}^{(\nu)} - M_{i,i+1,2,1}^{(\nu)} \\ [M_{i,j,2,1}^{(\nu)}]_{j=i+2}^t [M_{i,j,2,2}^{(\nu)}]_{j=i+1}^t \end{pmatrix}}{1} \right\}. \tag{4.11}
\end{aligned}$$

4.2.4 Maximum likelihood estimators

The parameters $S_i^{(\nu)}$, $\theta_i^{(\nu)}$, $f_i^{(\nu)}$, and the confounded pair $F_i^{(\nu)} p_{i+1}^{(\omega)} = p_{i+1}^{*(\nu)}$ are one-to-one functions of the $\lambda_{i,1}^{(\nu)}$, $\lambda_{i,2}^{(\nu)}$, $\tau_{i,1}^{(\nu)}$ and $\tau_{i,2}^{(\nu)}$:

$$f_i^{(\nu)} = \begin{cases} \tau_{i,2}^{(\nu)} \lambda_{i,1}^{(\nu)} & i = 1, \dots, t-1; \nu = 0, \dots, l \\ \lambda_{i,1}^{(\nu)} & i = t, \nu = 0, \dots, l \end{cases}$$

$$p_i^{*(\nu)} = \frac{\lambda_{i,1}^{(\omega)} \tau_{i,1}^{(\nu+1)}}{1 + (\lambda_{i,1}^{(\omega)} - 1) \tau_{i,1}^{(\nu+1)}} \quad \nu = 0, \dots, l$$

$$\theta_i^{(\nu)} = \frac{1 - \tau_{i,2}^{(\nu)}}{1 + \tau_{i,2}^{(\nu)} (\lambda_{i,2}^{(\nu)} - 1)} \quad \nu = 0, \dots, l$$

and

$$S_i^{(\nu)} = (1 + \tau_{i,2}^{(\nu)} (\lambda_{i,2}^{(\nu)} - 1)) \frac{\lambda_{i,1}^{(\nu)}}{\lambda_{i+1,1}^{(\omega)}} \{1 + \tau_{i+1,1}^{(\nu+1)} (\lambda_{i,1}^{(\nu)} - 1)\} \quad \nu = 0, \dots, l$$

Although we define $p_i^{*(0)} = F_{i-1}^{(0)} p_i^{(1)}$ it is important to bear in mind that this is not a capture probability for animals of age 0, which we cannot estimate because no marked animals of age 0 are ever captured. Rather, $p_i^{*(0)}$ is the joint probability that an animal of age 0 at $i-1$ is at risk of capture at i and is captured at i when it is of age 1.

Substituting the MLE's

$$\hat{\lambda}_{i,1}^{(\nu)} = \frac{R_{i,1}^{(\nu)}}{N_i^{(\nu)}}$$

$$\hat{\lambda}_{i,2}^{(\nu)} = \frac{R_{i,2}^{(\nu)}}{n_i^{(\nu)}}$$

$$\hat{\tau}_{i,1}^{(\nu)} = \frac{C_i^{(\nu)}}{T_i^{(\nu)}}$$

and

$$\hat{\tau}_{i,2}^{(\nu)} = \frac{O_i^{(\nu)}}{r_i^{(\nu)}}$$

and solving for $\hat{f}_i^{(\nu)}$, $\hat{p}_i^{*(\nu)}$, $\hat{\theta}_i^{(\nu)}$, and $\hat{S}_i^{(\nu)}$, we obtain the MLE's

$$\hat{f}_i^{(\nu)} = \begin{cases} \frac{O_i^{(0)}}{N_i^{(0)}} & \nu = 0, i = 1, \dots, t-1 \\ \frac{R_{i,1}^{(\nu)} O_i^{(\nu)}}{N_i^{(\nu)} \tau_i^{(\nu)}} & \nu = 1, \dots, l, i = 1, \dots, t-1 \\ \frac{R_{i,1}^{(\nu)}}{N_i^{(\nu)}} & \nu = 0, \dots, l, i = t \end{cases} \quad (4.12)$$

$$\hat{p}_i^{*(\nu)} = \frac{C_i^{(\nu+1)}}{\frac{N_i^{(\omega)} Z_i^{(\nu+1)}}{R_{i,1}^{(\omega)}} + C_i^{(\nu+1)}} \quad \nu = 0, \dots, l, i = 2, \dots, t \quad (4.13)$$

$$\hat{\theta}_i^{(\nu)} = \frac{\tau_i^{(\nu)} - O_i^{(\nu)}}{T_{i+1}^{(\nu+1)}} \quad \nu = 0, \dots, l, i = 1, \dots, t-1 \quad (4.14)$$

and

$$\hat{S}_i^{(\nu)} = \frac{R_{i,1}^{(\nu)}}{N_i^{(\nu)} \tau_i^{(\nu)}} \left\{ \frac{N_{i+1}^{(\omega)} Z_{i+1}^{(\nu+1)}}{R_{i+1,1}^{(\omega)}} + C_{i+1}^{(\nu+1)} \right\} \quad \nu = 1, \dots, l, i = 1, \dots, t-1. \quad (4.15)$$

For the youngest age class, $\hat{S}_i^{(0)}$ reduces to

$$\hat{S}_i^{(0)} = \frac{1}{N_i^{(0)}} \left\{ \frac{N_{i+1}^{(1)} Z_{i+1}^{(1)}}{R_{i+1,1}^{(1)}} + C_{i+1}^{(1)} \right\}$$

4.2.5 Asymptotic variances and covariances

The non-zero partial derivatives are:

$$\frac{\partial f_i^{(\nu)}}{\partial \lambda_{i,1}^{(\nu)}} = \begin{cases} \frac{f_i^{(\nu)}}{\lambda_{i,1}^{(\nu)}} & (i = 1, \dots, t-1) \\ 1 & i = t \end{cases}$$

$$\frac{\partial f_i^{(\nu)}}{\partial \tau_{i,2}^{(\nu)}} = \begin{cases} \frac{f_i^{(\nu)}}{\tau_{i,2}^{(\nu)}} & (i = 1, \dots, t-1) \\ 0 & i = t \end{cases}$$

$$\frac{\partial S_i^{(\nu)}}{\partial \lambda_{i,1}^{(\nu)}} = \frac{S_i^{(\nu)}}{\lambda_{i,1}^{(\nu)}},$$

$$\frac{\partial S_i^{(\nu)}}{\partial \lambda_{i+1,1}^{(\omega)}} = \frac{-S_i^{(\nu)}(1 - p_{i+1}^{*(\nu)})}{\lambda_{i+1,1}^{(\omega)}}$$

$$\begin{aligned}
\frac{\partial S_i^{(\nu)}}{\partial \lambda_{i,2}^{(\nu)}} &= \frac{S_i^{(\nu)}(1 - \theta_i^{(\nu)})}{\lambda_{i,2}^{(\nu)}} \\
\frac{\partial S_i^{(\nu)}}{\partial \tau_{i+1,1}^{(\nu+1)}} &= \frac{-S_i^{(\nu)} p_{i+1}^{*(\nu)} (1 - \lambda_{i+1,1}^{(\omega)})}{\tau_{i+1,1}^{(\nu+1)} \lambda_{i+1,1}^{(\omega)}} \\
\frac{\partial S_i^{(\nu)}}{\partial \tau_{i,2}^{(\nu)}} &= \frac{S_i^{(\nu)} \theta_i^{(\nu)} (\lambda_{i,2}^{(\nu)} - 1)}{1 - \tau_{i,2}^{(\nu)}} \\
\frac{\partial \theta_i^{(\nu)}}{\partial \lambda_{i,2}^{(\nu)}} &= \frac{-\theta_i^{(\nu)} (1 - \theta_i^{(\nu)})}{\lambda_{i,2}^{(\nu)}} \\
\frac{\partial \theta_i^{(\nu)}}{\partial \tau_{i,2}^{(\nu)}} &= \frac{-\theta_i^{(\nu)} (1 - \theta_i^{(\nu)})}{\tau_{i,2}^{(\nu)} (1 - \tau_{i,2}^{(\nu)})} \\
\frac{\partial p_i^{*(\nu)}}{\partial \lambda_{i,1}^{(\omega)}} &= \frac{p_i^{*(\nu)} (1 - p_i^{*(\nu)})}{\lambda_{i,1}^{(\omega)}} \\
\frac{\partial p_i^{*(\nu)}}{\partial \tau_{i,1}^{(\nu+1)}} &= \frac{p_i^{*(\nu)} (1 - p_i^{*(\nu)})}{\tau_{i,1}^{(\nu+1)} (1 - \tau_{i,1}^{(\nu+1)})},
\end{aligned}$$

leading to the following asymptotic variances and non-zero covariances.

$$\text{Var}(\hat{f}_i^{(\nu)}) = \begin{cases} \frac{f_i^{(\nu)}(1-f_i^{(\nu)})}{N_i^{(\nu)}} & \nu = 0 \\ (f_i^{(\nu)})^2 \left(\frac{1}{E[R_{i,1}^{(\nu)}]} - \frac{1}{N_i^{(\nu)}} + \frac{1}{E[O_i^{(\nu)}]} - \frac{1}{r_i^{(\nu)}} \right) & \nu = 1, \dots, l, i = 1, \dots, t-1 \\ (f_i^{(\nu)})^2 \left(\frac{1}{E[R_{i,1}^{(\nu)}]} - \frac{1}{N_i^{(\nu)}} \right) & \nu = 1, \dots, l, i = t \end{cases}$$

$$\begin{aligned}
\text{Var}(\hat{S}_i^{(\nu)}) &= (S_i^{(\nu)})^2 \left\{ \frac{1}{E[R_{i,1}^{(\nu)}]} - \frac{1}{N_i^{(\nu)}} + (1 - p_{i+1}^{*(\nu)})^2 \left(\frac{1}{E[R_{i+1,1}^{(\omega)}]} - \frac{1}{N_{i+1}^{(\omega)}} \right) \right. \\
&\quad + p_{i+1}^{*(\nu)} (1 - p_{i+1}^{*(\nu)}) \frac{(N_{i+1}^{(\omega)} - R_{i+1,1}^{(\omega)})^2}{N_{i+1}^{(\omega)} R_{i+1,1}^{(\omega)} T_{i+1}^{(\nu+1)}} + (1 - \theta_i^{(\nu)})^2 \left(\frac{1}{E[R_{i,2}^{(\nu)}]} - \frac{1}{n_i^{(\nu)}} \right) \\
&\quad \left. + \left[\frac{\theta_i^{(\nu)} (O_i^{(\nu)} - E[R_{i,2}^{(\nu)}])}{O_i^{(\nu)}} \right]^2 \left(\frac{1}{r_i^{(\nu)} - E[O_i^{(\nu)}]} - \frac{1}{r_i^{(\nu)}} \right) \right\} \\
&\nu = 0, \dots, l, i = 1, \dots, t-1
\end{aligned}$$

$$\text{Var}(\hat{\theta}_i^{(\nu)}) = [\theta_i^{(\nu)}(1 - \theta_i^{(\nu)})]^2 \left(\frac{1}{E[O_i^{(\nu)}]} + \frac{1}{(r_i^{(\nu)} - E[O_i^{(\nu)}])} + \frac{1}{E[R_{i,2}^{(\nu)}]} - \frac{1}{n_i^{(\nu)}} \right)$$

$\nu = 0, \dots, l, i = 1, \dots, t-1$

$$Var(\hat{p}_i^{(\nu)}) = [p_i^{*(\nu)}(1 - p_i^{*(\nu)})]^2 \left(\frac{1}{R_{i,1}^{(\omega)}} - \frac{1}{N_i^{(\omega)}} + \frac{1}{C_i^{(\nu+1)}} + \frac{1}{Z_i^{(\nu+1)}} \right)$$

$\nu = 0, \dots, l, i = 2, \dots, t$

$$Cov(\hat{f}_i^{(\nu)}, \hat{S}_i^{(\nu)}) = f_i^{(\nu)} S_i^{(\nu)} \left(\frac{1}{E[R_{i,1}^{(\nu)}]} - \frac{1}{N_i^{(\nu)}} + \frac{\theta_i^{(\nu)}(E[R_{i,2}^{(\nu)}] - n_i^{(\nu)})}{n_i^{(\nu)} r_i^{(\nu)}} \right)$$

$\nu = 0, \dots, l, i = 1, \dots, t - 1$

$$Cov(\hat{f}_{i+1}^{(\omega)}, \hat{S}_i^{(\nu)}) = -f_{i+1}^{(\omega)} S_i^{(\nu)} (1 - p_{i+1}^{*(\nu)}) \left(\frac{1}{E[R_{i+1,1}^{(\omega)}]} - \frac{1}{N_{i+1}^{(\omega)}} \right)$$

$\nu = 0, \dots, l - 1, i = 1, \dots, t - 1$

$$Cov(\hat{f}_i^{(\omega)}, \hat{p}_i^{*(\nu)}) = f_i^{(\omega)} p_i^{*(\nu)} (1 - p_i^{*(\nu)}) \left(\frac{1}{E[R_{i,1}^{(\omega)}]} - \frac{1}{N_i^{(\omega)}} \right)$$

$\nu = 0, \dots, l - 1, i = 1, \dots, t$

$$Cov(\hat{S}_i^{(\nu)}, \hat{S}_{i+1}^{(\omega)}) = -S_i^{(\nu)} S_{i+1}^{(\omega)} (1 - p_{i+1}^{*(\nu)}) \left(\frac{1}{E[R_{i+1,1}^{(\omega)}]} - \frac{1}{N_{i+1}^{(\omega)}} \right)$$

$\nu = 0, \dots, l - 1, i = 1, \dots, t - 2$

$$Cov(\hat{S}_i^{(l-1)}, \hat{S}_i^{(l)}) = -S_i^{(l-1)} S_i^{(l)} (1 - p_{i+1}^{*(l-1)}) (1 - p_{i+1}^{*(l)}) \left(\frac{1}{E[R_{i+1,1}^{(l)}]} - \frac{1}{N_{i+1}^{(l)}} \right)$$

$i = 1, \dots, t - 1$

$$Cov(\hat{S}_i^{(\nu)}, \hat{\theta}_i^{(\nu)}) = -S_i^{(\nu)} \theta_i^{(\nu)} (1 - \theta_i^{(\nu)})^2 \left(\frac{1}{E[R_{i,2}^{(\nu)}]} - \frac{1}{n_i^{(\nu)}} + \frac{\theta_i^{(\nu)}}{(1 - \theta_i^{(\nu)}) O_i^{(\nu)}} \right. \\ \left. \times \frac{(E[R_{i,2}^{(\nu)}] - O_i^{(\nu)})}{r_i^{(\nu)} - E[O_i^{(\nu)}]} \right)$$

$\nu = 0, \dots, l, i = 1, \dots, t - 1$

$$\begin{aligned} \text{Cov}(\hat{S}_i^{(\omega)}, \hat{p}_i^{*(\nu)}) &= -S_i^{(\omega)} p_i^{*(\nu)} (1 - p_i^{*(\nu)}) \left(\frac{1}{R_{i+1,1}^{(\nu+1)}} - \frac{1}{N_{i+1}^{(\nu+1)}} \right) \\ & \quad i = 1, \dots, t-1; \nu = 0, \dots, l-1 \end{aligned}$$

$$\begin{aligned} \text{Cov}(\hat{S}_i^{(\nu)}, \hat{p}_{i+1}^{*(\nu)}) &= \\ & -S_i^{(\nu)} p_{i+1}^{*(\nu)} (1 - p_{i+1}^{*(\nu)}) \left\{ (1 - p_{i+1}^{*(\nu)}) \left(\frac{1}{E[R_{i+1,1}^{(\omega)}]} - \frac{1}{N_{i+1}^{(\nu+1)}} \right) \right. \\ & \quad \left. + \frac{p_{i+1}^{*(\nu)}}{E[C_i^{(\nu+1)}]} \times \frac{(N_{i+1}^{(\omega)} - E[R_{i+1,1}^{(\omega)}])}{E[R_{i+1,1}^{(\omega)}]} \right\} \\ & \quad \nu = 0, \dots, l, i = 1, \dots, t-1 \end{aligned}$$

$$\begin{aligned} \text{Cov}(\hat{p}_i^{*(l-1)}, \hat{p}_i^{*(l)}) &= p_i^{*(l-1)} (1 - p_i^{*(l-1)}) p_i^{*(l)} (1 - p_i^{*(l)}) \left\{ \frac{1}{E[R_{i,1}^{(l)}]} - \frac{1}{N_i^{(l)}} \right\} \\ & \quad i = 1, \dots, t-1 \end{aligned}$$

4.2.6 Goodness-of-fit tests under random emigration

The residual component of the distribution of the MSS under age-dependence has a similar form to that for the one-age model. As a consequence the resulting goodness-of-fit test components derived using the methods of Chapter 3 are similar to those for the one-age model with the difference that each one-age component can be broken down into conditionally independent components contributed by each age class.

The first component of the residual distribution comprises the product ($i = 1, \dots, t-1; \nu = 0, \dots, l$) of terms

$$\frac{\begin{pmatrix} r_i^{(\nu)} - O_i^{(\nu)} \\ M_{i,i+1,p,1}^{(\nu)} \end{pmatrix} \begin{pmatrix} R_{i,2}^{(\nu)} \\ M_{i,i+1,2,1}^{(\nu)} \end{pmatrix}}{\begin{pmatrix} T_{i+1}^{(\nu+1)} \\ C_{i+1}^{(\nu+1)} \end{pmatrix}}$$

and leads to a series of contingency tables, each one based firstly on a partitioning of the sufficient statistic $T_{i+1}^{(\nu)}$ according to whether the animals were observed at $i - 1$ or not, and secondly according to whether the animals were captured at $i + 1$. Each group of animals of age ν at i ($\nu = 1, \dots, l + 1$) provides an independent contingency table, thus we form $(l + 1)(t - 2) 2 \times 2$ contingency tables which test whether the event “member of $T_{i+1}^{(\nu)}$ and captured at i ” is independent of the event “member of $T_{i+1}^{(\nu)}$ and observed at i ” i.e. a test for short-term effect of observation on the probability that the animal is captured. The contingency tables take the form shown in Table 4.5 for animals of age $l + 1$ at time $i + 1$.

Table 4.5: Example of a contingency table for the component 1 goodness-of-fit test for animals of age $l + 1$ at time $i + 1$

	Member of $T_{i+1}^{(l+1)}$	Member of $T_{i+1}^{(l+1)}$	
not observed at i	observed at i		
Captured at $i + 1$	$M_{i,i+1,p,1}^{(l)}$	$M_{i,i+1,2,1}^{(l)}$	$C_{i+1}^{(l+1)}$
Not captured at $i + 1$	$\sum_{j=i+2}^t M_{i,j,p,1}^{(l)}$	$\sum_{j=i+2}^t M_{i,j,2,1}^{(l)}$	$T_{i+1}^{(l+1)} - C_{i+1}^{(l+1)}$
	$T_{i+1}^{(l+1)} - R_{i,2}^{(l)}$	$R_{i,2}^{(l)}$	$T_{i+1}^{(l+1)}$

The second component of the residual distribution comprises the product ($i = 1, \dots, t - 2$) of terms

$$\frac{\prod_{h=l-1}^l \left(\begin{array}{c} r_i^{(h)} - O_i^{(h)} - M_{i,i+1,p,1}^{(h)} \\ [M_{i,j,p,1}^{(h)}]_{j=i+2}^t [M_{i,j,p,2}^{(h)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i,2}^{(h)} - M_{i,i+1,2,1}^{(h)} \\ [M_{i,j,2,1}^{(h)}]_{j=i+2}^t [M_{i,j,2,2}^{(h)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_{i+1}^{(l)} \\ [M_{i+1,j,p,1}^{(l)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(l)}]_{j=i+1}^t \end{array} \right)} \times \frac{\left(\begin{array}{c} R_{i+1,1}^{(l)} \\ [M_{i+1,j,1,1}^{(l)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(l)}]_{j=i+1}^t \end{array} \right)}{1}$$

$$\begin{aligned}
& \times \prod_{\nu=0}^{l-2} \left\{ \frac{\left(\begin{array}{c} r_i^{(\nu)} - O_i^{(\nu)} - M_{i,i+1,p,1}^{(\nu)} \\ [M_{i,j,p,1}^{(\nu)}]_{j=i+2}^t [M_{i,j,p,2}^{(\nu)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i+1,1}^{(\nu+1)} \\ [M_{i+1,j,1,1}^{(\nu+1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(\nu+1)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_{i+1}^{(\nu+1)} \\ [M_{i+1,j,p,1}^{(\nu+1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(\nu+1)}]_{j=i+1}^t \end{array} \right)} \right. \\
& \left. \times \frac{\left(\begin{array}{c} R_{i,2}^{(\nu)} - M_{i,i+1,2,1}^{(\nu)} \\ [M_{i,j,2,1}^{(\nu)}]_{j=i+2}^t [M_{i,j,2,2}^{(\nu)}]_{j=i+1}^t \end{array} \right)}{1} \right\} \quad (4.16)
\end{aligned}$$

For animals in age class l at i (i.e. of age l or older) this component leads to a series of contingency tables based firstly on the following partitioning of the sufficient statistic $r_{i+1}^{(l)}$:

$r_i^{(l)} - O_i^{(l)} - M_{i,i+1,p,1}^{(l)}$ - those members of $r_{i+1}^{(l)}$ that were aged l at i and that were not observed at i nor captured at $i+1$.

$R_{i+1,1}^{(l)}$ - those members of $r_{i+1}^{(l)}$ captured at $i+1$.

$R_{i,2}^{(l)} - M_{i,i+1,2,1}^{(l)}$ - those members of $r_{i+1}^{(l)}$ that were aged l at i and that were observed at i but not captured at $i+1$.

$r_i^{(l-1)} - M_{i,i,p,2}^{(l-1)} - M_{i,i+1,p,1}^{(l-1)}$ - those members of $r_{i+1}^{(l)}$ that were aged $l-1$ at i and that were not observed at i nor captured at $i+1$.

$R_{i,2}^{(l-1)} - M_{i,i+1,2,1}^{(l-1)}$ - those members of $r_{i+1}^{(l)}$ that were aged $l-1$ at i and that were observed at i but not captured at $i+1$.

For animals in age class ν at i ($\nu = 0, \dots, l-2$) the first partitioning of the sufficient statistic $r_{i+1}^{(\nu+1)}$ is:

$r_i^{(\nu)} - O_i^{(\nu)} - M_{i,i+1,p,1}^{(\nu)}$ - those members of $r_{i+1}^{(\nu+1)}$ that were not observed at i nor captured at $i+1$.

$R_{i,2}^{(\nu)} - M_{i,i+1,2,1}^{(\nu)}$ - those members of $r_{i+1}^{(\nu+1)}$ that were observed at i but not captured at $i + 1$.

$R_{i+1,1}^{(\nu+1)}$ - those members of $r_{i+1}^{(\nu+1)}$ captured at $i + 1$.

The second partitioning of $r_i^{(l)}$ for all age classes is according to the possible capture/observation classes after sampling time $i + 1$ (including animals observed in $i + 1, i + 2$).

From component (4.16) we form $(\nu(t - 2)2(t - i - 1) + 1) \times 3$ contingency tables, which for $\nu = 0, \dots, l - 2$ test whether membership in one of the capture/observation cells $M_{i,i+2,p,1}^{(\nu+1)}, \dots, M_{i,t,p,1}^{(\nu+1)}, M_{i,i+1,p,2}^{(\nu+1)}, \dots, M_{i,t,p,2}^{(\nu+1)}$ is independent of the events "captured at $i + 1$ ", "not captured at $i + 1$ and not observed at i ", and "not captured at $i + 1$ and observed at i ". In the case of age class l animals two additional events result from the mixed-age nature of this class. This test will be sensitive to short- and long-term capture effects on the probability that the animal is captured or seen again and to similar observation effects. The form of these contingency tables is shown in in Table 4.6 for animals in age class ν at i ($\nu < l$).

4.2.7 Testing for age-dependence

Because of the additional complexity of the model under age-dependence it is important to be able to test whether survival, capture, and observation rates are in fact age-dependent. One approach is to use the generalized likelihood ratio test, however a simpler test can be readily constructed in the form of contingency tables.

If we define \mathcal{S}_0 as the MSS under the null model (one-age model), and \mathcal{S}_1 as the MSS under the alternative (age-dependence model), then following Pollock (1981) and Brownie and Robson (1983) the test is based on the conditional distribution under model 0 of \mathcal{S}_1 given \mathcal{S}_0 , denoted $\text{Pr}_{H_0}(\mathcal{S}_1 | \mathcal{S}_0)$. If we let

$$N_i = \sum_{\nu=0}^l N_i^{(\nu)}$$

$$n_i = \sum_{\nu=0}^l n_i^{(\nu)}$$

Table 4.6: Example of a contingency table for the component 2 goodness-of-fit test for animals of age ν at time i ($\nu < l$).

	Member of $r_{i+1}^{(\nu)}$ not observed at i not captured at $i + 1$	Member of $r_{i+1}^{(\nu)}$ observed at i not captured at $i + 1$	Member of $r_{i+1}^{(\nu)}$ captured at $i + 1$	
Member of $M_{i+1,i+2,p,1}^{(\nu)}$	$M_{i,i+2,p,1}^{(\nu)}$	$M_{i,i+2,2,1}^{(\nu)}$	$M_{i+1,i+2,1,1}^{(\nu+1)}$	$M_{i+1,i+2,p,1}^{(\nu+1)}$
.	.	.	.	
.	.	.	.	
.	.	.	.	
Member of $M_{i+1,t,p,1}^{(\nu)}$	$M_{i,t,p,1}^{(\nu)}$	$M_{i,t,2,1}^{(\nu)}$	$M_{i+1,t,1,1}^{(\nu+1)}$	$M_{i+1,i+2,p,1}^{(\nu+1)}$
Member of $M_{i+1,i+1,p,2}^{(\nu)}$	$M_{i,i+1,p,2}^{(\nu)}$	$M_{i,i+1,2,2}^{(\nu)}$	$M_{i+1,i+1,1,2}^{(\nu+1)}$	$M_{i+1,i+1,p,2}^{(\nu+1)}$
.	.	.	.	
.	.	.	.	
.	.	.	.	
Member of $M_{i+1,t,p,2}^{(\nu)}$	$M_{i,t,p,2}^{(\nu)}$	$M_{i,t,2,2}^{(\nu)}$	$M_{i+1,t,1,2}^{(\nu+1)}$	$M_{i+1,i+2,p,2}^{(\nu+1)}$
	$r_i^{(\nu)} - O_i^{(\nu)} - M_{i,i+1,p,1}^{(\nu)}$	$R_{i,2}^{(\nu)} - M_{i,i+1,2,1}^{(\nu)}$	$R_{i+1}^{(\nu+1)}$	$r_{i+1}^{(\nu+1)}$

$$r_i = \sum_{\nu=0}^l r_i^{(\nu)}$$

$$T_i = \sum_{\nu=1}^l T_i^{(\nu+1)}$$

$$R_{i,1} = \sum_{\nu=0}^l R_{i,1}^{(\nu)}$$

$$R_{i,2} = \sum_{\nu=0}^l R_{i,2}^{(\nu)}$$

$$O_i = \sum_{\nu=0}^l O_i^{(\nu)}$$

and

$$C_i = \sum_{\nu=1}^l C_i^{(l+1)}$$

then condition on the marginal totals $R_{i,1}$, $R_{i,2}$, O_i and C_i respectively, the $R_{i,1}^{(\nu)}$, $R_{i,2}^{(\nu)}$, $O_i^{(\nu)}$ and $C_i^{(\nu)}$ are multinomial, and $\text{Pr}_{H_0}(\mathcal{S}_1|\mathcal{S}_0)$ the product of multiple hypergeometric distributions:

$$\begin{aligned} \text{Pr}_{H_0}(\mathcal{S}_1|\mathcal{S}_0) = & \prod_{i=1}^t \left\{ \frac{\prod_{\nu=0}^l \binom{N_i^{(\nu)}}{R_{i,1}^{(\nu)}}}{\binom{N_i}{R_{i,1}}} \right\} \prod_{i=1}^{t-1} \left\{ \frac{\prod_{\nu=0}^l \binom{n_i^{(\nu)}}{R_{i,2}^{(\nu)}}}{\binom{n_i}{R_{i,2}}} \right\} \\ & \times \prod_{i=1}^{t-1} \left\{ \frac{\prod_{\nu=0}^l \binom{r_i^{(\nu)}}{O_i^{(\nu)}}}{\binom{r_i}{O_i}} \right\} \prod_{i=2}^t \left\{ \frac{\prod_{\nu=1}^{l+1} \binom{T_i^{(\nu)}}{C_i^{(\nu)}}}{\binom{T_i}{C_i}} \right\}. \end{aligned} \quad (4.17)$$

Each multiple hypergeometric distribution gives rise to a contingency table and associated tests, with an example given in Table 4.7.

This technique of conditioning on \mathcal{S}_0 leads to uniformly most powerful tests (Bishop et al. 1975), provided the exact hypergeometric formulation is used. As discussed in Chapter 3, exact significance levels can be computed, but for large samples the chi-square approximation should be adequate. Conditional on the

Table 4.7: Example of a contingency table forming one component of the overall tests for age-dependence.

Age class	Released at i following capture		
	Captured or observed again	Not captured or observed again	
0	$R_{i,1}^{(0)}$	$N_i^{(0)} - R_{i,1}^{(0)}$	$N_i^{(0)}$
1	$R_{i,1}^{(1)}$	$N_i^{(1)} - R_{i,1}^{(1)}$	$N_i^{(1)}$
.	.	.	.
.	.	.	.
.	.	.	.
l	$R_{i,1}^{(l)}$	$N_i^{(l)} - R_{i,1}^{(l)}$	$N_i^{(l)}$
	$R_{i,1}$	$N_i - R_{i,1}$	N_i

marginal totals $R_{i,1}$, $R_{i,2}$, C_i , and O_i , each multiple hypergeometric term is independent of the others hence individual chi-square tests can be summed to form an overall asymptotic chi-square test of the one-age model vs the age-dependence model. This test has $l(4t - 3)$ degrees of freedom before pooling.

4.2.8 Age-dependent permanent emigration and Markov movement models

As in the single age class model, computation of the capture history probabilities is complicated by the dependence of the probability of being at risk of capture at i on whether or not the animal was at risk of capture at $i - 1$. To introduce age-dependence the parameters in the components of $Pr(h|\text{first release})$ must be indexed according to age. For example, for an animal first released at age ν the term $Pr(\text{last encounter}|\text{first release at age } \nu)$, where the last encounter is by a resighting between j and $j + 1$, is given by

$$Pr(\text{last encounter}|\text{first release at age } \nu) =$$

$$f_j^{(\nu+j-i)} \prod S_h^{(\omega_h)}$$

where

$$\omega_h = \begin{cases} \nu + h - i, & \nu + h - i < l \\ l, & \text{otherwise} \end{cases}$$

Age dependence in the parameters of

$$Pr(\text{encounter history between first and last encounter} | \text{first release at age } \nu \text{ and last encounter})$$

and

$$Pr(\text{never encountered again after last encounter} | \text{last encounter at age } \omega),$$

are introduced in a similar fashion. In particular, the $\gamma_{i,j,k}^{(\nu)}$'s are indexed according to age at last recapture and release and are defined recursively as follows.

Let

$$a_{i,j} = \begin{cases} \psi_{j-1,1,1}^{(\nu)} & j = i + 1 \\ a_{i,j-1}(1 - p_{j-1}^{(l)})\psi_{j-1,1,1}^{(l)} + b_{i,j-1}\psi_{j-1,2,1}^{(l)} & j = i + 2, \dots, t, \nu = l \\ a_{i,j-1}(1 - p_{j-1}^{(\omega_{j-1})})\psi_{j-1,1,1}^{(\omega_{j-1})} + b_{i,j-1}\psi_{j-1,2,1}^{(\omega_{j-1})} & j = i + 2, \dots, t, \\ & \nu = 0, 1, \dots, l - 1 \end{cases}$$

and

$$b_{i,j} = \begin{cases} (1 - \psi_{j-1,1,1}^{(\nu)}) & j = i + 1 \\ a_{i,j-1}(1 - p_{j-1}^{(l)})(1 - \psi_{j-1,1,1}^{(l)}) + b_{i,j-1}(1 - \psi_{j-1,2,1}^{(l)}) & j = i + 2, \dots, t; \nu = l \\ a_{i,j-1}(1 - p_{j-1}^{(\omega_{j-1})})(1 - \psi_{j-1,1,1}^{(\omega_{j-1})}) + b_{i,j-1}(1 - \psi_{j-1,2,1}^{(\omega_{j-1})}) & j = i + 2, \dots, t, \\ & \nu = 0, 1, \dots, l - 1 \end{cases}$$

then

$$\gamma_{i,j,k}^{(\nu)} = \begin{cases} a_{i,j} & k = 1 \\ a_{i,j}(1 - p_j^{(l)}) + b_{i,j} & k = 2, \nu = l \\ a_{i,j}(1 - p_j^{(\omega_j)}) + b_{i,j} & k = 2, \nu = 0, \dots, l - 1 \end{cases}$$

In the permanent emigration model we make the constraint $\psi_{i,2,1}^{(\nu)} = 0$, and as in the single age class model we let $F_i^{(\nu)} = \psi_{i,1,1}^{(\nu)}$. This leads to the explicit form for $\gamma_{i,j,1}^{(\nu)}$ as

$$\gamma_{i,j,1}^{(\nu)} = F_{j-1}^{(\omega_{j-1})} \prod_{h=i}^{j-2} F_h^{(\omega_h)} (1 - p_{(h+1)}^{(\omega_{h+1})}).$$

For both permanent and Markov emigration, the observation component of the model is expressed in terms of the $\gamma_{i,j,2}^{(\nu)}$'s hence closed-form maximum likelihood estimates do not appear to exist and numerical procedures must be used to compute the maximum-likelihood estimates. At time t $\gamma_{i,t,2}^{(\nu)}$ has the form

$$\begin{aligned} \kappa_1 F_{t-1}^{(\nu)} (1 - p_t^{(\omega)}) + \kappa_1 (1 - F_{t-1}^{(\nu)}) + \kappa_2 \\ = \kappa_1 (1 - F_{t-1}^{(\nu)} p_t^{(\omega)}) \end{aligned}$$

where

$$v = \begin{cases} \nu + t - i - 1, & \nu + t - i - 1 < l \\ l & \text{otherwise} \end{cases}$$

and

$$\omega = v + 1.$$

hence $F_{t-1}^{(\nu)}$ only appears in the product $F_{t-1}^{(\nu)} p_t^{(\omega)}$ ($\omega = \nu + 1, \nu = 0, \dots, l - 1; \omega = l, \nu = l$) and these parameters cannot be separately estimated. Unlike the random emigration model we can obtain estimates of $F_i^{(\nu)}$, ($i=1, \dots, t - 2$). Also, $p_i^{(0)}$ does not appear in the model and cannot be estimated for any i . Thus, in addition to $F_{t-1}^{(\nu)} p_t^{(\omega)}$ we can estimate $p_2^{(\nu)}, \dots, p_{t-1}^{(\nu)}$ ($\nu = 1, \dots, l$), $F_1^{(\nu)}, \dots, F_{t-2}^{(\nu)}$ ($\nu = 0, \dots, l$), $f_1^{(\nu)}, \dots, f_t^{(\nu)}$ ($\nu = 0, \dots, l$), $\theta_1^{(\nu)}, \dots, \theta_{t-1}^{(\nu)}$ ($\nu = 0, \dots, l$), and $S_1^{(\nu)}, \dots, S_{t-1}^{(\nu)}$ ($\nu = 0, \dots, l$).

In the stationary Markov movement model we make the constraint $\psi_{1,1,1}^{(\nu)} = \psi_{2,1,1}^{(\nu)} = \dots = \psi_{t-1,1,1}^{(\nu)} = \mu^{(\nu)}$ and $\psi_{1,2,1}^{(\nu)} = \psi_{2,3,1}^{(\nu)} = \dots = \psi_{t-1,2,1}^{(\nu)} = \lambda^{(\nu)}$ (i.e. movement probabilities are constant through time within each age group). As with the full model, the $\pi_{i,j,k}^{(\nu)}$ are expressed in terms of $\gamma_{i,j,k}^{(\nu)}$'s and solutions do not appear to exist in closed-form. The identifiable parameters are $p_2^{(\nu)}, \dots, p_{t-1}^{(\nu)}$ ($\nu = 1, \dots, l$), $f_1^{(\nu)}, \dots, f_t^{(\nu)}$ ($\nu = 0, \dots, l$), $\theta_1^{(\nu)}, \dots, \theta_{t-1}^{(\nu)}$ ($\nu = 0, \dots, l$), and $S_1^{(\nu)}, \dots, S_{t-1}^{(\nu)}$ ($\nu = 0, \dots, l$), $\mu^{(\nu)}$ ($\nu = 0, \dots, l$), and $\lambda^{(\nu)}$ ($\nu = 0, \dots, l$).

4.3 Marking Effect Models

Marking effect models are a special case of multi-strata models where stratification occurs as a consequence of the experiment, rather than from inherent characteristics of the animal. In the sections discussing goodness-of-fit for the single age class and the age-dependent models we noted that, among other things, one of the components tests for a short-term dependence of capture at i on the probability of subsequently being captured or observed. In this section we show how the model can be generalized to allow such a short-term effect. Robson (1969), Pollock (1975) and Pollock et al. (1991) discuss short-term marking effect models in the context of the single age class case without ancillary observations. Brownie and Robson (1983) discuss marking effects in their tag-resight model).

In the short-term marking effect model we follow Pollock (1975) and Brownie and Robson (1983) in assuming that capture and tagging at i affect survival to, and capture at $i + 1$, and observation in the interval $i, i + 1$. Subsequent recaptures do not influence survival or capture probabilities. As an example, many fish tags pierce the body of the fish. Such physical interference may influence the initial survival probability, and if unpleasant may reduce the subsequent recapture probability. However after a short recovery period it may be reasonable to assume that marked animals have the same survival and recapture probabilities as unmarked animals.

4.3.1 Notation and general model under random emigration

We adopt the same notation as that used for the age-dependent model but using just two classes of animals and assigning a different meaning to the superscripts.

Release cohort $C_{i,k}^{(0)}$ is that group of animals released at i following encounter by method k that have never been captured before i - i.e. the newly marked animals. Release cohort $C_{i,k}^{(1)}$ is that group of animals released at i following encounter by method k that have been captured at least once before i . As in previous models we use T_i to denote animals marked before i that are captured or observed at or after

i , but we partition this statistic into $T_i^{(1)}$, those members of T_i that were members of class 0 at $i - 1$ (i.e. just before capture period i they have been captured just once), and $T_i^{(2)}$, those members of T_i that were members of class 1 at $i - 1$ (i.e. just before i they have been captured at least twice). Hence, $C_i^{(\nu)}$ $\nu = 1, 2$ is those members of $T_i^{(\nu)}$ captured at i , and $Z_i^{(\nu)} = T_i^{(\nu)} - C_i^{(\nu)}$. Note that the index ν for $T_i^{(\nu)}$, $Z_i^{(\nu)}$, and $C_i^{(\nu)}$ takes the value 1 or 2. The indexing is arbitrary and is used to simplify the application of results developed under the age-dependence model to the marking effect case. In effect we are indexing these three statistics by the number of known captures immediately before i , rather than the mark class occupied at i . In contrast, r_i is partitioned according to class membership at i , hence $O_i^{(\nu)}$ is those animals in class ν at i that were observed in the interval $i, i + 1$. As in the 2-age model, $r_i^{(0)} = R_{i,1}^{(0)}$ and $r_i^{(1)} = R_{i,1}^{(1)} + Z_i^{(1)} + Z_i^{(2)}$.

All animals enter the study as members of a $C_{i,1}^{(0)}$ cohort. If the animal is next encountered by capture at j , it is transferred to cohort $C_{j,1}^{(1)}$. Animals next encountered by observation in the interval $j, j + 1$, ($j \neq i$) are transferred to release cohort $C_j^{(1)}$. If, however, they are observed in the interval $i, i + 1$ they are transferred to release cohort $C_i^{(0)}$ - i.e. they are still classed as being newly marked.

Consider our fictitious animal from Chapter 3 with capture history 05013. This animal was initially released as a member of $C_{2,1}^{(0)}$. Because the animal was observed in the interval 2,3, it contributed to $M_{i,i,1,2}^{(0)}$, then was re-released as a member of $C_{2,2}^{(0)}$ because it was still classified as "newly marked". Following this release the animal was next encountered by capture at time 4, hence contributed to $M_{2,4,2,1}^{(0)}$, then was re-released as a member of $C_{4,1}^{(1)}$. The final encounter of this animal via observation between times 5 and 6 means it contributed to $M_{4,1,1,2}^{(1)}$.

Note that we are unable to capture marked animals in mark class 1 at time 1 and hence there are no members of $C_1^{(1)}$. This means we cannot estimate the parameters $S_1^{(1)}$, $p_2^{*(1)}$, $\theta_1^{(1)}$, or $f_1^{(1)}$.

Comparison of the data and probabilities structure shows that the two-age model (Tables 4.1 through 4.4) and the marking effect model (Tables 4.8 through 4.11) are identical in structure but with the exception that there is no release of

class 1 animals in year 1. Also, $p_i^{*(0)}$ is defined differently in the two models.

Using as an example animals released at time 1 then next encountered by capture at time 3, we find using (4.8) that under a 2-age model

$$\pi_{1,3,1,1}^{(0)} = S_1^{(0)}(1 - F_1^{(0)}p_2^{(1)})S_2^{(1)}F_2^{(1)}p_2^{(1)} .$$

Under a temporary marking effect, the probability is identical with the exception that because the marking effect in capture probability induced on initial capture at i is expressed in the capture probability at $i + 1$ the correct capture probability at time 2 is $p_2^{(0)}$ and hence under temporary marking effect

$$\pi_{1,3,1,1}^{(0)} = S_1^{(0)}(1 - F_1^{(0)}p_2^{(0)})S_2^{(1)}F_2^{(1)}p_2^{(1)} .$$

However, in both cases the capture probabilities and emigration probabilities are not separately identifiable and we can re-write $\pi_{1,3,1,1}^{(0)}$ as

$$\pi_{1,3,1,1}^{(0)} = S_1^{(0)}(1 - p_2^{*(0)})S_2^{(1)}p_2^{*(1)} ,$$

and similarly

$$\pi_{1,3,1,1}^{(1)} = S_1^{(1)}(1 - p_2^{*(1)})S_2^{(1)}p_2^{*(1)} ,$$

where $p_i^{*(\nu)} = F_{i-1}^{(\nu)}p_i^{(1)}$ in the 2-age model and $p_i^{*(\nu)} = F_{i-1}^{(\nu)}p_i^{(\nu)}$ in the temporary marking effect model.

The structural similarity of the 2-age and the temporary marking effect models means that we can easily derive the marking effect model from the age dependence model by constraining $S_1^{(1)}$, $\theta_1^{(1)}$, $f_1^{(1)}$, and $p_2^{*(1)}$ out of the two age model. Note that we also have no observations of $R_{1,1}^{(1)}$, $R_{1,2}^{(1)}$, $O_1^{(1)}$, or $C_2^{(2)}$ thus the reduction in the dimension of the MSS equals the reduction in the number of parameters. Therefore the number of maximum likelihood equations equals the number of parameters to be estimated hence the MLE's under random emigration exist in closed-form. Moreover, the identical data and probability structures mean that the MLE's are identical to the two-age model estimators but making the appropriate substitution of statistics computed under the temporary marking effect model.

Table 4.8: Probability structure under random emigration for mark class 0 animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$.

A. Last released following capture					
Cohort	Next encountered by capture				
	$j = 2$	3	...	t	
$i = 1$	$S_1^{(0)} \theta_1^{(0)} p_2^{*(0)}$	$S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$ $\times S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times S_1^{(0)} \theta_1^{(0)} q_2^{*(0)} \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	
2	-	$S_2^{(0)} \theta_2^{(0)} p_3^{*(0)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times S_2^{(0)} \theta_2^{(0)} q_3^{*(0)} \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	
.	
.	
$t - 1$	-	-	...	$S_{t-1}^{(0)} \theta_{t-1}^{(0)} p_t^{*(0)}$	
Next encountered by observation					
Cohort	$j = 1$	2	...	$t - 1$	t
	$f_1^{(0)}$	$f_2^{(1)} S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$...	$f_{t-1}^{(1)} S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$f_t^{(1)} S_1^{(0)} \theta_1^{(0)} q_2^{*(0)}$ $\times \prod_{h=2}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$f_2^{(0)}$...	$f_{t-1}^{(1)} S_2^{(0)} \theta_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$f_t^{(1)} S_2^{(0)} \theta_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
.
.
$t - 1$	-	-	...	$f_{t-1}^{(0)}$	$f_t^{(1)} S_{t-1}^{(0)} \theta_{t-1}^{(0)} q_t^{*(0)}$
t	-	-	...	-	$f_t^{(0)}$

Table 4.9: Probability structure under random emigration for mark class 0 animals last released following observation (in the first resighting interval) in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$, and a temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1 - \theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}}$.

B. Last released following observation				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} p_2^{*(0)}$	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} q_2^{*(0)}$ $\times S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$\delta_1^{(0)} \theta_1^{(0)} S_1^{(0)} p_1^{*(0)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} q_t^{*(1)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	$\delta_2^{(0)} \theta_2^{(0)} S_2^{(0)} p_3^{*(0)}$...	$\delta_2^{(0)} \theta_2^{(0)} S_2^{(0)} q_2^{*(0)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$\delta_{t-1}^{(0)} \theta_{t-1}^{(0)} S_{t-1}^{(0)} p_t^{*(0)}$
Next encountered by observation				
Cohort	$j = 2$...	$t - 1$	t
	$i = 1$	$\delta_1^{(0)} \theta_1^{(0)} f_2^{(1)} S_1^{(0)} q_2^{*(0)}$...	$\delta_1^{(0)} \theta_1^{(0)} f_{t-1}^{(1)} S_1^{(0)} q_2^{*(0)}$ $\times \prod_{h=2}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$
2	-	...	$\delta_2^{(0)} \theta_2^{(0)} f_{t-1}^{(1)} S_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_2^{(0)} \theta_2^{(0)} f_t^{(1)} S_2^{(0)} q_3^{*(0)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	...	-	$\delta_{t-1}^{(0)} \theta_{t-1}^{(0)} f_t^{(0)} S_{t-1}^{(0)} q_t^{*(0)}$

Table 4.10: Probability structure under random emigration for mark class 1 animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$.

A. Last released following capture					
Cohort	Next encountered by capture				
	$j = 2$	3	...	t	
$i = 1$	-	...	-		
2	-	$S_2^{(1)} \theta_2^{(1)} p_3^{*(1)}$...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} q_t^{*(1)}$ $\times S_2^{(1)} \theta_2^{(1)} q_3^{*(1)} \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	
	
	
	
$t - 1$	-	-	...	$S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$	
Next encountered by observation					
Cohort	$j = 1$	2	...	$t - 1$	t
	<hr/>				
$i = 1$	-	-	...	-	-
2	-	$f_2^{(1)}$...	$f_{t-1}^{(1)} S_2^{(1)} \theta_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$f_t^{(1)} S_2^{(1)} \theta_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$f_{t-1}^{(1)}$	$f_t^{(1)} S_{t-1}^{(1)} \theta_{t-1}^{(1)} q_t^{*(1)}$
t	-	-	...	-	$f_t^{(1)}$

Table 4.11: Probability structure under random emigration for mark class 1 animals last released following observation in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t + 1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1 - \theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} p_i^{*(\nu)}}$.

B. Last released following observation				
Cohort	Next encountered by capture			
	$j = 2$	3	...	t
$i = 1$	-	-	...	-
2	-	$\delta_2^{(1)} \theta_2^{(1)} S_2^{(1)} p_3^{*(1)}$...	$\delta_2^{(1)} \theta_2^{(1)} S_2^{(1)} q_2^{*(1)}$ $\times S_{t-1}^{(1)} \theta_{t-1}^{(1)} p_t^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	-	...	$\delta_{t-1}^{(1)} \theta_{t-1}^{(1)} S_{t-1}^{(1)} p_t^{*(1)}$
Next encountered by observation				
Cohort	$j = 2$...	$t - 1$	t
	$j = 2$...	$t - 1$	t
$i = 1$	-	...	-	-
2	-	...	$\delta_2^{(1)} \theta_2^{(1)} f_{t-1}^{(1)} S_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-2} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$	$\delta_2^{(1)} \theta_2^{(1)} f_t^{(1)} S_2^{(1)} q_3^{*(1)}$ $\times \prod_{h=3}^{t-1} S_h^{(1)} \theta_h^{(1)} q_{h+1}^{*(1)}$

$t - 1$	-	...	-	$\delta_{t-1}^{(1)} \theta_{t-1}^{(1)} f_t S_{t-1}^{(1)} q_t^{*(1)}$

Thus we can substitute the statistics $R_i^{(\nu)}$, $C_i^{(\nu)}$, $T_i^{(\nu)}$, $Z_i^{(\nu)}$, and $r_i^{(\nu)}$, as defined under the tag-dependence model, directly into equations (4.12) through (4.15) and similarly for the asymptotic variances and covariances. We also construct goodness-of-fit test contingency tables in a similar way with the only restriction that components for class 1 animals are only defined over $i = 2, \dots, t$.

4.3.2 Test for marking effect

If we define \mathcal{S}_0 as the MSS under the null model (one-age model), and \mathcal{S}_1 as the MSS under the alternative (marking effect model), and if

$$N_i = N_i^{(0)} + N_i^{(1)} \quad i = 2, \dots, t$$

$$n_i = n_i^{(0)} + n_i^{(1)} \quad i = 2, \dots, t - 1$$

$$r_i = r_i^{(0)} + r_i^{(1)} \quad i = 2, \dots, t - 1$$

$$T_i = T_i^{(1)} + T_i^{(2)} \quad i = 3, \dots, t$$

$$R_{i,1} = R_{i,1}^{(0)} + R_{i,1}^{(1)} \quad i = 2, \dots, t$$

$$R_{i,2} = R_{i,2}^{(0)} + R_{i,2}^{(1)} \quad i = 2, \dots, t - 1$$

$$O_i = O_i^{(0)} + O_i^{(1)} \quad i = 2, \dots, t - 1$$

and

$$C_i = C_i^{(1)} + C_i^{(2)} \quad i = 3, \dots, t$$

then following (4.17)

$$\Pr_{H_0}(\mathcal{S}_1 | \mathcal{S}_0) =$$

$$\prod_{i=2}^t \left\{ \frac{\begin{pmatrix} N_i^{(0)} \\ R_{i,1}^{(0)} \end{pmatrix} \begin{pmatrix} N_i^{(1)} \\ R_{i,1}^{(1)} \end{pmatrix}}{\begin{pmatrix} N_i \\ R_{i,1} \end{pmatrix}} \right\} \prod_{i=2}^{t-1} \left\{ \frac{\begin{pmatrix} n_i^{(0)} \\ R_{i,2}^{(0)} \end{pmatrix} \begin{pmatrix} n_i^{(1)} \\ R_{i,2}^{(1)} \end{pmatrix}}{\begin{pmatrix} n_i \\ R_{i,2} \end{pmatrix}} \right\} \\ \times \prod_{i=2}^{t-1} \left\{ \frac{\begin{pmatrix} r_i^{(0)} \\ O_i^{(0)} \end{pmatrix} \begin{pmatrix} r_i^{(1)} \\ O_i^{(1)} \end{pmatrix}}{\begin{pmatrix} r_i \\ O_i \end{pmatrix}} \right\} \prod_{i=3}^t \left\{ \frac{\begin{pmatrix} T_i^{(1)} \\ C_i^{(1)} \end{pmatrix} \begin{pmatrix} T_i^{(2)} \\ C_i^{(2)} \end{pmatrix}}{\begin{pmatrix} T_i \\ C_i \end{pmatrix}} \right\}.$$

giving rise to $(4t - 7)$ conditionally independent contingency tables before pooling, each contributing one degree of freedom.

4.4 Joint Age-Dependence and Marking Effect Model

The structural equivalence of the probability structures under the 2-age model and the short-term marking effect model means that it is important that the experimenter consider whether either effect is likely to be present. The marked animals in the population immediately before sampling at i are all survivors from previous marking occasions. In contrast, the unmarked segment of the population will contain some survivors from previous capture occasions, but in addition will include animals born into the population between $i - 1$ and i . Thus, newly marked animals at i will tend to be younger on average than previously marked animals. In this case, a test for marking effect may indicate that a marking effect is present when in fact the cause is an age-effect. Alternatively, the presence of an apparent age-effect may occur as a consequence of an unmodelled marking effect.

It is possible to further generalize the model of the previous section to allow simultaneous age-dependence and marking effect. We use a similar notation to the age dependent model, but where the superscript (ν) is replaced by the superscript (ν, k) , and $k = 0$ for animals captured for the first time at i and $k = 1$ if the animal

has been previously captured. As with the temporary marking effect model the statistics $T_i^{(\nu,k)}$, $Z_i^{(\nu,k)}$, and $C_i^{(\nu,k)}$ are indexed by $k = 1$ or $k = 2$, indicating the known number of captures immediately before time i (i.e. one or at least two). To the assumptions of the age-dependent model we add the assumptions of the marking effect model discussed in the previous section.

The data-structure and model structure are identical to the age-dependence model but with the addition that cohorts can be split according to whether or not they were first captures or recaptures at i . But note that age 0 animals can only ever appear in mark class 0 (i.e. an age 0 animal at i cannot have been captured before i).

In this section we restrict our discussion to the joint age- and marking effect model under random emigration as this leads to explicit estimators and tests. The general algebraic structure of the model under permanent or Markov emigration can be derived as a straight-forward extension of the algebraic structure given in section 4.2.8.

4.4.1 The probability structure under random emigration

As in the age-dependence and the marking effect models we compute the m-array cell probabilities making use of our knowledge of the events that must have taken place for the animal to contribute to a particular $M_{i,j,m,n}^{(\nu,k)}$. For example, we know that animals contributing to $M_{1,3,1,1}^{(0,0)}$ must have:

1. Survived from time 1 to 2 as members of age class 0 and mark class 0, an event which happened with probability $S_1^{(0,0)}$.
2. Given they were alive at 2 we know the animals were not observed between 1 and 2 an event which occurred with probability $\theta_2^{(0,0)}$.
3. Given they were alive at 2 we know that they did not get captured at 2. The probability of this event is one minus the probability of the complementary event “remained at risk of capture between 1 and 2 and captured at 2” which has probability $F_1^{(0,0)} p_2^{(1,0)}$ (remembering that the temporary effect of capture

at $i - 1$ on the capture probability persists until immediately after capture time i).

4. Given they were alive and not captured at 2 we know they then survived from 2 to 3 as members of age class 1 and mark class 1, were not observed between 1 and 2, and became at risk of capture at 3. The joint probability of these events is $S_2^{(1,1)}\theta_2^{(1,1)}F_2^{(1,1)}$.
5. Finally, given they were alive at 3 we know they were also captured at 3, now as members of age-class 2 and mark class 1. This event has probability $p_3^{(2,1)}$.

Thus,

$$\begin{aligned}\pi_{1,3,1,2}^{(0,0)} &= S_1^{(0,0)}\theta_1^{(0,0)}(1 - F_1^{(0,0)}p_2^{(1,0)})S_2^{(1,1)}\theta_2^{(1,1)}F_2^{(1,1)}p_3^{(2,1)} \\ &= S_1^{(0,0)}\theta_1^{(0,0)}(1 - p_2^{*(1,0)})S_2^{(1,1)}\theta_2^{(1,1)}p_3^{*(2,1)} \\ &= \alpha_{2,1}^{(1,1)}\beta_1^{(0,0)}\beta_2^{(1,1)}\end{aligned}$$

The cell probability for $M_{1,3,2,2}^{(0,0)}$ is computed in an identical manner with the exception that the survival probability from 1 to 2 is now conditional on the fact that the animals were observed. Hence

$$\pi_{1,3,2,2}^{(0,0)} = \alpha_{2,1}^{(1,1)}\delta_1^{(0,0)}\beta_1^{(0,0)}\beta_2^{(1,1)},$$

where

$$\delta_i^{(\nu,k)} = \frac{1 - \theta_i^{(\nu,k)}}{\theta_i^{(\nu,k)} f_i^{(\nu,k)} \rho_i^{(\nu,k)}}.$$

4.4.2 The likelihood under random emigration

Let

$$\alpha_{i,h}^{(\nu,k)} = \begin{cases} S_i^{(\nu,k)}\theta_i^{(\nu,k)}F_i^{(\nu,k)}p_{i+1}^{(\omega,k)} & h = 1 \\ f_i^{(\nu,k)} & h = 2 \end{cases}$$

$$\beta_i^{(\nu)} = S_i^{(\nu,k)}\theta_i^{(\nu,k)}(1 - F_i^{(\nu,k)}p_{i+1}^{(\omega,k)}) \quad (4.18)$$

and

$$\delta_i^{(\nu,k)} = \frac{1 - \theta_i^{(\nu,k)}}{\theta_i^{(\nu,k)} f_i^{(\nu,k)} \rho_i^{(\nu,k)}}, \quad (4.19)$$

$$\lambda_{i,1}^{(\nu,k)} = \begin{cases} \alpha_{i,2}^{(\nu,k)} & i = t \\ (\alpha_{i,1}^{(\nu,k)} + \alpha_{i,2}^{(\nu,k)}) + \beta_i^{(\nu,k)} \lambda_{i+1,1}^{(\omega,1)} & i = 1, \dots, t-1 \end{cases},$$

$$\lambda_{i,2}^{(\nu,k)} = \delta_i^{(\nu,k)} (\lambda_{i,1}^{(\nu,k)} - \alpha_{i,2}^{(\nu,k)}),$$

$$\tau_{i+1,1}^{(\nu+1,k+1)} = \frac{\alpha_{i,1}^{(\nu,k)}}{\lambda_{i,1}^{(\nu,k)} - \alpha_{i,2}^{(\nu,k)}},$$

and

$$\tau_{i,2}^{(\nu,k)} = \frac{\alpha_{i,2}^{(\nu,k)}}{\lambda_{i,1}^{(\nu,k)}},$$

where ω is defined by (4.1). Define the statistics

$$Z_i^{(\nu+1,1)} = R_{i-1,1}^{(\nu,0)} + R_{i-1,2}^{(\nu,0)} - C_i^{(\nu+1,1)} - O_{i-1}^{(\nu,0)} \quad i = 2, \dots, t$$

$$Z_i^{(\nu,2)} = \sum_{k=1}^2 Z_{i-1}^{(\nu-1,k)} + R_{i-1,1}^{(\nu-1,1)} + R_{i-1,2}^{(\nu-1,1)} - C_i^{(\nu,2)} - O_{i-1}^{(\nu-1,1)} \quad i = 3, \dots, t; \nu = 3, \dots, l$$

$$Z_i^{(l+1,2)} = \left\{ \sum_{k=1}^2 Z_{i-1}^{(l+1,k)} + Z_{i-1}^{(l,k)} \right\} + R_{i-1,1}^{(l,1)} + R_{i-1,2}^{(l,1)} - C_i^{(l+1,2)} - O_{i-1}^{(l)} \quad i = 2, \dots, t$$

$$T_i^{(\nu,k)} = Z_i^{(\nu,k)} + C_i^{(\nu,k)} \quad i = 2, \dots, t; \nu = 1, \dots, l+1.$$

and

$$\tau_i^{(\nu,k)} = \begin{cases} R_{i,1}^{(\nu,0)} & k = 0 \\ \sum_{k=1}^2 Z_i^{(\nu,k)} + R_{i,1}^{(\nu,1)} & \nu = 1, \dots, l-1, k = 1 \\ \sum_{h=l}^{l+1} \sum_{k=0}^1 Z_i^{(h,k)} + R_{i,1}^{(l)} & \nu = l, k = 1 \end{cases}.$$

Also, define the partial column totals

$$M_{1,j,p,k}^{(\nu,0)} = M_{1,j,1,k}^{(\nu,0)},$$

$$M_{i+1,j,p,n}^{(l,1)} = \begin{cases} M_{2,j,1,n}^{(l,1)} + \sum_{h=l-1}^l M_{1,j,1,n}^{(h,0)} + M_{1,j,2,n}^{(h,0)} & i = 1 \\ M_{i+1,j,1,n}^{(l,1)} + \sum_{h=l-1}^l \sum_{k=0}^1 (M_{i,j,p,n}^{(h,k)} + M_{i,j,2,n}^{(h,k)}) & i = 2, \dots, t-1 \end{cases},$$

$$M_{i+1,j,p,n}^{(\nu,1)} = \begin{cases} M_{2,j,1,n}^{(\nu,1)} + M_{1,j,1,n}^{(\nu-1,0)} + M_{1,j,2,n}^{(\nu-1,0)} & i = 1 \\ M_{i+1,j,1,n}^{(\nu,1)} + \sum_{k=0}^1 M_{i,j,p,n}^{(\nu-1,k)} + M_{i,j,2,n}^{(\nu-1,k)} & i = 2, \dots, t-1 \end{cases}$$

and

$$M_{i,j,p,n}^{(\nu,0)} = M_{i,j,1,n}^{(\nu,0)}$$

Factorization of the likelihood into $Pr(\text{MSS})$ and $Pr(\text{Data}|\text{MSS})$ terms under random emigration is carried out as for the one-age and l -age models making use of the factorizations:

$$\begin{aligned} Pr(M_{i,i+1,p,1}^{(\nu,k)}, \dots, M_{i,i,p,1}^{(\nu,k)}, M_{i,i,p,2}^{(\nu,k)}, \dots, M_{i,i,p,2}^{(\nu,k)} | r_i^{(\nu)}) = \\ Pr(M_{i,i,p,2}^{(\nu,k)} | r_i^{(\nu,k)}) Pr(M_{i,i+1,p,1}^{(\nu,k)} | r_i^{(\nu,k)} - M_{i,i,p,2}^{(\nu,k)}) \\ \times Pr(M_{i,i+2,p,1}^{(\nu,k)}, \dots, M_{i,i,p,1}^{(\nu,k)}, M_{i,i+1,p,2}^{(\nu,k)}, \dots, m_{i,i,p,2}^{(\nu,k)} | r_i^{(\nu,k)} - M_{i,i,p,2}^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)}) \end{aligned}$$

and

$$\begin{aligned} Pr(M_{i,i+1,2,1}^{(\nu,k)}, \dots, M_{i,i,2,1}^{(\nu,k)}, M_{i,i+1,2,2}^{(\nu,k)}, \dots, M_{i,i,2,2}^{(\nu,k)} | R_{i,2}^{(\nu,k)}) = \\ Pr(M_{i,i+1,2,1}^{(\nu,k)} | R_{i,2}^{(\nu,k)}) \\ \times Pr(M_{i,i+2,2,1}^{(\nu,k)}, \dots, M_{i,i,2,1}^{(\nu,k)}, M_{i,i+1,2,2}^{(\nu,k)}, \dots, M_{i,i,2,2}^{(\nu,k)} | R_{i,2}^{(\nu,k)} - M_{i,i+1,2,1}^{(\nu,k)}) \end{aligned}$$

Note that

1.

$$\begin{aligned} Pr(M_{i,i,p,2}^{(\nu,k)} | r_i^{(\nu,k)}) &= Pr(O_i^{(\nu,k)} | r_i^{(\nu,k)}) \\ &= \binom{r_i^{(\nu,k)}}{O_i^{(\nu,k)}} (\tau_{i,2}^{(\nu,k)})^{O_i^{(\nu,k)}} (1 - \tau_{i,2}^{(\nu,k)})^{r_i^{(\nu,k)} - O_i^{(\nu,k)}}, \end{aligned}$$

2.

$$\begin{aligned} Pr(M_{i,i+1,p,1}^{(\nu,k)} | r_i^{(\nu,k)} - M_{i,i,p,2}^{(\nu,k)}) = \\ \binom{r_i^{(\nu,k)} - O_i^{(\nu,k)}}{M_{i,i+1,p,1}^{(\nu,k)}} (\tau_{i+1,1}^{(\nu+1,k+1)})^{M_{i,i+1,p,1}^{(\nu,k)}} (1 - \tau_{i+1,1}^{(\nu+1,k+1)})^{r_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)}}, \end{aligned}$$

and

$$Pr(M_{i,i+1,2,1}^{(\nu,k)} | R_{i,2}^{(\nu,k)}) = \begin{pmatrix} R_{i,2}^{(\nu,k)} \\ M_{i,i+1,2,1}^{(\nu,k)} \end{pmatrix} (\tau_{i+1,1}^{(\nu+1,k+1)})^{M_{i,i+1,2,1}^{(\nu,k)}} \\ \times (1 - \tau_i^{(\nu+1,k+1)})^{R_{i,2}^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)}},$$

hence $(M_{i,i+1,p,1}^{(\nu,k)} | \tau_i^{(\nu,k)} - M_{i,i,p,2}^{(\nu,k)})$ and $(M_{i,i+1,2,1}^{(\nu,k)} | R_{i,2}^{(\nu,k)})$ can be pooled to form a

$$\frac{\begin{pmatrix} \tau_i^{(\nu,k)} - O_i^{(\nu,k)} \\ M_{i,i+1,p,1}^{(\nu,k)} \end{pmatrix} \begin{pmatrix} R_{i,2}^{(\nu,k)} \\ M_{i,i+1,2,1}^{(\nu,k)} \end{pmatrix}}{\begin{pmatrix} T_{i+1}^{(\nu+1,k+1)} \\ C_{i+1}^{(\nu+1,k+1)} \end{pmatrix}} (\tau_{i+1,1}^{(\nu+1,k+1)})^{M_{i,i+1,p,1}^{(\nu,k)}} \\ \times (1 - \tau_i^{(\nu+1,k+1)})^{\tau_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)}},$$

term. In addition, common conditional multinomial terms for the remaining components in the above factorization mean that we can pool observations from

3.

$$(M_{1,3,p,1}^{(\nu,0)}, \dots, M_{1,t,p,1}^{(\nu,0)}, M_{1,2,p,2}^{(\nu,0)}, \dots, M_{1,t,p,2}^{(\nu,0)} | \tau_1^{(\nu,0)} - O_1^{(\nu,0)} - M_{1,2,p,1}^{(\nu,0)}), \\ (M_{1,3,2,1}^{(\nu,0)}, \dots, M_{1,t,2,1}^{(\nu,0)}, M_{1,2,2,2}^{(\nu,0)}, \dots, M_{1,t,2,2}^{(\nu,0)} | R_{1,2}^{(\nu,0)} - M_{1,2,2,1}^{(\nu,0)}),$$

and

$$(M_{2,3,1,1}^{(\nu+1,1)}, \dots, M_{2,t,1,1}^{(\nu+1,1)}, M_{2,2,1,2}^{(\nu+1,1)}, \dots, M_{2,t,1,2}^{(\nu+1,1)} | R_{2,1}^{(\nu+1,1)}),$$

for $\nu = 0, \dots, l-2$ to form a

$$\prod_{\nu=0}^{l-2} \left\{ \frac{\begin{pmatrix} \tau_1^{(\nu,0)} - O_1^{(\nu,0)} - M_{1,2,p,1}^{(\nu,0)} \\ [M_{1,j,p,1}^{(\nu,0)}]_{j=3}^t [M_{1,j,p,2}^{(\nu,0)}]_{j=2}^t \end{pmatrix} \begin{pmatrix} R_{1,2}^{(\nu,0)} - M_{1,2,2,1}^{(\nu,0)} \\ [M_{1,j,2,1}^{(\nu,0)}]_{j=3}^t [M_{1,j,2,2}^{(\nu,0)}]_{j=2}^t \end{pmatrix}}{\begin{pmatrix} \tau_2^{(\nu+1,1)} \\ [M_{2,j,p,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,p,2}^{(\nu+1,1)}]_{j=2}^t \end{pmatrix}} \right. \\ \left. \times \begin{pmatrix} R_{2,1}^{(\nu+1,1)} \\ [M_{2,j,1,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,1,2}^{(\nu+1,1)}]_{j=2}^t \end{pmatrix} \right\}$$

term,

4.

$$\begin{aligned} & (M_{1,3,p,1}^{(h,0)}, \dots, M_{1,t,p,1}^{(h,0)}, M_{1,2,p,2}^{(h,0)}, \dots, M_{1,t,p,2}^{(h,0)} | r_1^{(h,0)} - O_1^{(h,0)} - M_{1,2,p,1}^{(h,0)}), \\ & (M_{1,3,2,1}^{(h,0)}, \dots, M_{1,t,2,1}^{(h,0)}, M_{1,2,2,2}^{(h,0)}, \dots, M_{1,t,2,2}^{(h,0)} | R_{1,2}^{(h,0)} - M_{1,2,2,1}^{(h,0)}), \end{aligned}$$

and

$$(M_{2,3,1,1}^{(l,1)}, \dots, M_{2,t,1,1}^{(l,1)}, M_{2,2,1,2}^{(l,1)}, \dots, M_{2,t,1,2}^{(l,1)} | R_{2,1}^{(l,1)}),$$

for $(h = l - 1, l)$ to form a

$$\begin{aligned} & \frac{\prod_{h=l-1}^l \left(\begin{array}{c} r_1^{(h,0)} - O_1^{(h,0)} - M_{1,2,p,1}^{(h,0)} \\ [M_{1,j,p,1}^{(h,0)}]_{j=3}^t [M_{1,j,p,2}^{(h,0)}]_{j=2}^t \end{array} \right) \left(\begin{array}{c} R_{1,2}^{(h,0)} - M_{1,2,2,1}^{(h,0)} \\ [M_{1,j,2,1}^{(h,0)}]_{j=3}^t [M_{1,j,2,2}^{(h,0)}]_{j=2}^t \end{array} \right)}{\left(\begin{array}{c} r_2^{(l,1)} \\ [M_{2,j,p,1}^{(l,1)}]_{j=3}^t [M_{2,j,p,2}^{(l,1)}]_{j=2}^t \end{array} \right)} \\ & \quad \times \left(\begin{array}{c} R_{2,1}^{(l,1)} \\ [M_{2,j,1,1}^{(l,1)}]_{j=3}^t [M_{2,j,1,2}^{(l,1)}]_{j=2}^t \end{array} \right) \end{aligned}$$

term,

5.

$$\begin{aligned} & (M_{i,i+2,p,1}^{(\nu,k)}, \dots, M_{i,t,p,1}^{(\nu,k)}, M_{i,i+1,p,2}^{(\nu,k)}, \dots, M_{i,t,p,2}^{(\nu,k)} | r_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)}), \\ & (M_{i,i+2,2,1}^{(\nu,k)}, \dots, M_{i,t,2,1}^{(\nu,k)}, M_{i,i+1,2,2}^{(\nu,k)}, \dots, M_{i,t,2,2}^{(\nu,k)} | R_{i,2}^{(\nu,k)} - M_{i,i+1,2,1}^{(\nu,k)}), \end{aligned}$$

and

$$(M_{i+1,i+2,1,1}^{(\nu+1,1)}, \dots, M_{i+1,t,1,1}^{(\nu+1,1)}, M_{i+1,i+1,1,2}^{(\nu+1,1)}, \dots, M_{i+1,t,1,2}^{(\nu+1,1)} | R_{i+1,1}^{(\nu+1,1)}),$$

for $\nu = 0, \dots, l - 2$, $i = 2, \dots, t - 2$, $k = 0, 1$, to form a

$$\prod_{\nu=0}^{l-2} \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} r_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)} \\ [M_{i,j,p,1}^{(\nu,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(\nu,k)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i,2}^{(\nu,k)} - M_{i,2,2,1}^{(\nu,k)} \\ [M_{i,j,2,1}^{(\nu,k)}]_{j=i+2}^t [M_{i,j,2,2}^{(\nu,k)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_i^{(\nu+1,1)} \\ [M_{i+1,j,p,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)} \right\}$$

$$\times \left(\begin{array}{c} R_{i+1,1}^{(\nu+1,1)} \\ [M_{i+1,j,1,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)$$

term and finally

6.

$$(M_{i,i+2,p,1}^{(h,k)}, \dots, M_{i,t,p,1}^{(h,k)}, M_{i,i+1,p,2}^{(h,k)}, \dots, M_{i,t,p,2}^{(h,k)} | r_i^{(h,k)} - O_i^{(h,k)} - M_{i,i+1,p,1}^{(h,k)}),$$

$$(M_{i,i+2,2,1}^{(h,k)}, \dots, M_{i,t,2,1}^{(h,k)}, M_{i,i+1,2,2}^{(h,k)}, \dots, M_{i,t,2,2}^{(h,k)} | R_{i,2}^{(h,k)} - M_{i,i+1,2,1}^{(h,k)}),$$

and

$$(M_{i+1,i+2,1,1}^{(l,1)}, \dots, M_{i+1,t,1,1}^{(l,1)}, M_{i+1,i+1,1,2}^{(l,1)}, \dots, M_{i+1,t,1,2}^{(l,1)} | R_{i+1,1}^{(l,1)}),$$

for $(h = l - 1, l), (k = 0, 1)$ to form a

$$\prod_{i=2}^{t-2} \left\{ \frac{\prod_{h=l-1}^l \prod_{k=0}^1 \left(\begin{array}{c} r_i^{(h,k)} - O_i^{(h,k)} - M_{i,i+1,p,1}^{(h,k)} \\ [M_{i,j,p,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(h,k)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i,2}^{(h,k)} - M_{i,i+1,2,1}^{(h,k)} \\ [M_{i,j,2,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,2,2}^{(h,k)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_{i+1}^{(l,1)} \\ [M_{i+1,j,p,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(l,1)}]_{j=i+1}^t \end{array} \right)} \times \frac{\left(\begin{array}{c} R_{i+1,1}^{(l,1)} \\ [M_{i+1,j,1,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(l,1)}]_{j=i+1}^t \end{array} \right)}{1} \right\}$$

term.

Utilizing these results we find that under random emigration, the $Pr(\text{MSS})$ component of the likelihood is given by

$$Pr(\text{MSS}) = \prod_{\nu=0}^l \left\{ \prod_{i=k+1}^t \prod_{k=0}^1 \left\{ \left(\begin{array}{c} N_i^{(\nu,k)} \\ R_{i,1}^{(\nu,k)} \end{array} \right) (\lambda_{i,1}^{(\nu,k)})^{R_{i,1}^{(\nu,k)}} (1 - \lambda_{i,1}^{(\nu,k)})^{N_i^{(\nu,k)} - R_{i,1}^{(\nu,k)}} \right\} \right. \\ \times \prod_{i=k+1}^{t-1} \prod_{k=0}^1 \left\{ \left(\begin{array}{c} n_i^{(\nu,k)} \\ R_{i,2}^{(\nu,k)} \end{array} \right) (\lambda_{i,2}^{(\nu,k)})^{R_{i,2}^{(\nu,k)}} (1 - \lambda_{i,2}^{(\nu,k)})^{n_i^{(\nu,k)} - R_{i,2}^{(\nu,k)}} \right\} \\ \left. \times \prod_{k=1}^2 \prod_{i=k+1}^t \left\{ \left(\begin{array}{c} T_i^{(\nu+1,k)} \\ C_i^{(\nu+1,k)} \end{array} \right) (\tau_{i,1}^{(\nu+1,k)})^{C_i^{(\nu+1,k)}} (1 - \tau_{i,1}^{(\nu+1,k)})^{T_i^{(\nu+1,k)} - C_i^{(\nu+1,k)}} \right\} \right\}$$

$$\times \prod_{i=k+1}^{t-1} \prod_{k=0}^1 \left\{ \left(\begin{array}{c} \tau_i^{(\nu,k)} \\ O_i^{(\nu,k)} \end{array} \right) (\tau_{i,2}^{(\nu,k)})^{O_i^{(\nu,k)}} (1 - \tau_{i,2}^{(\nu,k)})^{\tau_i^{(\nu,k)} - O_i^{(\nu,k)}} \right\} . \quad (4.20)$$

4.4.3 Parameter estimates

The parameters $S_i^{(\nu,k)}$, $\theta_i^{(\nu,k)}$, $f_i^{(\nu,k)}$, and the confounded pair $F_i^{(\nu,k)} p_{i+1}^{(\omega,k)} = p_{i+1}^{*(\nu,k)}$ are one-to-one functions of the $\lambda_{i,1}^{(\nu,k)}$, $\lambda_{i,2}^{(\nu,k)}$, $\tau_{i,1}^{(\nu,k)}$ and $\tau_{i,2}^{(\nu,k)}$:

$$f_i^{(\nu,k)} = \begin{cases} \tau_{i,2}^{(\nu,k)} \lambda_{i,1}^{(\nu,k)} & i = 1, \dots, t-1 \\ \lambda_{i,1}^{(\nu,k)} & i = t \end{cases}$$

$$p_i^{*(\nu,k)} = \frac{\lambda_{i,1}^{(\omega,k)} \tau_{i,1}^{(\nu+1,k+1)}}{1 + (\lambda_{i,1}^{(\omega,1)} - 1) \tau_{i,1}^{(\nu+1,k+1)}}$$

$$\theta_i^{(\nu,k)} = \frac{1 - \tau_{i,2}^{(\nu,k)}}{1 + \tau_{i,2}^{(\nu,k)} (\lambda_{i,2}^{(\nu,k)} - 1)}$$

and

$$S_i^{(\nu,k)} = \left(1 + \tau_{i,2}^{(\nu,k)} (\lambda_{i,2}^{(\nu,k)} - 1) \right) \frac{\lambda_{i,1}^{(\nu,k)}}{\lambda_{i+1,1}^{(\omega,1)}} \left\{ 1 + \tau_{i+1,2}^{(\nu+1)} (\lambda_{i,1}^{(\nu,k)} - 1) \right\} .$$

These have a close similarity with equations (4.12) through (4.15) thus the MLE's and asymptotic variances and covariances can be obtained directly from the MLE's and asymptotic variances and covariances by appropriate substitution of $N_i^{(\nu,k)}$, $n_i^{(\nu,k)}$, $T_i^{(\nu,k)}$, $\tau_i^{(\nu,k)}$, $R_{i,1}^{(\nu,k)}$, $R_{i+1,1}^{(\nu,1)}$, $C_i^{(\nu,k)}$, and $O_i^{(\nu,k)}$ for $N_i^{(\nu)}$, $n_i^{(\nu)}$, $T_i^{(\nu)}$, $\tau_i^{(\nu)}$, $R_{i,1}^{(\nu)}$, $R_{i+1,1}^{(\nu,1)}$, $C_i^{(\nu)}$, and $O_i^{(\nu)}$ respectively in equations (4.12) through (4.15). The MLE's are given by

$$\hat{f}_i^{(\nu,k)} = \begin{cases} \frac{O_i^{(0,0)}}{N_i^{(0,0)}} & \nu = 0, k = 0 \\ \frac{R_{i,1}^{(\nu,k)} O_i^{(\nu,k)}}{N_i^{(\nu,k)} \tau_i^{(\nu,k)}} & \nu = 1, \dots, l, k = 0, 1, i = 1, \dots, t-1 \\ \frac{R_{i,1}^{(\nu,k)}}{N_i^{(\nu,k)}} & \nu = 1, \dots, l, k = 0, 1, i = t \end{cases} \quad (4.21)$$

$$\hat{p}_i^{*(\nu,k)} = \frac{C_i^{(\nu+1,k+1)}}{\frac{N_i^{(\omega,1)} Z_i^{(\nu+1,k+1)}}{R_{i,1}^{(\omega,1)}} + C_i^{(\nu+1,k+1)}} \quad i = 2, \dots, t, k = 1, 2$$

$$\hat{\theta}_i^{(\nu,k)} = \frac{n_i^{(\nu,k)} (r_i^{(\nu,k)} - O_i^{(\nu,k)})}{r_i^{(\nu,k)} n_i^{(\nu,k)} + O_i^{(\nu,k)} (R_{i,2}^{(\nu,k)} - n_i^{(\nu,k)})} \quad i = 1, \dots, t-1, k = 0, 1 \quad (4.22)$$

and

$$\hat{S}_i^{(\nu,k)} = \left\{ \frac{R_{i,1}^{(\nu,k)}}{N_i^{(\nu,k)} T_i^{(\nu,k)}} + \frac{R_{i,1}^{(\nu,k)} R_{i,2}^{(\nu,k)} L_{i,2}^{(\nu,k)}}{n_i^{(\nu,k)} N_i^{(\nu,k)} T_{i+1}^{(\nu+1,k+1)} r_i^{(\nu,k)}} \right\} \left\{ \frac{N_{i+1}^{(\omega,1)} Z_{i+1}^{(\nu+1,k+1)}}{R_{i+1,1}^{(\omega,1)}} + C_{i+1}^{(\nu+1,k+1)} \right\}$$

$$i = 1, \dots, t-1, k = 0, 1,$$

and their asymptotic variances by

$$Var(\hat{f}_i^{(\nu,k)}) = \begin{cases} \frac{f_i^{(\nu,k)}(1-f_i^{(\nu,k)})}{N_i^{(\nu,k)}} & \nu = 0 \\ (f_i^{(\nu,k)})^2 \left(\frac{1}{E[R_{i,1}^{(\nu,k)}]} - \frac{1}{N_i^{(\nu,k)}} + \frac{1}{E[O_i^{(\nu,k)}]} - \frac{1}{r_i^{(\nu,k)}} \right) & \nu > 0, i = 1, \dots, t-1 \\ (f_i^{(\nu,k)})^2 \left(\frac{1}{E[R_{i,1}^{(\nu,k)}]} - \frac{1}{N_i^{(\nu,k)}} \right) & \nu > 0, i = t \end{cases} \quad (4.23)$$

$$Var(\hat{S}_i^{(\nu,k)}) = (S_i^{(\nu,k)})^2 \left\{ \frac{1}{E[R_{i,1}^{(\nu,k)}]} - \frac{1}{N_i^{(\nu,k)}} + (1 - p_{i+1}^{*(\nu,k)})^2 \left(\frac{1}{E[R_{i+1,1}^{(\omega,1)}]} - \frac{1}{N_{i+1}^{(\omega,1)}} \right) \right. \\ \left. + p_{i+1}^{*(\nu,k)} (1 - p_{i+1}^{*(\nu,k)}) \frac{(N_{i+1}^{(\omega,1)} - R_{i+1,1}^{(\omega,1)})^2}{N_{i+1}^{(\omega,1)} R_{i+1,1}^{(\omega,1)} T_{i+1}^{(\nu+1,k+1)}} \right. \\ \left. + (1 - \theta_i^{(\nu,k)})^2 \left(\frac{1}{E[R_{i,2}^{(\nu,k)}]} - \frac{1}{n_i^{(\nu,k)}} \right) \right. \\ \left. + (\theta_i^{(\nu,k)})^2 \frac{n_i^{(\nu,k)} - E[R_{i,2}^{(\nu,k)}]}{n_i^{(\nu,k)}} \left(\frac{1}{r_i^{(\nu,k)} - E[O_i^{(\nu,k)}]} - \frac{1}{r_i^{(\nu,k)}} \right) \right\}$$

$$Var(\hat{\theta}_i^{(\nu,k)}) = [\theta_i^{(\nu,k)}(1 - \theta_i^{(\nu,k)})]^2 \left(\frac{1}{E[O_i^{(\nu,k)}]} + \frac{1}{(r_i^{(\nu,k)} - E[O_i^{(\nu,k)}])} \right. \\ \left. + \frac{1}{E[R_{i,2}^{(\nu,k)}]} - \frac{1}{n_i^{(\nu,k)}} \right) \quad (4.24)$$

$$Var(p_i^{*(\nu,k)}) = [p_i^{*(\nu,k)}(1 - p_i^{*(\nu,k)})]^2 \left(\frac{1}{R_{i,1}^{(\omega,1)}} - \frac{1}{N_i^{(\omega,1)}} + \frac{1}{C_{i+1}^{(\nu+1,k+1)}} + \frac{1}{Z_{i+1}^{(\nu+1,k+1)}} \right)$$

As in the previous models we have considered, the overall goodness of fit test can be derived directly from the residual $Pr(\text{Data}|\text{MSS})$ term of the likelihood which

is given by

$$Pr(\text{Data}|\text{MSS}) =$$

$$\begin{aligned} & \prod_{\nu=0}^l \left\{ \prod_{k=0}^1 \prod_{i=k+1}^{t-1} \frac{\begin{pmatrix} r_i^{(\nu,k)} - O_i^{(\nu,k)} \\ M_{i,i+1,p,1}^{(\nu,k)} \end{pmatrix} \begin{pmatrix} R_{i,2}^{(\nu,k)} \\ M_{i,i+1,2,1}^{(\nu,k)} \end{pmatrix}}{\begin{pmatrix} T_{i+1}^{(\nu+1,k+1)} \\ C_{i+1}^{(\nu+1,k+1)} \end{pmatrix}} \right\} \\ & \times \frac{\prod_{h=l-1}^l \begin{pmatrix} r_1^{(h,0)} - O_1^{(h,0)} - M_{1,2,p,1}^{(h,0)} \\ [M_{1,j,p,1}^{(h,0)}]_{j=3}^t [M_{1,j,p,2}^{(h,0)}]_{j=2}^t \end{pmatrix} \begin{pmatrix} R_{1,2}^{(h,0)} - M_{1,2,2,1}^{(h,0)} \\ [M_{1,j,2,1}^{(h,0)}]_{j=3}^t [M_{1,j,2,2}^{(h,0)}]_{j=2}^t \end{pmatrix}}{\begin{pmatrix} r_2^{(l,1)} \\ [M_{2,j,p,1}^{(l,1)}]_{j=3}^t [M_{2,j,p,2}^{(l,1)}]_{j=2}^t \end{pmatrix}} \\ & \quad \times \frac{\begin{pmatrix} R_{2,1}^{(l,1)} \\ [M_{2,j,1,1}^{(l,1)}]_{j=3}^t [M_{2,j,1,2}^{(l,1)}]_{j=2}^t \end{pmatrix}}{1} \\ & \times \prod_{\nu=0}^{l-2} \left\{ \frac{\begin{pmatrix} r_1^{(\nu,0)} - O_1^{(\nu,0)} - M_{1,2,p,1}^{(\nu,0)} \\ [M_{1,j,p,1}^{(\nu,0)}]_{j=3}^t [M_{1,j,p,2}^{(\nu,0)}]_{j=2}^t \end{pmatrix} \begin{pmatrix} R_{1,2}^{(\nu,0)} - M_{1,2,2,1}^{(\nu,0)} \\ [M_{1,j,2,1}^{(\nu,0)}]_{j=3}^t [M_{1,j,2,2}^{(\nu,0)}]_{j=2}^t \end{pmatrix}}{\begin{pmatrix} r_2^{(\nu+1,1)} \\ [M_{2,j,p,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,p,2}^{(\nu+1,1)}]_{j=2}^t \end{pmatrix}} \right. \\ & \quad \left. \times \frac{\begin{pmatrix} R_{2,1}^{(\nu+1,1)} \\ [M_{2,j,1,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,1,2}^{(\nu+1,1)}]_{j=2}^t \end{pmatrix}}{1} \right\} \\ & \times \prod_{i=2}^{t-2} \left\{ \frac{\prod_{h=l-1}^l \prod_{k=0}^1 \begin{pmatrix} r_i^{(h,k)} - O_i^{(h,k)} - M_{i,i+1,p,1}^{(h,k)} \\ [M_{i,j,p,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(h,k)}]_{j=i+1}^t \end{pmatrix} \begin{pmatrix} R_{i,2}^{(h,k)} - M_{i,i+1,2,1}^{(h,k)} \\ [M_{i,j,2,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,2,2}^{(h,k)}]_{j=i+1}^t \end{pmatrix}}{\begin{pmatrix} r_{i+1}^{(l,1)} \\ [M_{i+1,j,p,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(l,1)}]_{j=i+1}^t \end{pmatrix}} \right. \\ & \quad \left. \times \frac{\begin{pmatrix} R_{i+1,1}^{(l,1)} \\ [M_{i+1,j,1,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(l,1)}]_{j=i+1}^t \end{pmatrix}}{1} \right\} \end{aligned}$$

$$\times \prod_{\nu=0}^{l-2} \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} r_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)} \\ [M_{i,j,p,1}^{(\nu,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(\nu,k)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i,2}^{(\nu,k)} - M_{i,2,2,1}^{(\nu,k)} \\ [M_{i,j,2,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,2,2}^{(h,k)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_i^{(\nu+1,1)} \\ [M_{i+1,j,p,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)} \times \frac{\left(\begin{array}{c} R_{i+1,1}^{(\nu+1,1)} \\ [M_{i+1,j,1,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)}{1} \right\}.$$

The generalization of the age-dependence model goodness-of-fit test involves additional terms arising from the partitioning of the data according to recapture status on capture at i (i.e. recapture vs first capture). Because of the extensive splitting of the data set, first by age classes and second according to recapture status, the parameter estimates will tend to have low precision, except in large-scale tagging programs such as some fisheries experiments. Of greatest interest may be the tests between models. These will be of two types, according to the null-hypothesis H_0 : age-dependence or H_0 : marking effect.

For the first test, H_0 : age-dependence vs H_1 : age-dependence and marking effect, the conditional distribution $\Pr_{H_0}(\mathcal{S}_1|\mathcal{S}_0)$ where $(\mathcal{S}_1$ and $\mathcal{S}_0)$ are the MSS for H_1 and H_0 respectively is given by

$$\Pr_{H_0}(\mathcal{S}_1|\mathcal{S}_0) = \prod_{\nu=1}^l \left\{ \prod_{i=2}^t \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} N_i^{(\nu,k)} \\ R_{i,1}^{(\nu,k)} \end{array} \right)}{\left(\begin{array}{c} N_i^{(\nu)} \\ R_{i,1}^{(\nu)} \end{array} \right)} \right\} \prod_{i=2}^{t-1} \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} n_i^{(\nu,k)} \\ R_{i,2}^{(\nu,k)} \end{array} \right)}{\left(\begin{array}{c} n_i^{(\nu)} \\ R_{i,2}^{(\nu)} \end{array} \right)} \right\} \right. \\ \left. \times \prod_{i=2}^{t-1} \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} r_i^{(\nu,k)} \\ O_i^{(\nu,k)} \end{array} \right)}{\left(\begin{array}{c} r_i^{(\nu)} \\ O_i^{(\nu)} \end{array} \right)} \right\} \prod_{i=3}^{t-1} \left\{ \frac{\prod_{k=1}^2 \left(\begin{array}{c} T_i^{(\nu+1,k)} \\ C_i^{(\nu+1,k)} \end{array} \right)}{\left(\begin{array}{c} T_i^{(\nu+1)} \\ C_i^{(\nu+1)} \end{array} \right)} \right\} \right\}.$$

Note that age-class 0 animals make no contribution to this test as there are no observations of age class 0 animals in mark class 1.

For the second test, H_0 : marking effect vs H_1 : age-dependence and marking effect, $\text{Pr}_{H_0}(\mathcal{S}_1|\mathcal{S}_0)$ is given by

$$\begin{aligned} \text{Pr}_{H_0}(\mathcal{S}_1|\mathcal{S}_0) = & \prod_{k=0}^1 \left\{ \prod_{i=2}^t \left\{ \frac{\prod_{\nu=k}^l \begin{pmatrix} N_i^{(\nu,k)} \\ R_{i,1}^{(\nu,k)} \end{pmatrix}}{\begin{pmatrix} N_i^{(k)} \\ R_{i,1}^{(k)} \end{pmatrix}} \right\} \prod_{i=2}^{t-1} \left\{ \frac{\prod_{\nu=k}^l \begin{pmatrix} n_i^{(\nu,k)} \\ R_{i,2}^{(\nu,k)} \end{pmatrix}}{\begin{pmatrix} n_i^{(k)} \\ R_{i,2}^{(k)} \end{pmatrix}} \right\} \right\} \\ & \times \prod_{i=2}^{t-1} \left\{ \frac{\prod_{\nu=k}^l \begin{pmatrix} r_i^{(\nu,k)} \\ O_i^{(\nu,k)} \end{pmatrix}}{\begin{pmatrix} r_i^{(k)} \\ O_i^{(k)} \end{pmatrix}} \right\} \prod_{i=3}^{t-1} \left\{ \frac{\prod_{\nu=k+1}^{l+1} \begin{pmatrix} T_i^{(\nu,k+1)} \\ C_i^{(\nu,k+1)} \end{pmatrix}}{\begin{pmatrix} T_i^{(k+1)} \\ C_i^{(k+1)} \end{pmatrix}} \right\} \right\}. \end{aligned}$$

Including the tests developed for just the age-dependence and marking effect models we have alternative pathways for hypothesis testing, each testing the sequence Model 1 v Model 2 v Model 3. In both pathways, Model 1 is the one age model without marking effect and Model 3 has both types of dependence. In one pathway Model 2 has just a marking effect and in the other pathway Model 2 has just age-dependence. Within each pathway the tests are nested, however tests are not nested between pathways. It is possible that both the tests of age-dependence and marking effect vs the one-age model with no marking effect are significant, but that neither are significant when the comparison is with the marking effect and age-dependence model. In such cases the experimenters must rely on their judgement based on an understanding of the biology of the animals as to which generalization may be more appropriate, although Akaike's Information Criterion (Lebreton et al. 1992) may be useful as an objective means of differentiating between models. Note several publications deal specifically with the use of this model selection criterion in open mark-recapture models (Anderson et al. 1994, Burnham and Anderson 1992, Burnham et al. 1994,1995a,1995b).

4.5 Observations Obtained After t

In many studies resightings may be obtained after time t , up to time v , where time t is the final period in which animals were captured. This is particularly likely when observations of marked animals are reported by members of the public. To obtain estimates as efficiently as possible, these observations should be included in the analysis.

Because there are no recaptures after time t , and also because of the age-dependence, there are some important structural limitations to the data. These are:

- There are no $C_{i,1}^{(\nu,k)}$ or $C_{i,2}^{(\nu,0)}$ cohorts for $i > t$ and for any ν or k .
- For $\nu < l$, additional $C_{i,2}^{(\nu,1)}$ release cohorts can only occur for $i = t, \dots, t + \nu$. At times greater than $t + \nu$ all marked animals are known to be older than age ν .
- For $\nu = l$ additional $C_{i,2}^{(\nu,1)}$ release cohorts can only occur for $i = t, \dots, v - 1$.

In addition we have the usual restriction that there are no $C_i^{(0,1)}$ cohorts, because marked animals of age 0 cannot be captured, and there are also, by definition, no $C_1^{(\nu,1)}$ cohorts ($\nu = 1, \dots, l$) (i.e. no releases of marked animals in mark class 1 at time 1).

4.5.1 Probability structure under random emigration

Let

$$\omega_x = \min(l, \nu + x - i).$$

For $i = 1, \dots, t$ and $j = t + 1, \dots, v$ the probability structure for observations of members of $C_{i,1}^{(\nu,k)}$ is given by

$$\pi_{i,j,1,2}^{(\nu,k)} = \alpha_{j,2}^{(\omega_j,1)} \beta_i^{(\nu,k)} \prod_{h=i+1}^{j-1} \beta_h^{(\omega_h,1)},$$

where $\alpha_{j,2}^{(\nu,1)} = f_j^{(\nu,1)}$ and $\beta_t^{(\nu,k)}$ is defined as in (4.18). Because animals are not captured after t , $\beta_j^{(\nu,1)}$ is given by

$$\beta_j^{(\nu,1)} = S_i^{(\nu,k)} \theta_i^{(\nu,k)} \quad j = t + 1, \dots, v - 1 .$$

Now for $j > t$ the parameters $\alpha_{j,2}^{(\omega_j,1)}$, and $\beta_t^{(\omega_t,1)}, \beta_{t+1}^{(\omega_{t+1},1)}, \dots, \beta_{j-1}^{(\omega_{j-1},1)}$ always occur in the product

$$\alpha_{j,2}^{(\omega_j,1)} \beta_i^{(\nu,k)} \prod_{h=i+1}^{j-1} \beta_h^{(\omega_h,1)}$$

hence these parameters are not individually identifiable. Instead we define the parameters

$$\xi_j^{(\nu,k)} = \alpha_{j,2}^{(\omega_j,1)} \beta_t^{(\nu,k)} \prod_{h=t+1}^{j-1} \beta_h^{(\omega_h,1)} ,$$

and for $j = t + 1, \dots, v$ re-write the observation probabilities as

$$\pi_{i,j,1,2}^{(\nu,k)} = \begin{cases} \beta_i^{(\nu,k)} \prod_{h=i+1}^{t-1} \beta_h^{(\omega_h,1)} \xi_j^{(\omega_j,1)} & i = 1, \dots, t - 1 \\ \xi_j^{(\nu,k)} & i = t \end{cases} .$$

For $i = 1, \dots, t$ and $j = t + 1, \dots, v$ the probability structure for observations of members of $C_{i,2}^{(\nu,k)}$ is given by

$$\pi_{i,j,2,2}^{(\nu,k)} = \delta_i^{(\nu,k)} \pi_{i,j,1,2}^{(\nu,k)} .$$

However, for $i = t + 1, \dots, t + \nu$ ($t + \nu < l$) or $i = t + 1, \dots, v - 1$ ($\nu = l$) the probability structure for observations of members of $C_{i,2}^{(\nu,1)}$ is given by

$$\pi_{i,j,2,2}^{(\nu,1)} = \delta_i^{(\nu,1)} \alpha_{j,2}^{(\omega_j,1)} \prod_{h=i}^{j-1} \beta_h^{(\omega_h,1)} . \quad (4.25)$$

As with $\xi_j^{(\nu,k)}$ the parameters in the product (4.25) are completely confounded.

4.5.2 Additional components to the likelihood under random emigration

If we have observations of marked animals from beyond the final capture period then after the $t - 1$ th “peeling” and “pooling” cycle we are left with the term

$$P_{\mathcal{R}}(M_{t,t,1,2}^{(0,0)}, \dots, M_{t,v,1,2}^{(0,0)} | R_{t,1}^{(0,0)})$$

$$\begin{aligned}
& \times \prod_{\nu=1}^l \prod_{k=0}^1 \left\{ \frac{\begin{pmatrix} r_{t-1}^{(\nu,k)} - O_{t-1}^{(\nu,k)} - C_t^{(\nu,k+1)} \\ [M_{t-1,j,p,2}^{(\nu,k)}]_{j=t}^{\nu} \end{pmatrix} \begin{pmatrix} R_{t-1,2}^{(\nu,k)} - M_{t-1,t,2,2}^{(\nu,k)} \\ [M_{t-1,j,2,2}^{(\nu,k)}]_{j=t}^{\nu} \end{pmatrix} \begin{pmatrix} R_{t,1}^{(\omega,1)} \\ [M_{t,j,2,2}^{(\omega,1)}]_{j=t}^{\nu} \end{pmatrix}}{\begin{pmatrix} r_t^{(\omega,1)} \\ [M_{t,j,p,2}^{(\omega,1)}]_{j=t}^{\nu} \end{pmatrix}} \right. \\
& \quad \times P_{\mathcal{R}}(M_{t,t,p,2}^{(\nu,k)}, \dots, M_{t,v,1,2}^{(\nu,k)} | r_t^{(\nu,k)}) \left. \right\} \\
& \quad \times \prod_{\nu=0}^l P_{\mathcal{R}}(M_{t,t+1,2,2}^{(\nu,0)}, \dots, M_{t,v,2,2}^{(\nu,0)} | R_{t,2}^{(\nu,0)}) \\
& \quad \times \prod_{\nu=1}^{l-1} \prod_{i=t}^{t+\nu} P_{\mathcal{R}}(M_{i,i+1,2,2}^{(\nu,1)}, \dots, M_{i,v+1,2,2}^{(\nu,1)}) \\
& \quad \times \prod_{i=t}^{\nu-1} P_{\mathcal{R}}(M_{i,i+1,2,2}^{(l,1)}, \dots, M_{i,v+1,2,2}^{(l,1)}),
\end{aligned}$$

where $M_{i,v+1,2,2}^{(\nu,1)}$ is the number of animals released at i following observation in age class ν that were never observed again.

If we define the additional statistics as follows

$$\begin{aligned}
r_t^{(\nu,0)} &= R_{t,1}^{(\nu,0)} \\
O_t^{\nu,0} &= M_{t,t,1,2}^{(\nu,0)} \\
M_{t,j,p,2}^{(\nu,0)} &= M_{t,j,1,2}^{(\nu,0)}
\end{aligned}$$

then factoring observations for the t th release cohorts we find for $k = 0$ and $\nu = 0, \dots, l$, or $k = 1$ and $\nu = 1, \dots, l$

$$\begin{aligned}
& P_{\mathcal{R}}(M_{t,t,p,2}^{(\nu,k)}, \dots, M_{t,v,p,2}^{(\nu,k)} | r_t^{(\nu,k)}) \\
& = P_{\mathcal{R}}(M_{t,t,p,2}^{(\nu,k)} | r_t^{(\nu,k)}) P_{\mathcal{R}}(M_{t,t+1,p,2}^{(\nu,k)}, \dots, M_{t,v,p,2}^{(\nu,k)} | r_t^{(\nu,k)} - M_{t,t,p,2}^{(\nu,k)})
\end{aligned}$$

where

$$(M_{t,t,p,2}^{(\nu,k)} | r_t^{(\nu,k)}) = (O_t^{(\nu,k)} | r_t^{(\nu,k)})$$

is binomial $B(r_t^{(\nu,k)}, \tau_{t,2}^{(\nu,k)})$,

$$\tau_{t,2}^{(\nu,k)} = \frac{\alpha_{t,2}^{(\nu,k)}}{\lambda_{t,2}^{(\nu,k)}}.$$

Also,

$$(M_{t,t+1,1,2}^{(\nu,k)}, \dots, M_{t,v,1,2}^{(\nu,k)} | r_t^{(\nu,k)} - O_t^{(\nu,k)})$$

is multinomial with conditional cell probabilities

$$\frac{\xi_j^{(\nu,k)}}{\sum_{h=t+1}^v \xi_h^{(\nu,k)}}$$

for $j = t + 1, \dots, v$. For $\nu = 0, \dots, l$:

$$Pr(M_{t,t+1,2,2}^{(\nu,k)}, \dots, M_{t,v,2,2}^{(\nu,k)} | R_{t,2}^{(\nu,k)})$$

is multinomial with conditional cell probabilities

$$\begin{aligned} & \frac{\delta_t^{(\nu,k)} \xi_j^{(\nu,k)}}{\delta_t^{(\nu,k)} \sum_{h=t+1}^v \xi_h^{(\nu,k)}} \\ &= \frac{\xi_j^{(\nu,k)}}{\sum_{h=t+1}^v \xi_h^{(\nu,k)}} \end{aligned}$$

for $j = t + 1, \dots, v$, hence observations of $(M_{t,t+1,2,2}^{(\nu,k)}, \dots, M_{t,v,2,2}^{(\nu,k)} | R_{t,2}^{(\nu,k)})$ can be pooled with $(M_{t,t+1,1,2}^{(\nu,k)}, \dots, M_{t,v,1,2}^{(\nu,k)} | r_t^{(\nu,k)} - O_t^{(\nu,k)})$. Thus we obtain the additional terms in the likelihood

$$\begin{aligned} & \binom{n_t^{(0,0)}}{R_{t,2}^{(0,0)}} (\lambda_{t,2}^{(0,0)})^{R_{t,2}^{(0,0)}} (1 - \lambda_{t,2}^{(0,0)})^{n_t^{(0,0)} - R_{t,2}^{(0,0)}} \\ & \times \prod_{\nu=1}^l \prod_{k=0}^1 \binom{n_t^{(\nu,k)}}{R_{t,2}^{(\nu,k)}} (\lambda_{t,2}^{(\nu,k)})^{R_{t,2}^{(\nu,k)}} (1 - \lambda_{t,2}^{(\nu,k)})^{n_t^{(\nu,k)} - R_{t,2}^{(\nu,k)}} \\ & \times \binom{r_t^{(0,0)}}{O_t^{(0,0)}} (\tau_{t,2}^{(0,0)})^{O_t^{(0,0)}} (1 - \tau_{t,2}^{(0,0)})^{r_t^{(0,0)} - O_t^{(0,0)}} \\ & \times \prod_{\nu=1}^l \prod_{k=0}^1 \binom{r_t^{(\nu,k)}}{O_t^{(\nu,k)}} (\tau_{t,2}^{(\nu,k)})^{O_t^{(\nu,k)}} (1 - \tau_{t,2}^{(\nu,k)})^{r_t^{(\nu,k)} - O_t^{(\nu,k)}} \\ & \times \frac{\binom{r_t^{(0,0)} - O_t^{(0,0)}}{[M_{t,j,1,2}^{(0,0)}]_{j=t+1}^v} \binom{R_{t,2}^{(0,0)}}{[M_{t,j,2,2}^{(0,0)}]_{j=t+1}^v}}{\binom{r_t^{(0,0)} - O_t^{(0,0)} + R_{t,2}^{(0,0)}}{[M_{t,j,\dots,2}^{(0,0)}]_{j=t+1}^v}} \end{aligned}$$

$$\begin{aligned}
& \times \begin{pmatrix} \tau_t^{(0,0)} - O_t^{(0,0)} + R_{t,2}^{(0,0)} \\ [M_{t,j,\cdot,2}^{(0,0)}]_{j=t+1}^v \end{pmatrix} \prod_{j=t+1}^v \left(\frac{\xi_j^{(0,0)}}{\sum_{h=t+1}^v \xi_h^{(0,0)}} \right)^{M_{t,j,\cdot,2}^{(0,0)}} \\
& \times \prod_{\nu=1}^l \prod_{k=0}^1 \frac{\begin{pmatrix} \tau_t^{(\nu,k)} - O_t^{(\nu,k)} \\ [M_{t,j,1,2}^{(\nu,k)}]_{j=t+1}^v \end{pmatrix} \begin{pmatrix} R_{t,2}^{(\nu,k)} \\ [M_{t,j,2,2}^{(\nu,k)}]_{j=t+1}^v \end{pmatrix}}{\begin{pmatrix} \tau_t^{(\nu,k)} - O_t^{(\nu,k)} + R_{t,2}^{(\nu,k)} \\ [M_{t,j,\cdot,2}^{(\nu,k)}]_{j=t+1}^v \end{pmatrix}} \\
& \times \begin{pmatrix} \tau_t^{(\nu,k)} - O_t^{(\nu,k)} + R_{t,2}^{(\nu,k)} \\ [M_{t,j,\cdot,2}^{(\nu,k)}]_{j=t+1}^v \end{pmatrix} \prod_{j=t+1}^v \left(\frac{\xi_j^{(\nu,k)}}{\sum_{h=t+1}^v \xi_h^{(\nu,k)}} \right)^{M_{t,j,\cdot,2}^{(\nu,k)}} \\
& \times \prod_{\nu=1}^l \prod_{i=t+1}^{\min(t+\nu, v-1)} \begin{pmatrix} n_i^{\nu,k} \\ [M_{i,j,2,2}^{(\nu,k)}]_{j=i+1}^{v+1} \end{pmatrix} \prod_{j=i+1}^{v+1} \left(\pi_{i,j,2,2}^{(\nu,1)} \right)^{M_{i,j,2,2}^{(\nu,1)}}
\end{aligned}$$

where

$$M_{t,j,\cdot,2}^{(\nu,k)} = M_{t,j,1,2}^{(\nu,k)} + M_{t,j,2,2}^{(\nu,k)} .$$

4.5.3 Additional parameter estimates under random emigration

Due to the additional observations, we have extra parameters to estimate. In addition, the parameter $\tau_{t,2}^{(\nu,k)}$ is defined and estimation of this parameter now contributes to the estimation of $f_t^{(\nu,k)}$. From

$$\begin{aligned}
\tau_{t,2}^{(\nu,k)} &= \frac{\alpha_{t,2}^{(\nu,k)}}{\lambda_{t,1}^{(\nu,k)}} \\
&= \frac{f_t^{(\nu,k)}}{\lambda_{t,1}^{(\nu,k)}} ,
\end{aligned}$$

and substituting the MLE's for $\tau_{t,2}^{(\nu,k)}$ and $\lambda_{t,1}^{(\nu,k)}$ we obtain

$$\begin{aligned}
\hat{f}_t^{(\nu,k)} &= \hat{\lambda}_{t,1}^{(\nu,k)} \hat{\tau}_{t,2}^{(\nu,k)} \\
&= \frac{R_{t,1}^{(\nu,k)} O_t^{(\nu,k)}}{N_t^{(\nu,k)} r_t^{(\nu,k)}}
\end{aligned}$$

and is identical to (4.21) for $i \neq t$.

We can also estimate $\theta_t^{(\nu,k)}$. From

$$\lambda_{t,2}^{(\nu,k)} = \delta_t^{(\nu,k)} (\lambda_{t,1}^{(\nu,k)} - \alpha_{t,2}^{(\nu,k)})$$

we obtain

$$\theta_t^{(\nu,k)} = \frac{1 - \tau_{t,2}^{(\nu,k)}}{1 + \tau_{t,2}^{(\nu,k)} (\lambda_{t,2}^{(\nu,k)} - 1)}.$$

Substituting the MLE's for $\tau_{t,2}^{(\nu,k)}$, and $\lambda_{t,2}^{(\nu,k)}$ we obtain

$$\hat{\theta}_t^{(\nu,k)} = \frac{n_t^{(\nu,k)} (r_t^{(\nu,k)} - O_t^{(\nu,k)})}{r_t^{(\nu,k)} n_t^{(\nu,k)} + O_t^{(\nu,k)} (R_{t,2}^{(\nu,k)} - n_t^{(\nu,k)})}$$

which is identical to (4.22) but with $i = t$. Asymptotic variances for $\hat{f}_t^{(\nu,k)}$ and $\hat{\theta}_t^{(\nu,k)}$ are given by (4.23) and (4.24) respectively (in the case of $\hat{f}_t^{(\nu,k)}$ substituting t for i in (4.23)).

In addition to $\hat{f}_t^{(\nu,k)}$ and $\hat{\theta}_t^{(\nu,k)}$ we can estimate values for the parameters $\xi_i^{(\nu,k)}$ and $\pi_{i,j,2,2}^{(\nu,k)}$. However, because they represent products of confounded parameters they are of little direct interest, although they may have a use for computing expected values in order to assess model fit (Brownie et al. 1985:17).

Since $(M_{t,t+1,\dots,2}^{(\nu,k)}, \dots, M_{t,t,\nu,\dots,2}^{(\nu,k)} | r_t^{(\nu,k)} - O_t^{(\nu,k)} + R_{t,2}^{(\nu,k)})$ is multinomial with conditional cell probabilities

$$\begin{aligned} \pi_j^{*(\nu,k)} &= \frac{\xi_j^{(\nu,k)}}{\sum_{h=t+1}^{\nu} \xi_h^{(\nu,k)}} \\ &= \frac{\xi_j^{(\nu,k)}}{\lambda_{t,1}^{(\nu,k)} - \alpha_{t,2}^{(\nu,k)}}, \end{aligned}$$

substituting MLE's for $\pi_j^{*(\nu,k)}$, $\lambda_{t,1}^{(\nu,k)}$, and $f_t^{(\nu,k)} = \alpha_{t,2}^{(\nu,k)}$ we obtain

$$\hat{\xi}_j^{(\nu,k)} = \frac{M_{t,j,\dots,2}^{(\nu,k)}}{(r_t^{(\nu,k)} - O_t^{(\nu,k)} + R_{t,2}^{(\nu,k)})} \frac{R_{t,1}^{(\nu,k)} (r_t^{(\nu,k)} - O_t^{(\nu,k)})}{N_t^{(\nu,k)} r_t^{(\nu,k)}}.$$

Because the $\pi_{i,j,2,2}^{(\nu,k)}$ simply represent the cell probabilities for the $M_{i,j,2,2}^{(\nu,1)}$'s their MLE's are given by

$$\hat{\pi}_{i,j,2,2}^{(\nu,1)} = \frac{M_{i,j,2,2}^{(\nu,1)}}{n_i^{(\nu,1)}} \quad i = t+1, \dots, \nu-1; \quad j = i+1, \dots, \nu.$$

4.5.4 Additional components to the goodness-of-fit tests

When $\nu > t$ we have an additional component to the residual $Pr(\text{Data}|\text{MSS})$ after factorization cycle t . This term is used in goodness of fit testing and is given

$$\begin{aligned} & \frac{\begin{pmatrix} r_{t-1}^{(0,0)} - O_{t-1}^{(0,0)} - C_t^{(0,1)} \\ [M_{t-1,j,p,2}^{(0,0)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t-1,2}^{(0,0)} - M_{t-1,t,2,2}^{(0,0)} \\ [M_{t-1,j,2,2}^{(0,0)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t,1}^{(1,1)} \\ [M_{t,j,2,2}^{(1,1)}]_{j=t}^\nu \end{pmatrix}}{\begin{pmatrix} r_t^{(1,1)} \\ [M_{t,j,p,2}^{(1,1)}]_{j=t}^\nu \end{pmatrix}} \\ & \times \prod_{\nu=1}^{l-2} \prod_{k=0}^1 \frac{\begin{pmatrix} r_{t-1}^{(\nu,k)} - O_{t-1}^{(\nu,k)} - C_t^{(\nu,k+1)} \\ [M_{t-1,j,p,2}^{(\nu,k)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t-1,2}^{(\nu,k)} - M_{t-1,t,2,2}^{(\nu,k)} \\ [M_{t-1,j,2,2}^{(\nu,k)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t,1}^{(\nu+1,1)} \\ [M_{t,j,2,2}^{(\nu+1,1)}]_{j=t}^\nu \end{pmatrix}}{\begin{pmatrix} r_t^{(\nu+1,1)} \\ [M_{t,j,p,2}^{(\nu+1,1)}]_{j=t}^\nu \end{pmatrix}} \\ & \times \prod_{k=0}^1 \frac{\prod_{\nu=1}^{l-2} \begin{pmatrix} r_{t-1}^{(\nu,k)} - O_{t-1}^{(\nu,k)} - C_t^{(\nu,k+1)} \\ [M_{t-1,j,p,2}^{(\nu,k)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t-1,2}^{(\nu,k)} - M_{t-1,t,2,2}^{(\nu,k)} \\ [M_{t-1,j,2,2}^{(\nu,k)}]_{j=t}^\nu \end{pmatrix} \begin{pmatrix} R_{t,1}^{(l,1)} \\ [M_{t,j,2,2}^{(l,1)}]_{j=t}^\nu \end{pmatrix}}{\begin{pmatrix} r_t^{(l,1)} \\ [M_{t,j,p,2}^{(l,1)}]_{j=t}^\nu \end{pmatrix}}. \end{aligned}$$

These terms give rise to an additional $2l - 1$ conditionally independent contingency tables. In addition, factorization cycle t gives rise to the term

$$\begin{aligned} & \frac{\begin{pmatrix} r_t^{(0,0)} - O_t^{(0,0)} \\ [M_{t,j,1,2}^{(0,0)}]_{j=t+1}^\nu \end{pmatrix} \begin{pmatrix} R_{t,2}^{(0,0)} \\ [M_{t,j,2,2}^{(0,0)}]_{j=t+1}^\nu \end{pmatrix}}{\begin{pmatrix} r_t^{(0,0)} - O_t^{(0,0)} + R_{t,2}^{(0,0)} \\ [M_{t,j,\cdot,2}^{(0,0)}]_{j=i+1}^\nu \end{pmatrix}} \\ & \times \prod_{\nu=1}^l \prod_{k=0}^1 \frac{\begin{pmatrix} r_t^{(\nu,k)} - O_t^{(0,0)} \\ [M_{t,j,1,2}^{(\nu,k)}]_{j=t+1}^\nu \end{pmatrix} \begin{pmatrix} R_{t,2}^{(\nu,k)} \\ [M_{t,j,2,2}^{(\nu,k)}]_{j=t+1}^\nu \end{pmatrix}}{\begin{pmatrix} r_t^{(\nu,k)} - O_t^{(\nu,k)} + R_{t,2}^{(\nu,k)} \\ [M_{t,j,\cdot,2}^{(\nu,k)}]_{j=i+1}^\nu \end{pmatrix}}, \end{aligned}$$

leading to an additional $2l + 1$ conditionally independent contingency tables.

4.5.5 Age-dependence and marking effect models under permanent and Markov emigration with $v > t$

Under permanent and random emigration computation of observation cell probabilities makes use of $\gamma_{i,j,1}^{(\nu,k)}$, the probability an animal released at time i as a member of age class ν and mark class k is not recaptured between i and j , nor at j . Because we do not capture animals after t we find

$$\gamma_{i,j}^{(\nu,k)} = \begin{cases} \gamma_{i,t}^{(\nu,k)} & i = 1, \dots, t-1, j = t+1, \dots, v \\ 1 & i = t \end{cases} \quad (4.26)$$

In addition to the parameters that can be estimated when $v = t$ we can estimate the parameters $\xi_i^{(\nu,k)}$ ($i = t+1, \dots, v$) and $\pi_{i,j,2,2}^{(\nu,1)}$ ($i = t+1, \dots, v-1, j = t+1, \dots, v$). These products of confounded parameters are defined exactly as under random emigration.

Chapter 5

Modified and Reduced Parameter Models

In this section we consider a number of important reduced parameter versions of the models discussed in Chapters 3 and 4. In some cases these reduced parameter models lead to closed form MLE's that correspond to published mark-recapture estimators. In other cases reduced parameter models do not lead to closed-form solutions and we discuss how these models can be fitted.

5.1 Models with No Resightings

If we make the constraint $f_i^{(\nu,k)} = (1 - \theta_i^{(\nu,k)}) = 0$ then the $M_{i,j,m,2}^{(\nu,k)}$ ($m=1,2$) and hence $O_i^{(\nu,k)}$, and $n_i^{(\nu,k)}$ are all structurally zero. If we also assume that emigration is permanent (in the age-dependent model including one-age as a special case) or random (in the single age class model only) and omit the subscripts used to denote the type of release cohort we find that the estimators of survival and capture probabilities and their respective variances reduce to

$$\hat{S}_i^{(\nu,k)} = \frac{R_i^{(\nu,k)}}{N_i^{(\nu,k)} r_i^{(\nu,k)}} \left\{ \frac{N_{i+1}^{(\omega,1)} Z_{i+1}^{(\nu+1,k+1)}}{R_{i+1}^{(\omega,1)}} + C_{i+1}^{(\nu+1,k+1)} \right\},$$

$$Var(\hat{S}_i^{(\nu,k)}) = (S_i^{(\nu,k)})^2 \left\{ \frac{1}{E[R_i^{(\nu,k)}]} - \frac{1}{N_i^{(\nu,k)}} + (1 - p_{i+1}^{*(\nu,k)})^2 \left(\frac{1}{E[R_{i+1}^{(\omega,1)}]} - \frac{1}{N_{i+1}^{(\omega,1)}} \right) \right\}$$

$$\left. + p_{i+1}^{*(\nu,k)}(1 - p_{i+1}^{*(\nu,k)}) \frac{(N_{i+1}^{(\omega,1)} - E[R_{i+1}^{(\omega,1)}])^2}{N_{i+1}^{(\omega,1)} E[R_{i+1}^{(\omega,1)}] E[T_{i+1}^{(\nu+1,k+1)}]} \right\}$$

$$p_i^{*(\hat{\nu},k)} = \frac{C_i^{(\nu+1,k+1)}}{\frac{N_i^{(\omega,1)} Z_i^{(\nu+1,k+1)}}{R_i^{(\omega,1)}} + C_i^{(\nu+1,k+1)}} \quad i = 2, \dots, t$$

and

$$Var(\hat{p}_i^{*(\nu,k)}) = [p_i^{*(\nu,k)}(1 - p_i^{*(\nu,k)})]^2 \left(\frac{1}{E[R_i^{(\omega,1)}]} - \frac{1}{N_i^{(\omega,1)}} + \frac{1}{E[C_i^{(\nu+1,k+1)}]} + \frac{1}{Z_i^{(\nu+1,k+1)}} \right)$$

which in the one-age case with no marking effect are the Jolly-Seber estimators of $S_i = \phi_i$ and $p_i^* = p_i$.

Importantly, in the single age-class case we are unable to discriminate between the case of random emigration or permanent emigration as the probability structure for the model is identical in either case (Burnham 1993). The type of emigration does effect the interpretation of the parameters however. For example, if emigration is permanent in the one-age model without a marking effect then $p_i^* = p_i$ and $S_i = S_i F_i$ is the joint probability a marked animal survives from $i, i + 1$ and is at risk of capture at $i + 1$. If emigration is random, then $p_i^* = p_i F_{i-1}$ and S_i is the true survival rate.

In the age-dependent model we can distinguish between the two models. If we have the age-dependent model under permanent emigration and no ancillary observations and no marking effect then the model reduces to that developed by Pollock (1981). To simplify the discussion we will just consider the two-age case. For this model, under permanent emigration a minimal sufficient statistic is given by $R_i^{(0)}$ ($i=1, \dots, t-1$), $R_i^{(1)}$ ($i=1, \dots, t-1$), and C_i ($i=2, \dots, t-1$) (Brownie et al. 1986) where C_i is the total number of animals captured at i . This sufficient statistic has dimension $3t - 4$ with $3t - 4$ estimable parameters given in closed-form by Pollock et al. (1990).

Under random emigration, however, we find from 4.11 that a MSS is given by $R_i^{(0)}$ ($i=1, \dots, t-1$), $R_i^{(1)}$ ($i=1, \dots, t-1$), $C_i^{(1)}$ ($i=2, \dots, t-1$) and $C_i^{(2)}$ ($i=2, \dots, t-1$)

which has dimension $4t - 6$ with $4t - 6$ estimable parameters in the model. Closed-form solutions to the $\hat{p}_i^{*(\nu)}$ and $\hat{S}_i^{(\nu)}$'s are given in Chapter 4. The additional $t - 1$ identifiable parameters in the random emigration model when compared to the permanent emigration model are $p_i^{*(0)}$ ($i = 2, \dots, t - 1$) and $p_t^{*(0)} S_t$. Thus the models lead to different likelihoods and different parameter estimates. Moreover if we examine the probability structure (Tables 5.1 and 5.2) we find that the permanent emigration model is in fact a constrained version of the random emigration model. If in the random emigration model (Table 5.1) we make the constraint $p_i^{*(0)} = p_i^{*(1)}$ ($i = 2, \dots, t - 1$) then we obtain a reduced model which is identical in structure to the permanent emigration model developed by Pollock (1981).

Table 5.1: Probability structure for a $t = 4$ two-age Jolly-Seber model with no marking effect under random emigration where $p_i^{*(1)} = F_{i-1}^{(1)} p_i^{(1)}$ and $p_i^{*(0)} = F_{i-1}^{(0)} p_i^{(1)}$.

	j=2	3	4
Adults			
i=1	$S_1^{(1)} p_2^{*(1)}$	$S_1^{(1)} (1 - p_2^{*(1)}) S_2^{(1)} p_3^{*(1)}$	$S_1^{(1)} (1 - p_2^{*(1)}) S_2^{(1)} (1 - p_3^{*(1)}) S_3^{(1)} p_4^{*(1)}$
2		$S_2^{(1)} p_3^{*(1)}$	$S_2^{(1)} (1 - p_3^{*(1)}) S_3^{(1)} p_4^{*(1)}$
3			$S_3^{(1)} p_4^{*(1)}$
Young			
i=1	$S_1^{(0)} p_2^{*(0)}$	$S_1^{(0)} (1 - p_2^{*(0)}) S_2^{(1)} p_3^{*(1)}$	$S_1^{(0)} (1 - p_2^{*(0)}) S_2^{(1)} (1 - p_3^{*(1)}) S_3^{(1)} p_4^{*(1)}$
2		$S_2^{(0)} p_3^{*(0)}$	$S_2^{(0)} (1 - p_3^{*(0)}) S_3^{(1)} p_4^{*(1)}$
3			$S_3^{(0)} p_4^{*(0)}$

The structural equivalence between the constrained random emigration model and the permanent emigration model means that we can formally test the null hypothesis that emigration is permanent against the alternative of random emigration. From Brownie et al. (1986) the log-likelihood function (ignoring the normalizing constant) for the recaptures of marked animals in a two-age Jolly-Seber model under permanent emigration with no marking effect is given by

$$\mathcal{L}_p = \sum_{\nu=0}^1 \left\{ \sum_{i=1}^{t-1} R_i^{(\nu)} \ln(\lambda_{i,p}^{(\nu)}) + (N_i^{(\nu)} - R_i^{(\nu)}) \ln(1 - \lambda_{i,p}^{(\nu)}) \right\} + \sum_{i=2}^{t-1} C_i \ln(\tau_{i,p}) Z_i \ln(1 - \tau_{i,p})$$

Table 5.2: Probability structure for a $t = 4$ two-age Jolly-Seber model with no marking effect under permanent emigration where $S_i^{(\nu)} = S_i^{(\nu)} F_i^{(\nu)}$.

	j=2	3	4
Adults			
i=1	$S_1^{*(1)} p_2^{(1)}$	$S_1^{*(1)} (1 - p_2^{(1)}) S_2^{*(1)} p_3^{(1)}$	$S_1^{*(1)} (1 - p_2^{(1)}) S_2^{*(1)} (1 - p_3^{(1)}) S_3^{*(1)} p_4^{(1)}$
2		$S_2^{*(1)} p_3^{(1)}$	$S_2^{*(1)} (1 - p_3^{(1)}) S_3^{*(1)} p_4^{(1)}$
3			$S_3^{*(1)} p_4^{(1)}$
Young			
i=1	$S_1^{*(0)} p_2^{(1)}$	$S_1^{*(0)} (1 - p_2^{(1)}) S_2^{*(1)} p_3^{(1)}$	$S_1^{*(0)} (1 - p_2^{(1)}) S_2^{*(1)} (1 - p_3^{(1)}) S_3^{*(1)} p_4^{(1)}$
2		$S_2^{*(0)} p_3^{(1)}$	$S_2^{*(0)} (1 - p_3^{(1)}) S_3^{*(1)} p_4^{(1)}$
3			$S_3^{*(0)} p_4^{(1)}$

where $C_i = C_i^{(1)} + C_i^{(2)}$, $Z_i = Z_i^{(1)} + Z_i^{(2)}$. From Chapter 4 the log-likelihood function under the random emigration model (ignoring the normalizing constant) is given by

$$\begin{aligned} \mathcal{L}_r = & \sum_{\nu=0}^1 \sum_{i=1}^{t-1} R_i^{(\nu)} \ln(\lambda_{i,r}^{(\nu)}) + (N_i^{(\nu)} - R_i^{(\nu)}) \ln(1 - \lambda_{i,r}^{(\nu)}) \\ & + \sum_{i=2}^{t-1} C_i^{(\nu+1)} \ln(\tau_{i,r}^{(\nu+1)}) Z_i^{(\nu+1)} \ln(1 - \tau_{i,r}^{(\nu+1)}) . \end{aligned}$$

Noting that $\hat{\lambda}_{i,p}^{(\nu)} = \hat{\lambda}_{i,r}^{(\nu)}$, $\hat{\tau}_{i,p} = \frac{C_i}{T_i}$, and $\hat{\tau}_{i,r}^{(\nu)} = \frac{C_i^{(\nu)}}{T_i^{(\nu)}}$, where $T_i = Z_i + C_i$, we find that the log-likelihood-ratio test statistic is given by

$$\begin{aligned} X^2 = & -2 \sum_{i=2}^{t-1} \left\{ C_i \ln\left(\frac{C_i}{T_i}\right) + Z_i \ln\left(\frac{Z_i}{T_i}\right) - \sum_{\nu=1}^2 C_i^{(\nu)} \ln\left(\frac{C_i^{(\nu)}}{T_i^{(\nu)}}\right) + Z_i^{(\nu)} \ln\left(\frac{Z_i^{(\nu)}}{T_i^{(\nu)}}\right) \right\} \\ = & -2 \sum_{i=2}^{t-1} \sum_{\nu=1}^2 C_i^{(\nu)} \ln\left(\frac{C_i^{(\nu)} T_i}{Z_i T_i^{(\nu)}}\right) + Z_i^{(\nu)} \ln\left(\frac{Z_i^{(\nu)} T_i}{Z_i T_i^{(\nu)}}\right) , \end{aligned}$$

with $t - 2$ degrees of freedom.

Alternatively we can construct contingency tables to test between models. If S_0 is the set of minimally sufficient statistics under the null, permanent emigration, model and S_1 is the set of minimally sufficient statistics under the alternative,

random emigration, model then

$$Pr(\mathcal{S}_i | \mathcal{S}_0) = \prod_{i=2}^{t-1} \frac{\begin{pmatrix} C_i^{(1)} \\ T_i^{(1)} \end{pmatrix} \begin{pmatrix} C_i^{(2)} \\ T_i^{(2)} \end{pmatrix}}{\begin{pmatrix} C_i \\ T_i \end{pmatrix}}$$

leading to the set of $t - 2$ conditionally independent contingency tables of the form given in Table 5.3. As discussed in Chapter 4 the contingency table approach is

Table 5.3: Contingency table used to test the “random” vs “permanent” emigration models

	Young at $i - 1$, captured at i or after i	Adult at $i - 1$, captured at or after i	
Captured at i	$C_i^{(1)}$	$C_i^{(2)}$	C_i
Not captured at $i + 1$	$Z_i^{(1)}$	$Z_i^{(2)}$	Z_i
	$T_i^{(1)}$	$T_i^{(2)}$	T_i

generally preferred if “exact” significance can be assessed using the hypergeometric distribution. If a chi-square approximation is used instead of the exact procedure, then the contingency table and likelihood ratio tests would have the same asymptotic power.

Although we have described the test as a comparison of the “permanent” and the “temporary” emigration models, we are really testing whether age-group at $i - 1$ has an effect on capture probability at i . This test will be sensitive to any mechanism that leads to such an age-group dependence. Random emigration is just one particularly important alternative that leads to capture probabilities at time i differing between animals who were young at $i - 1$ and those animals who were adult at $i - 1$. Therefore rejection of the permanent emigration model in favour of the random emigration should not be taken as strict evidence of random emigration. Rather rejection of the permanent emigration assumption is simply evidence of age-dependent capture probabilities, with a number of possible explanations including random emigration.

In contrast, in the full model (i.e. with resightings) the permanent emigration model has *more* estimable parameters than the random emigration model. Moreover, the two models are no longer nested and we have no formal test for discriminating between the two models. Note, however, if we make the constraint $F_i^{(\nu,k)} = 1$ (i.e. no emigration) in the one age-class permanent emigration model we obtain a probability structure that is identical to the random emigration model, with the difference that $p_i^{*(\nu,k)} = p_i^{(\nu,k)}$. Thus, in the one age-class case the likelihood ratio test between the permanent emigration and no-emigration models ($F_i^{(\nu,k)} = 1$) is in fact a test of the composite “either no, or random, emigration” hypothesis against the alternative of permanent emigration.

Finally, if the random emigration age-dependence model is valid, then we can use our estimator of $p_i^{*(\nu,k)}$ to estimate the relative movement rates $\rho_i^{(k)}$ of animals in the oldest two age classes. Since

$$p_{i+1}^{*(l-1,k)} = F_i^{(l-1,k)} p_{i+1}^{(l,k)}$$

and

$$p_{i+1}^{*(l,k)} = F_i^{(l,k)} p_{i+1}^{(l,k)}$$

then

$$\hat{\rho}_i^{(k)} = \frac{\widehat{F}_i^{(l,k)}}{F_i^{(l-1,k)}} = \frac{\hat{p}_{i+1}^{*(l,k)}}{\hat{p}_{i+1}^{*(l-1,k)}}.$$

with asymptotic variance

$$Var(\hat{\rho}_i^{(k)}) = \frac{Var(\hat{p}_{i+1}^{*(l,k)})}{[p_{i+1}^{*(l-1,k)}]^2} + \frac{[Var(p_{i+1}^{*(l,k)})]^2 \hat{p}_{i+1}^{*(l-1,k)}}{[p_{i+1}^{*(l-1,k)}]^4} - \frac{2 [p_{i+1}^{*(l,k)}]^2 Cov(\hat{p}_{i+1}^{*(l,k)}, \hat{p}_{i+1}^{*(l-1,k)})}{[p_{i+1}^{*(l-1,k)}]^3}.$$

However, this estimator may not be very useful as it depends on the assumption that animals in age class l and mark class k at time i have the same capture probabilities regardless of their age class at time $i - 1$.

5.1.1 Benefit of including ancillary observations

Relative efficiency of the survival rate estimator

Using our closed-form expressions for the variance of the parameter estimates under random emigration we can compare the relative efficiency of the survival rate estimator under the Jolly-Seber model with the survival rate estimator obtained using our model. This is easily done by generating expected values of the statistics under particular parameter combinations then substituting these expected values into the variance expressions.

For simplicity, a single age-class $t = 5$ study with all parameters equal through time (although not structurally constrained) was considered. In addition the observation and death processes was constrained so that death followed a homogeneous Poisson process, and first observation within $(i, i + 1)$ a non-homogeneous process with heterogeneity due entirely to the death of individuals. In this case it can be shown (Terry Moore pers. comm.) that

$$\theta_i = (1 - f_i)^{\frac{\ln(S_i)}{S_i - 1}}. \quad (5.1)$$

Denoting \hat{S}_i as the estimate obtained with ancillary observations and \hat{S}_i^{JS} as the estimate of S_i under the Jolly-Seber model using the same data, but without ancillary observations, relative efficiency was measured by

$$\frac{Var(\hat{S}_i^{JS})}{Var(\hat{S}_i)}.$$

This was computed only for estimates of S_1 , S_2 , and S_3 as no estimate of S_4 is possible in a $t = 5$ Jolly-Seber model. Note that the measure of relative efficiency is based on $Var(\hat{S}_i | S_i)$. This is the only component of the survival probability variance estimate that is affected by the inclusion of ancillary observations.

Relative efficiency was an increasing function of p , f , and i (Tables 5.1, 5.2, and 5.3), and always greater than one. Relative efficiency for larger values of f was not as great when p was also large. Higher survival rate appears to elevate the rate at which relative efficiency increased with the observation probability (i.e. an increase in the second derivative of relative efficiency with respect to f), and as a

consequence the increase in relative efficiency with i was also greater for the higher survival rates.

Intuitively, including ancillary observations improves the survival rate estimates because we obtain observations on animals that were never captured following release. Without ancillary observations these animals do not contribute to $R_{i,1}$ or Z_i . Thus efficiency will be improved by influences, such as increasing f_i , which lead to an increase in the expected values of $R_{i,1}$ and Z_i . The relative increase in $E[R_{i,1}]$ and $E[Z_i]$ resulting from the inclusion of ancillary observations would be greatest when p was small relative to f . For example in a study where p was close to 1, there would be a relatively small gain from including ancillary observations as most live animals are recaptured in any case. Similarly $E[R_{i,1}]$ and $E[Z_i]$ increase with t thus the relative benefit of including ancillary observations would be greater in short rather than long studies. This is evident from Table 5.4 where relative efficiency with various f , S , and p are given for estimates of S_1 , S_2 , and S_3 in a $t = 10$ study, however the difference between a $t = 5$ and $t = 10$ study appears slight.

The effect of heterogeneous capture probabilities

An important assumption of the Jolly-Seber model and the extensions to it that we have considered in Chapter 3 is that all animals have the same capture probability at time i - the homogeneous capture probability assumption. As we have shown in Chapter 4 we can relax this assumption and allow animals to have different capture probabilities according to known classes of animals. In some cases there may be inherent heterogeneity with some animals more or less vulnerable to capture as a consequence of factors that can be difficult to explicitly incorporate in the model. For example poorly conditioned animals may have higher capture probabilities if traps are baited with food. These animals may also have lower survival rates.

The effects of heterogeneous capture probabilities on the Jolly-Seber estimators are well known (see section 1.4.4). Essentially, the marked members of the population will tend to be those with high capture probabilities, and the estimate of

Figure 5.1: Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.3$ (Relative efficiency = $\frac{\text{Var}(\hat{S}_i^{JS})}{\text{Var}(\hat{S}_i)}$).

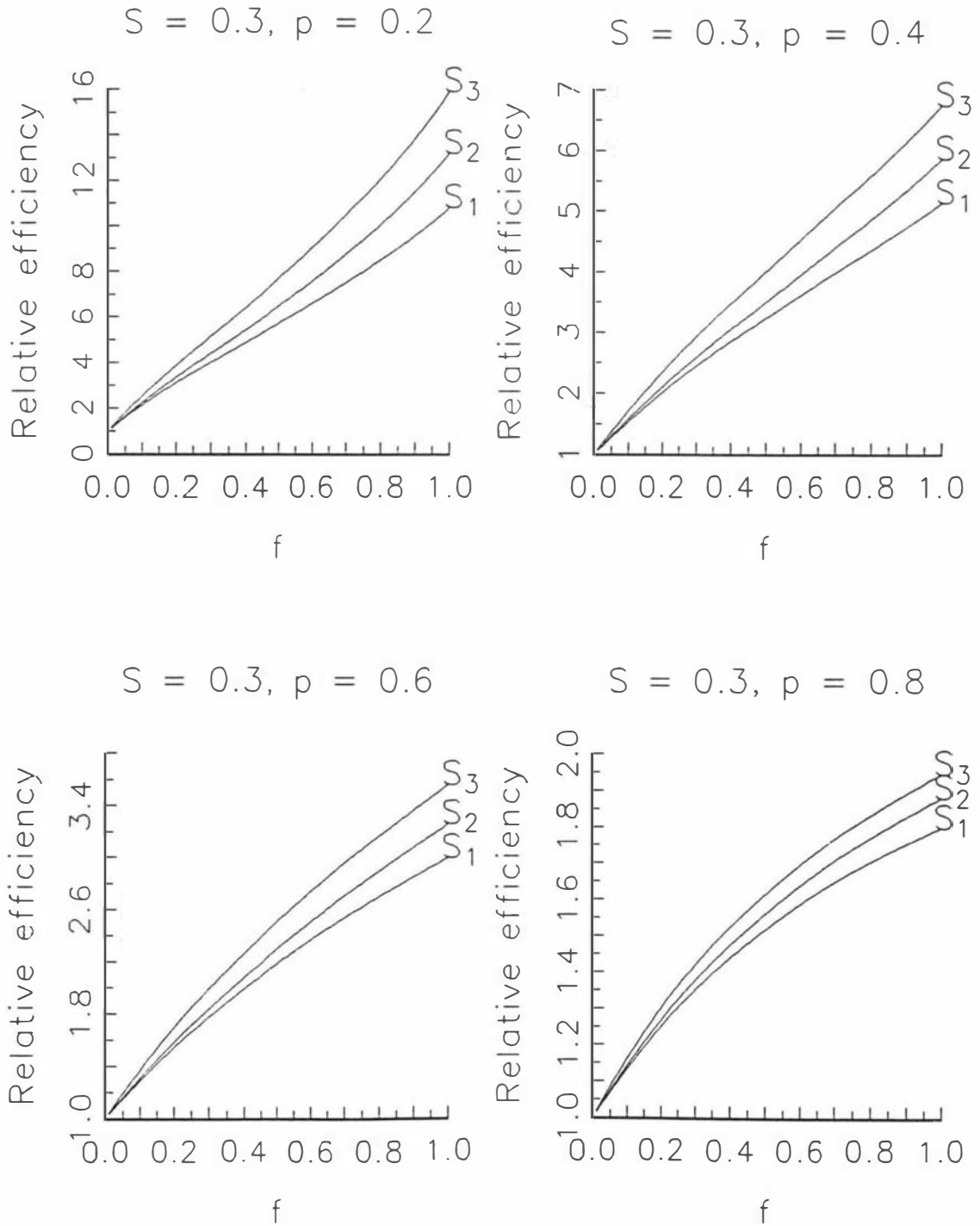


Figure 5.2: Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.5$ (Relative efficiency = $\frac{\text{Var}(\hat{S}_i^{JS})}{\text{Var}(\hat{S}_i)}$).

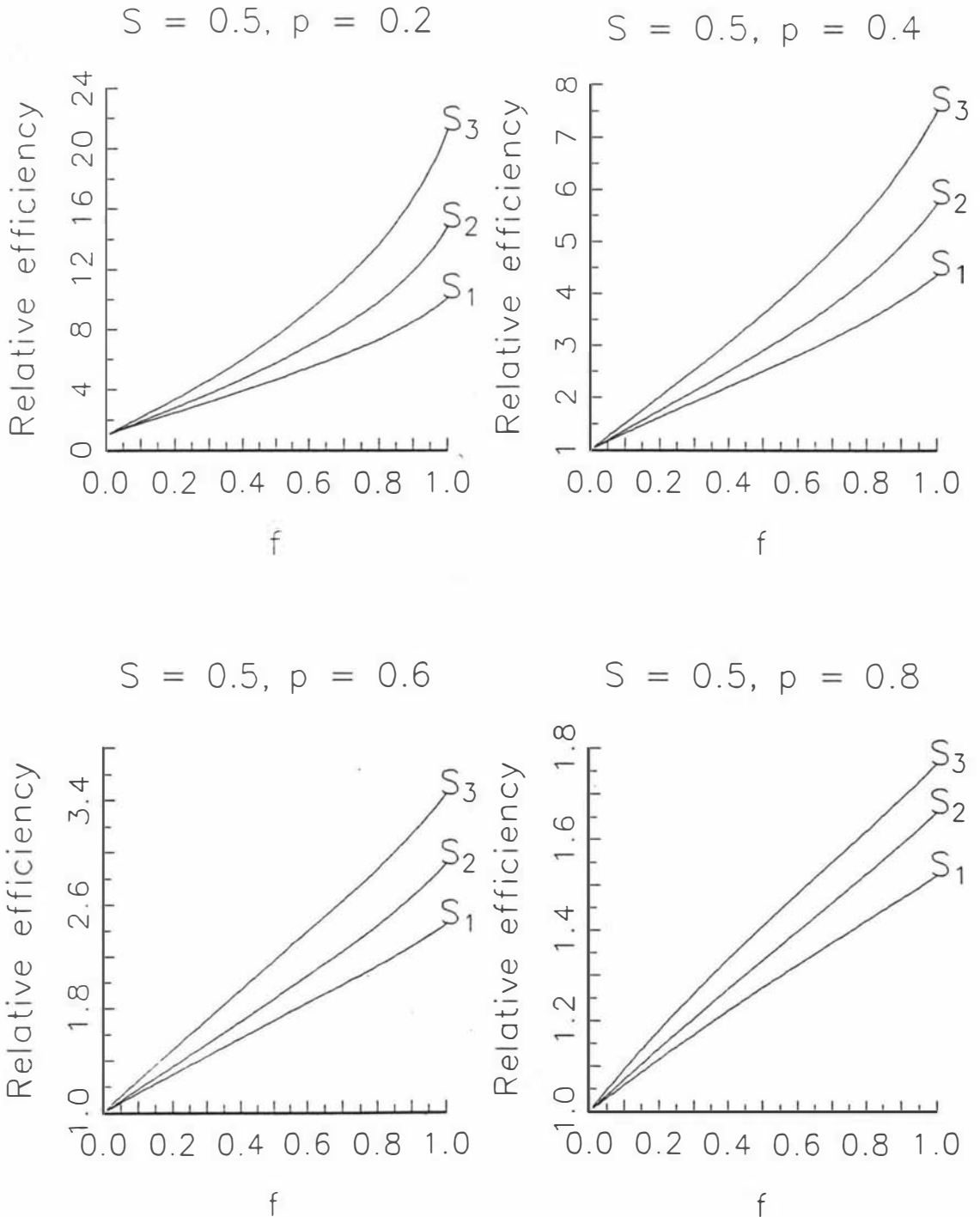


Figure 5.3: Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.8$ (Relative efficiency = $\frac{\text{Var}(\hat{S}_i^{JS})}{\text{Var}(\hat{S}_i)}$).

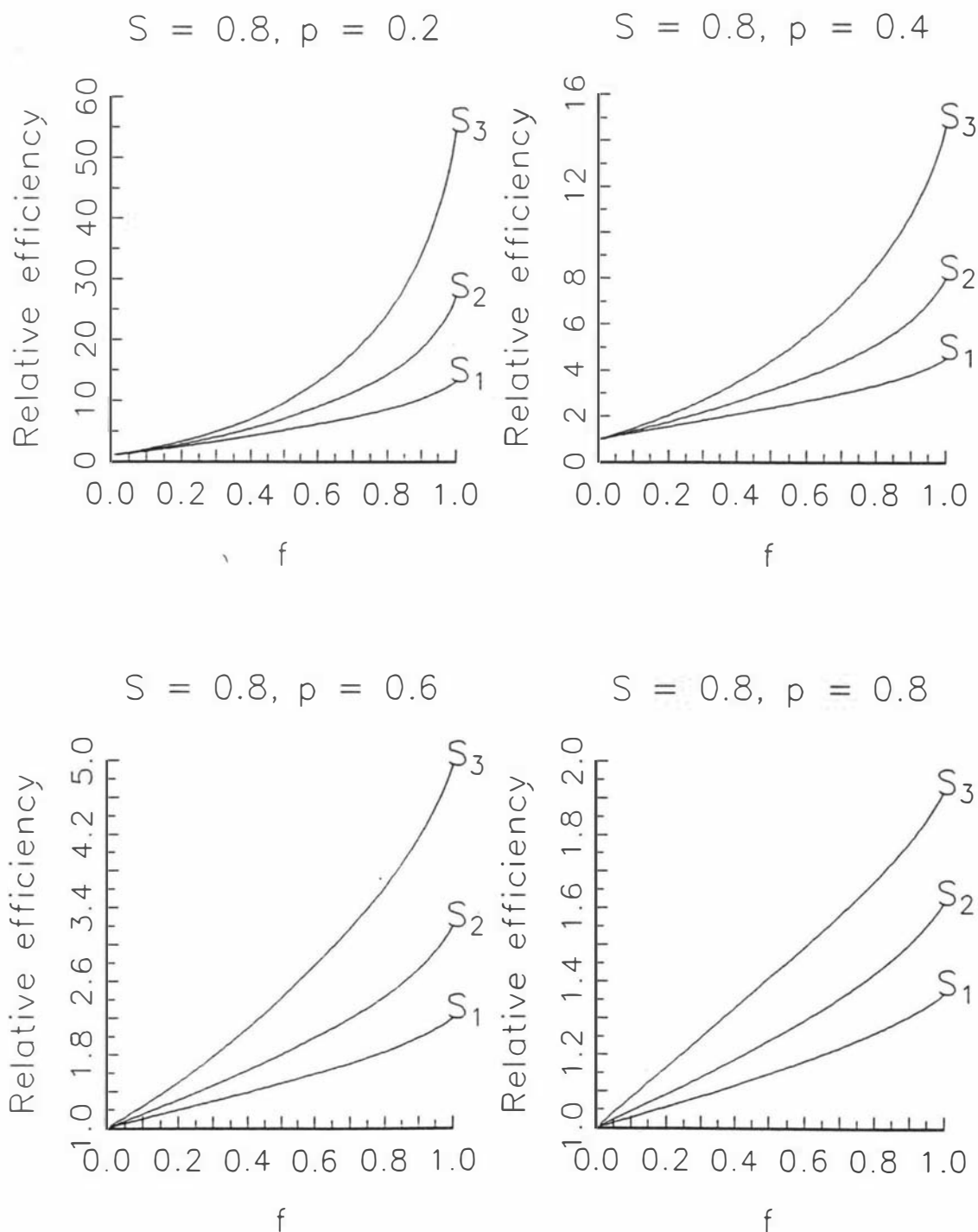
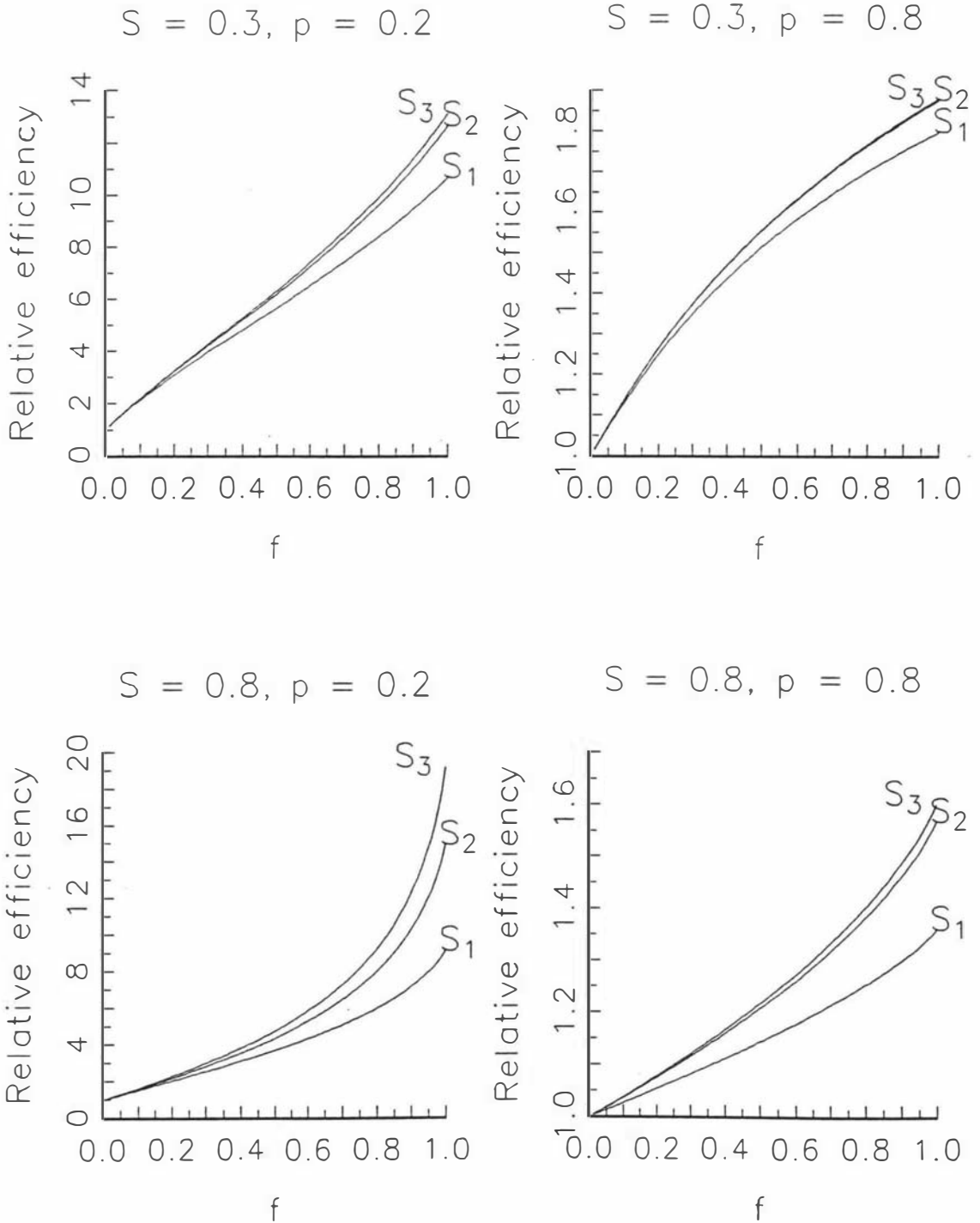


Figure 5.4: Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 10$ and various survival and capture probabilities (Relative efficiency $= \frac{\text{Var}(\hat{S}_i^{JS})}{\text{Var}(\hat{S}_i)}$).



subsequent capture probability will as a consequence also be high. This in turn will lead to under-estimation of the size of the population. Bias of the survival rate estimator, although non-zero, is generally small.

If the method of obtaining observations is unrelated to the capture method then individual capture probabilities may be unrelated to the probability a marked animal is observed. In these circumstances we might expect that the effect of heterogeneous capture probabilities is reduced by the inclusion of ancillary observations as we rely less on physical capture of the animals in collecting information on marked animals. In addition we expect the survival rate estimator to have even less bias as we are able to obtain information on the survival of low capture probability individuals through the observation process.

To examine the effect of heterogeneous capture probabilities on the estimators the expected values of the statistics $R_{i,1}$, C_i , and Z_i were obtained from a one-age mark-recapture study under random emigration with ancillary observations and where all animals are released on observation. The animal population was made up of low and high capture probability individuals with capture probabilities p_l and p_h respectively. The extent of heterogeneity was measured by the parameter Δ_p , where $p_l = \bar{p} - \frac{\Delta_p}{2}$ and $p_h = \bar{p} + \frac{\Delta_p}{2}$. All remaining parameters were held constant through time (although not constrained in the model), with θ_i given by 5.1. Asymptotic bias in the capture and survival rate estimators relative to the asymptotic bias of the Jolly-Seber estimators was measured for various combinations of \bar{p} , S , f , and Δ_p . Relative asymptotic bias (relative bias) was measured by

$$\text{Relative bias} = \frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{*JS} - \bar{p}},$$

where \hat{p}_i^* is the capture probability estimate in the model with ancillary observations assuming random emigration and \hat{p}_i^{*JS} the corresponding Jolly-Seber capture probability estimate obtained from the same data by ignoring resightings.

As suggested above, mark-recapture estimators incorporating ancillary observation appear to be more robust to heterogeneous capture probabilities (Figures 5.5, 5.6, 5.7, and 5.8) with relative bias of capture probability and survival rate estimates reduced by the inclusion of ancillary observations in all the cases considered.

However, bias in the capture probability estimator is still a potential problem. Even if observation probabilities are high, approaching 1, heterogeneous capture probabilities still lead to biased capture probability estimates (Tables 5.4 and 5.5). In contrast, absolute bias in the survival rate estimator was close to zero, less than 2% of S_i in all the cases considered.

Trap-dependence and marking effect are a type of heterogeneity of capture probabilities among marked animals that is induced by the experiment. As we have shown in Chapter 4 we can incorporate certain kinds of marking effect into the model. Under a permanent marking effect where marking permanently lowers an animal's subsequent capture probability, the Jolly-Seber point estimate of survival rate remains a valid estimator of the survival rate (i.e the model is correct for marked animals), however the variance estimator is affected depending on the type of trap-response (Nichols et al. 1984, Pollock et al. 1990).

“Trap-happiness”, occurs when trapping leads to an increase in subsequent capture probability, and hence an increase in the precision of the survival rate estimator. “Trap-shyness” leads to reduced precision, however we would expect that the effect of trap-shyness in reducing precision would be mitigated to a certain extent by the inclusion of ancillary observations, provided trap-shy animals are not also less likely to be observed.

Figure 5.5: Average asymptotic bias of \hat{p}_i^* relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individuals. $\Delta_p = p_h - p_l$, $t=5$, $S_i = 0.3$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\bar{p}_{JS} - \bar{p}}$, $P = \bar{p}$).

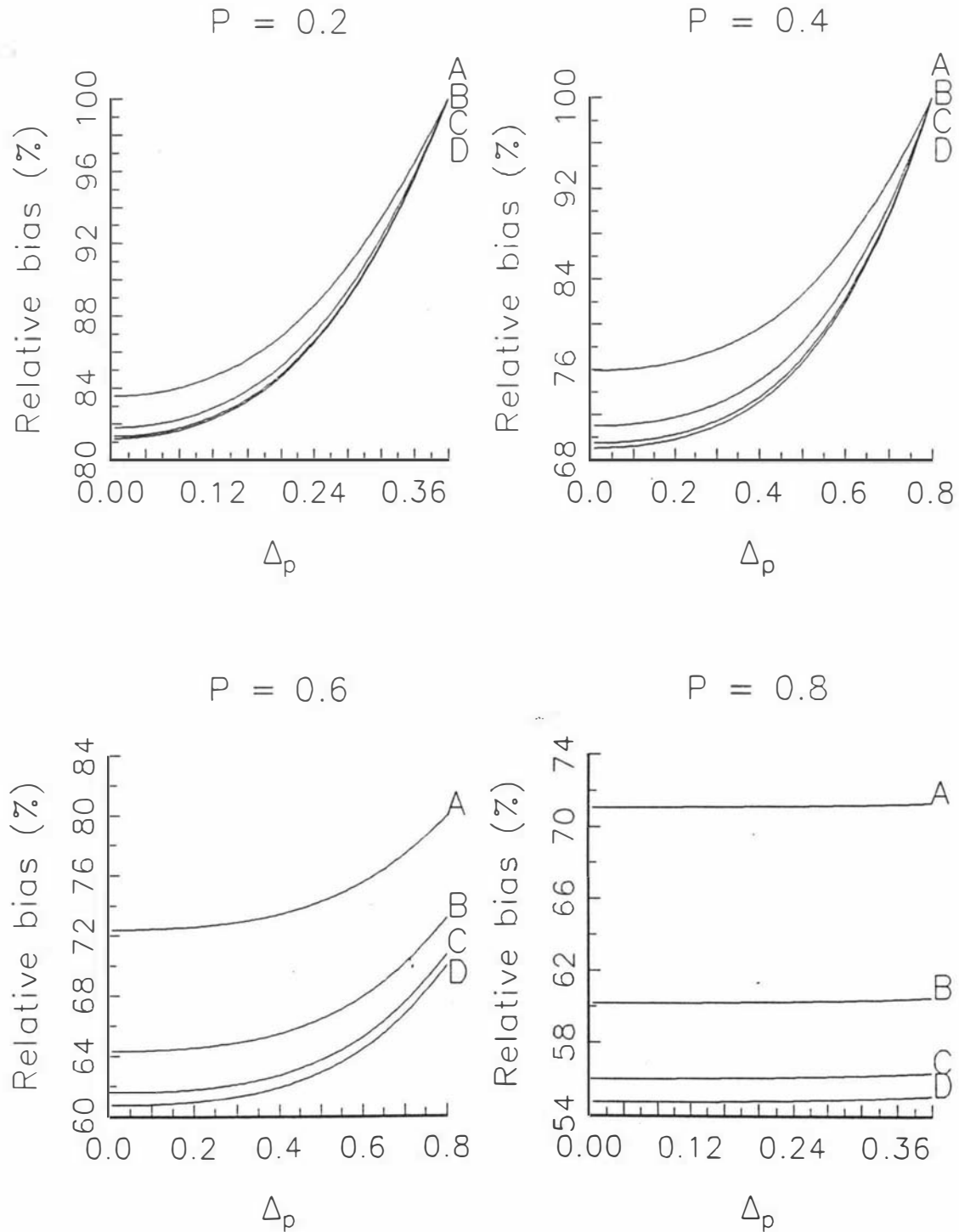


Figure 5.6: Average asymptotic bias of \hat{p}_i^* relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, $t=5$, $S_i = 0.8$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{JS} - \bar{p}}$, $P = \bar{p}$).

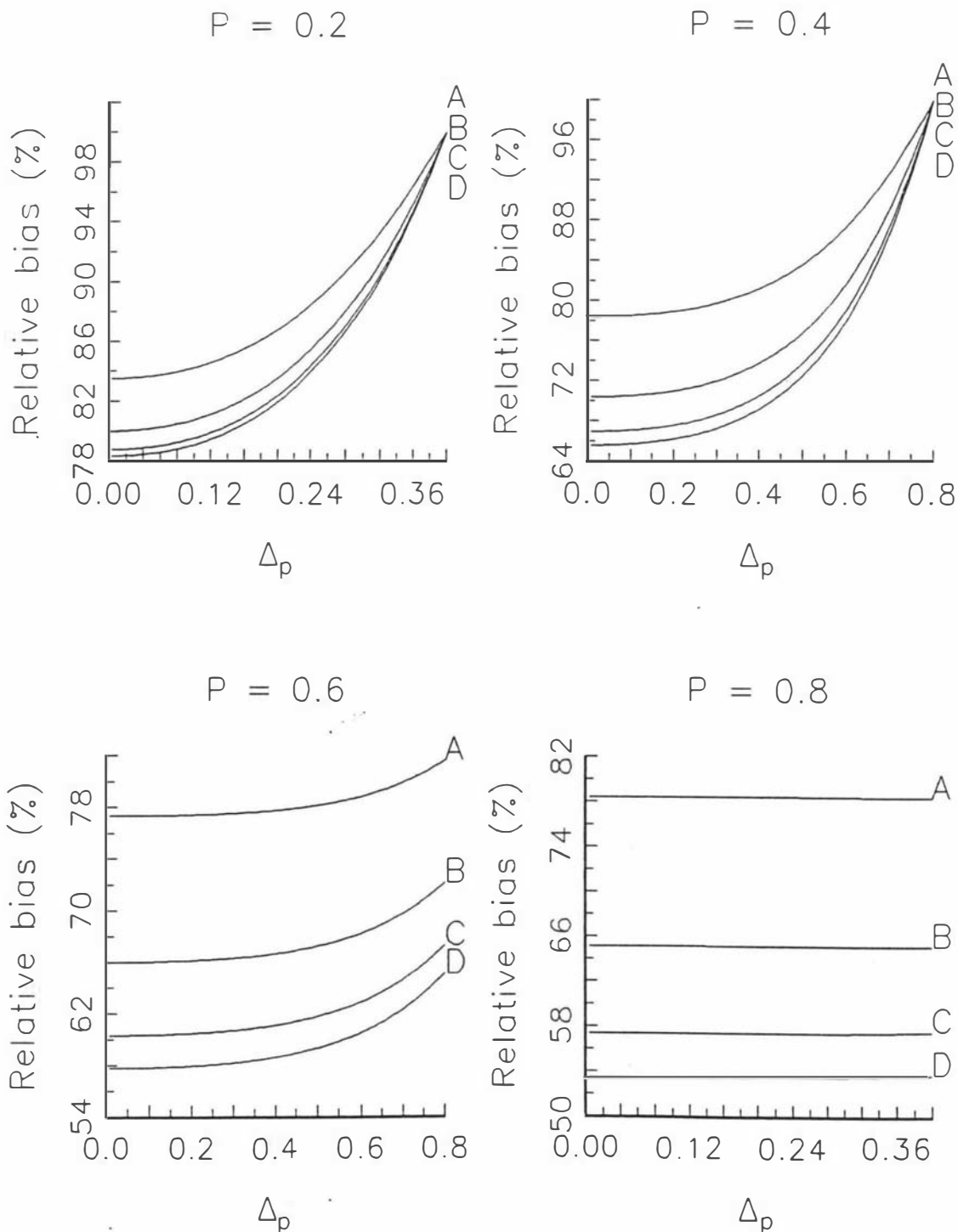


Figure 5.7: Average asymptotic bias of \hat{S}_i^* relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, $t=5$, $S_i = 0.3$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\bar{p}}$, $P = \bar{p}$).

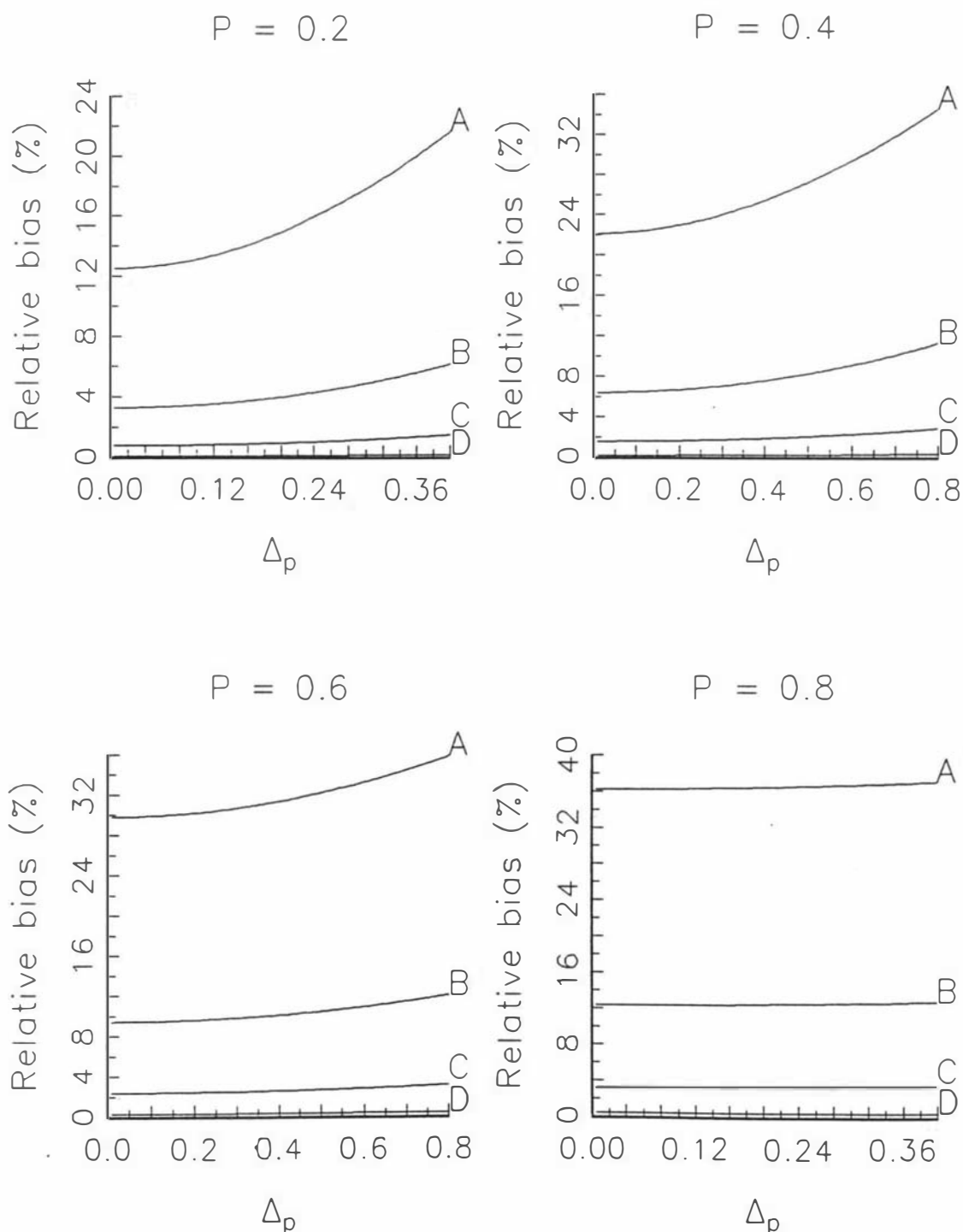


Figure 5.8: Average asymptotic bias of \hat{S}_i^* relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, $t=5$, $S_i = 0.8$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\bar{p}_i^* / S - \bar{p}}$, $P = \bar{p}$).

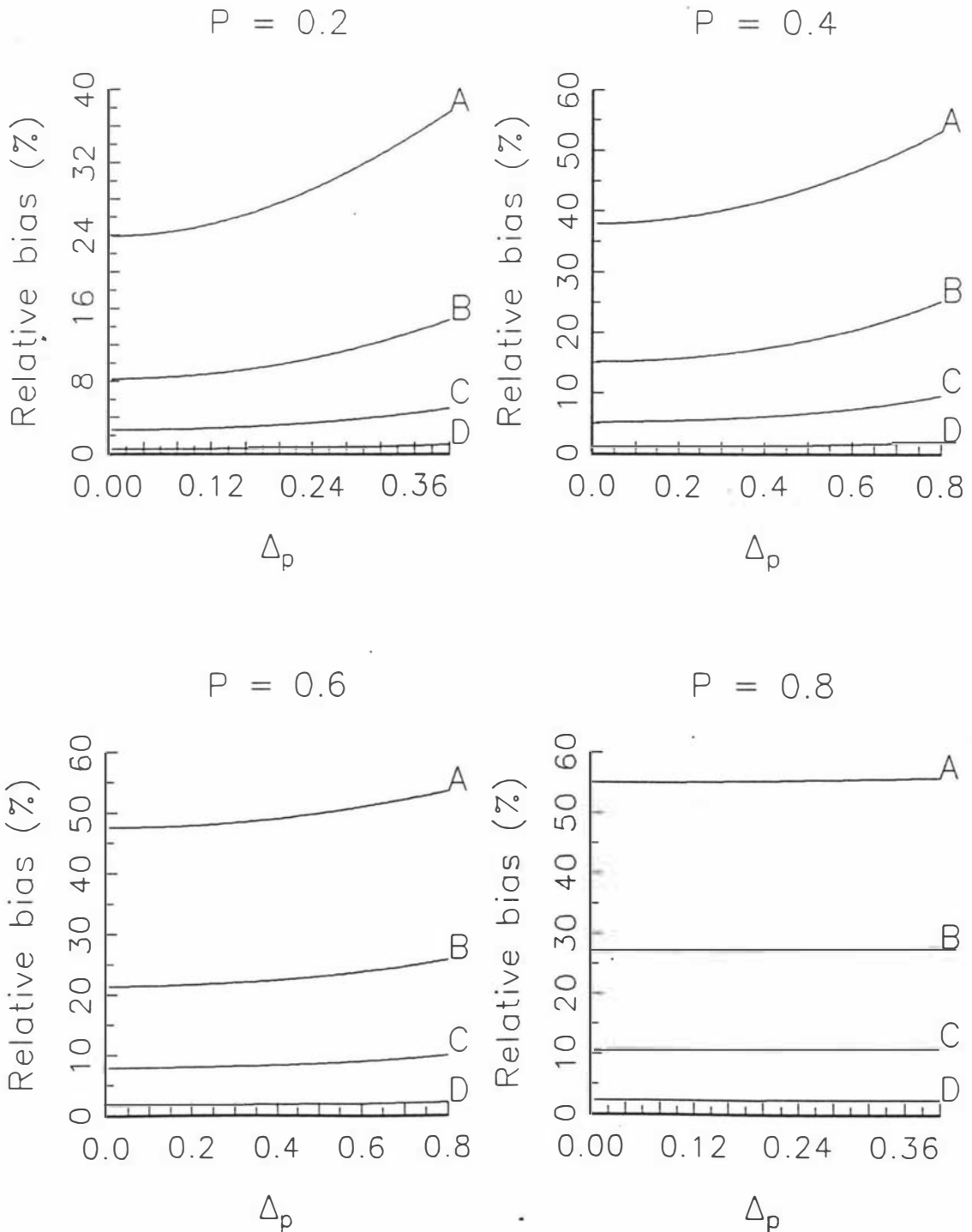


Table 5.4: Average bias of the capture ($\bar{p}_i - \bar{p}$) and survival ($\bar{S}_i - \bar{S}$) rate estimators for a $t = 5$ one-age mark recapture experiment with ancillary observations and a population made up of high (p_h) and low (p_l) capture probability individuals ($p_l = \bar{p} - \frac{\Delta_p}{2}$ and $p_h = \bar{p} + \frac{\Delta_p}{2}$), and with $S_i = 0.3$.

$S_i = 0.3 \Delta_p = 0.1$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.0122	.0061	.0041	.0032	-.0003	-.0002	-.0002	-.0002
$f=0.4$.0120	.0058	.0038	.0028	-.0001	-.0001	-.0001	-.0001
$f=0.6$.0119	.0057	.0036	.0026	-.0000	-.0000	-.0000	-.0000
$f=0.8$.0119	.0057	.0036	.0026	-.0000	-.0000	-.0000	-.0000
$S_i = 0.3 \Delta_p = 0.3$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.1116	.0553	.0373	.0285	-.0011	-.0018	-.0016	-.0058
$f=0.4$.1105	.0527	.0340	.0249	-.0003	-.0005	-.0005	-.0005
$f=0.6$.1101	.0518	.0329	.0236	-.0001	-.0001	-.0001	-.0001
$f=0.8$.1101	.0516	.0326	.0232	-.0000	-.0000	-.0000	-.0000
$S_i = 0.3 \Delta_p = 0.5$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.1556	.1046			-.0034	-.0039	
$f=0.4$.1494	.0958			-.0010	-.0012	
$f=0.6$.1474	.0928			-.0003	-.0003	
$f=0.8$.1468	.0919			-.0000	-.0000	

Table 5.4 continued.

$$S_i = 0.3 \Delta_p = 0.7$$

	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.3069	.2069			-.0025	-.0059	
$f=0.4$.3013	.1915			-.0008	-.0020	
$f=0.6$.2994	.1860			-.0002	-.0005	
$f=0.8$.2988	.1843			-.0000	-.0001	

Table 5.5: Average bias of the capture ($\bar{p}_i - \bar{p}$) and survival ($\bar{S}_i - \bar{S}$) rate estimators for a $t = 5$ one-age mark recapture experiment with ancillary observations and a population made up of high (p_h) and low (p_l) capture probability individuals ($p_l = \bar{p} - \frac{\Delta p}{2}$ and $p_h = \bar{p} + \frac{\Delta p}{2}$), and with $S_i = 0.8$.

$S_i = 0.8 \Delta_p = 0.1$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.0115	.0054	.0033	.0022	-.0008	-.0005	-.0003	-.0001
$f=0.4$.0112	.0049	.0029	.0019	-.0003	-.0002	-.0001	-.0001
$f=0.6$.0110	.0047	.0027	.0017	-.0001	-.0001	-.0000	-.0000
$f=0.8$.0110	.0046	.0026	.0016	-.0000	-.0000	-.0000	-.0000
$S_i = 0.8 \Delta_p = 0.3$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.1088	.0497	.0303	.0203	-.0029	-.0035	-.0022	-.0013
$f=0.4$.1066	.0456	.0265	.0172	-.0010	-.0014	-.0010	-.0006
$f=0.6$.1058	.0439	.0245	.0154	-.0003	-.0005	-.0004	-.0003
$f=0.8$.1055	.0432	.0237	.0145	-.0001	-.0001	-.0001	-.0001
$S_i = 0.8 \Delta_p = 0.5$								
	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.1438	.0869			-.0064	-.0053	
$f=0.4$.1342	.0763			-.0026	-.0024	
$f=0.6$.1299	.0710			-.0009	-.0009	
$f=0.8$.1282	.0686			-.0002	-.0002	

Table 5.5 continued.

$$S=0.8 \Delta_p = 0.7$$

	\bar{p}_i				\bar{S}_i			
	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$	$\bar{p} = 0.2$	$\bar{p} = 0.4$	$\bar{p} = 0.6$	$\bar{p} = 0.8$
$f=0.2$.2971	.1778			-.0044	-.0082	
$f=0.4$.2881	.1584			-.0019	-.0038	
$f=0.6$.2837	.1486			-.0007	-.0014	
$f=0.8$								

5.2 Tag-Resight Model

If all observations on marked animals subsequent to release are obtained by resighting (i.e. we have no recaptures), and if all animals are released on resighting, then the problem reduces to that considered by Cormack (1964) and Brownie and Robson (1983). The models they developed are appropriate only under a set of circumstances more restrictive than those we have considered, specifically the case where the observations for time i are obtained exactly at i . Moreover, because of concern that newly marked animals will likely be associated with the capture location they recommend ignoring observations at i from animals released at i .

In the one-age model with no marking effect we make the constraint $p_i = 0$ because there are no recaptures. Also, if observations are made exactly at i , then we make the constraint

$$(1 - \theta_i) = f_i$$

as animals alive at i and still alive at $i + 1$ are no more likely to have been observed at i than those not alive at i . Also, because the $M_{i,i,k,2}$ ($k=1,2$) are ignored, and the cell probabilities for $C_{i,1}$ cohorts are identical to those for $C_{i,2}$ cohorts, we can pool data from the two types of release cohort forming $M_{i,j,..,2} = M_{i,j,1,2} + M_{i,j,2,2}$. The probability structure of the observations $M_{i,i+1,..,2}, \dots, M_{i,t,..,2}$ ($i=1, \dots, t-1$) is shown in Table 5.6 for a $t=4$ one-age study. Note that in the absence of

Table 5.6: Probability structure for a $t = 4$ one-age tag-resight model. All observations are obtained exactly at sampling time i , and observations at i of animals released at i ignored.

	j=2	3	4
i=1	$S_1 f_2$	$S_1(1 - f_2)S_2 f_3$	$S_1(1 - f_2)S_2(1 - f_3)S_3 f_4$
2		$S_2 f_3$	$S_2(1 - f_3)S_3 f_4$
3			$S_3 f_4$

recaptures, the random emigration and permanent emigration models have identical probability structures since the parameter F_i no longer appears in the model. This

is not unexpected as the emigration is defined with respect to the capture site and we assume that observations are obtained on animals throughout their geographic range. Also note from Table 5.6 that the probability structure of the one-age tag-resight model is identical to the probability structure for marked animals in the Jolly-Seber model (see Table 1.2).

The discarding of the $M_{i,i,..,2}$ and the need for observations to be made at i over a very short period are major limitations of the above model. The discarding of the $M_{i,i,..,2}$ is a practical consideration rather than a necessary step for modelling purposes. It is made necessary by the requirement for a short observation period that coincides with the captures. Because captures and observations are made simultaneously it is likely that newly tagged animals will not have dispersed away from the capture site and as a consequence they will have a higher probability of observation. If observations are delayed for some time after captures, say to allow time for dispersal of newly marked animals, then the model is invalid because of mortality during the intervening period (Brownie and Robson 1983:446).

The need for observations to be carried out over a short interval of time concurrent with trapping is a major practical limitation. In practice, observations may occur over a lengthy period relative to the between-captures period leading to violation of the assumptions of the model. A major advantage of the models described in Chapters 3 and 4 is that we have relaxed this assumption, thus generalizing the tag-resight model discussed by Cormack (1964) and Brownie and Robson (1983).

To fit an age-dependent tag-resight model using the framework of Chapters 3 and 4 we make the constraints $p_i^{(\nu)} = 0 \forall i, \nu$. Because the constrained models are of full rank (we lose a $C_i^{(\nu)}$ corresponding to each $p_i^{(\nu)}$ constrained out) the closed-form maximum likelihood estimators of the reduced model are simply the respective maximum likelihood estimators for $S_i^{(\nu)}$, $f_i^{(\nu)}$, and $\theta_i^{(\nu)}$ given in Chapters 3 and 4, but where $R_{i,k}^{(\nu)}$, $T_i^{(\nu)}$, and $r_i^{(\nu)}$ include no recaptures. Thus, for the age-dependence model with no marking effect the MLE's are given by equations 4.12 through 4.15 and the asymptotic variances and covariances given in section 4.2.5.

Since all animals are released on observation the MLE for $S_i^{(\nu)}$ reduces to

$$\hat{S}_i^{(\nu)} = \left\{ \frac{R_{i,1}^{(\nu)}}{N_i^{(\nu)} r_i^{(\nu)}} \right\} \left\{ \frac{N_{i+1}^{(\omega)} Z_{i+1}^{(\nu+1)}}{R_{i+1,1}^{(\omega)}} + C_{i+1}^{(\nu+1)} \right\} \quad i = 1, \dots, t-1.$$

Incorporating the constraint $p_i^{(\nu)} = 0$ the asymptotic variance is given by

$$\begin{aligned} \text{Var}(\hat{S}_i^{(\nu)}) = & (S_i^{(\nu)})^2 \left\{ \frac{1}{E[R_{i,1}^{(\nu)}]} - \frac{1}{N_i^{(\nu)}} + \frac{1}{E[R_{i+1,1}^{(\omega)}]} - \frac{1}{N_{i+1}^{(\omega)}} \right. \\ & + (1 - \theta_i^{(\nu)})^2 \left(\frac{1}{E[R_{i,2}^{(\nu)}]} - \frac{1}{n_i^{(\nu)}} \right) \\ & \left. + (\theta_i^{(\nu)})^2 \frac{n_i^{(\nu)} - E[R_{i,2}^{(\nu)}]}{n_i^{(\nu)}} \left(\frac{1}{r_i^{(\nu)} - E[O_i^{(\nu)}]} - \frac{1}{r_i^{(\nu)}} \right) \right\}. \end{aligned}$$

Note that the release of all animals on “observation” is not a requirement, if some animals are removed from the population on observation we simply use (4.15) to estimate the survival rate.

Using this framework we can fit the model with and without an age-effect but importantly, we *cannot* fit a marking effect model, because there are no releases at i of animals marked before i and captured at i . For simplicity, we consider just the one-age case, and in the following discussion the superscript ν refers to mark class. The probability structure for a $t = 4$ one-age tag-resight study with temporary marking effect is illustrated in Table 5.7. Note that since all animals are released on resighting $\rho_i = 1 \forall i$. Comparison with Tables 4.1 and 4.2 shows that is identical to the probability structure for observations in the marking effect model of section 4.3 but without any $C_{i,1}^{(1)}$ cohorts and including the constraint $p_i^{(\nu)} = 0$. Note that omitting the $C_{i,1}^{(1)}$ cohorts does not reduce the number of parameters but does reduce the MSS as there are no $R_{i,1}^{(1)}$ observations. Thus the MSS has smaller dimension than the number of parameters, and unique estimates cannot be found for all parameters in the model. Consequently, to fit a marking effect model we must reduce the size of the parameter space by imposing constraints. One possible set of constraints is $(1 - \theta_i^{(\nu)}) = f_i^{(\nu)}$ as used by Cormack (1964) and Brownie and Robson (1983) (i.e. we assume a short observation period that coincides with

Table 5.7: Probability structure for a $t = 4$ one-age tag-resight study with a temporary marking response. For animals released at i , class 0 animals are those animals marked at i and class 1 animals are those animals marked before i . Note:

$$\delta_i^{(\nu)} = \frac{(1-\theta_i^{(\nu)})}{\theta_i^{(\nu)} f_i^{(\nu)}}$$

(A). Marked at i				
	$j = 1$	2	3	4
Released following capture				
$i = 1$	$f_1^{(0)}$	$S_1^{(0)} \theta_1^{(0)} f_2^{(1)}$	$S_1^{(0)} \theta_1^{(0)} S_2^{(1)} \theta_2^{(1)} f_3^{(1)}$	$S_1^{(0)} \theta_1^{(0)} S_2^{(1)} \theta_2^{(1)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$
2		$f_2^{(0)}$	$S_2^{(0)} \theta_2^{(0)} f_3^{(1)}$	$S_2^{(0)} \theta_2^{(0)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$
3			$f_3^{(0)}$	$S_3^{(0)} \theta_3^{(0)} f_4^{(1)}$
4				$f_4^{(0)}$
Released following observation				
$i = 1$		$\delta_1^{(0)} S_1^{(0)} \theta_1^{(0)} f_2^{(1)}$	$\delta_1^{(0)} S_1^{(0)} \theta_1^{(0)} S_2^{(1)} \theta_2^{(1)} f_3^{(1)}$	$\delta_1^{(0)} S_1^{(0)} \theta_1^{(0)} S_2^{(1)} \theta_2^{(1)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$
2			$\delta_2^{(0)} S_2^{(0)} \theta_2^{(0)} f_3^{(1)}$	$\delta_2^{(0)} S_2^{(0)} \theta_2^{(0)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$
3				$\delta_3^{(0)} S_3^{(0)} \theta_3^{(0)} f_4^{(1)}$
(B). Marked before i				
	$j = 1$	2	3	4
Released following capture				
$i = 1$	-	-	-	-
2	-	-	-	-
3	-	-	-	-
4	-	-	-	-
Released following observation				
$i = 1$	-	-	-	-
2			$\delta_2^{(1)} S_2^{(1)} \theta_2^{(1)} f_3^{(1)}$	$\delta_2^{(1)} S_2^{(1)} \theta_2^{(1)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$
3				$\delta_3^{(1)} S_3^{(1)} \theta_3^{(1)} f_4^{(1)}$

captures - the “short observation period” assumption). With this assumption $f_i^{(0)}$ only appears in cells corresponding to the $M_{i,i}^{(0)}$ therefore the remaining parameters can be estimated by ignoring the $M_{i,i}^{(0)}$ and combining the $C_{i,1}^{(o)}$ and $C_{i,2}^{(o)}$ data. Thus, the model reduces to the the marking effect model of Brownie and Robson (1983).

It would be useful if we could test the assumptions made by Brownie and Robson (1983) of (i) a short observation period and (ii) a marking effect on observation probabilities. In the absence of a marking effect, we can formally test the short observation period assumption. We do this by comparing the full model (i.e. $(1 - \theta_i) \neq f_i$) with the constrained model ($(1 - \theta_i) = f_i$). Factoring the likelihood we find that the MSS for the reduced model is the same as for the full model (because the $\delta_i = \frac{(1-\theta_i)}{\theta_i f_i \rho_i}$ term remains in the model), hence the reduced model is not of full rank and explicit MLE's do not appear to exist. The model can be fitted using numerical procedures and comparison between models can be made using the generalized likelihood ratio test. However, this test of the short observation period assumption is only appropriate if it is assumed there is no short-term marking effect on the observation probabilities.

Similarly, assuming a short observation period we can test whether there is an effect of marking on the observation probability. We do this using the model structure given in Table 5.7 with the constraint $(1 - \theta_i) = f_i$ and fit models with and without the constraint $f_i^{(1)} = f_i^{(0)}$, $i = 2, \dots, t$. If there is no effect of marking on observation probabilities there is potentially a large gain in precision as we are able to incorporate the $M_{i,i}^{(0)}$'s in the analysis.

Thus, we can fit a model where we assume a long observation period with no marking effect on observation probabilities and a model where we assume a short observation period and a temporary marking effect on observation probabilities. However, we cannot assume both a long observation period and a marking effect on observation probabilities, thus we cannot fully test the two assumptions using formal testing procedures based on nested models. Instead we must use discrimination procedures such as Akaike's Information Criterion (Lebreton et al. 1992) to select between the competing models.

If a short-term influence of marking on observation probabilities is likely but there is no evidence that the short-term observation period assumption is invalid then the models of Cormack (1964) and Brownie and Robson (1983) are appropriate. However, it is not generally advisable to assume a short-observation period unless there is a strong reason for believing the assumption is valid. Even if the likelihood ratio test fails to reject the assumption, this may be a consequence of low power, and the survival rate estimator may as a consequence be biased. However, if we do not assume a short observation period, we are unable to test the marking effect assumption. Thus, if it is believed that a marking effect is likely in a tag-resight experiment, steps should be taken to ensure that the short observation period assumption is valid, and the observation period coincides with the capture period.

5.3 Tag-Resight when Only Young Animals Are Captured

A closely related problem to that discussed at the end of the previous section occurs in a tag-resight model when animals can be captured and marked only while young. This situation is common in many colonially nesting bird species where birds can only be captured while still in the pre-flight stage. The problem has been considered from the perspective of tag-return data and several models proposed, although Anderson et al. (1985) have strongly argued that the assumptions of these models are unlikely to hold in most cases. For example, Barker and Buchanan (1993) showed that if tag-returns from animals in the first year following tagging (i.e. while the animals are still young) are ignored, the tag-recovery data can be modelled using model M_1 of Brownie et al. (1985) by assuming time-invariant juvenile survival rates. Although in many cases this approach may be reasonable, it is unsatisfactory in that it is not possible to formally test the adequacy of the assumption apart from the general goodness-of-fit statistic.

As noted by Pollock et al. (1990), a tag-resight approach can be used to obtain

data from adult animals that are unavailable through live-recaptures. The advantage that this approach has over the tag-return models discussed by Anderson et al. (1985) is that adults are released into a new cohort following observation, thus allowing separate estimation of juvenile and adult parameters. Writing out the probability structure for a $t = 4$ study (noting that $\rho_i = 1 \forall i$) it is evident that not all parameters in the model will be identifiable without captures of adults (Table 5.8). Comparison with Table 5.7 shows that the tag-resight marking effect model is identical to the two-age tag-resight model with animals only captured as young. Therefore we can only fit a tag-resight model to data from animals captured only as young if we assume a short observation period coincident with the capture period.

5.3.1 Tag-return models

The tag-resight models lead naturally to a discussion of the tag-return models where observations are obtained only from dead animals. If $p_i^{(\nu,k)} = 0$ and $\eta_i^{(\nu,k)} = 0$ (no recaptures, or recaptures are ignored, and all animals are lost on observation) then the statistics $M_{i,j,1,1}^{(\nu,k)}$, $M_{i,j,2,k}^{(\nu,k)}$, $C_i^{(\nu,k)}$ and $R_{i,2}^{(\nu,k)}$ are all structurally zero and the one-age model without marking effect described in Chapter 3 reduces to the Seber-Robson-Youngs bird-banding model described by Brownie et al. (1985). The age-dependence generalization of Chapter 4 without marking effect reduces to model H_1 of Brownie et al. (1985) if $l = 2$ and model H_4 if $l = 3$.

Because animals are never recaptured (or recaptures are ignored) the marking effect model with the constraints $p_i^{(\nu,k)} = 0$ and $\eta_i^{(\nu,k)} = 0$ is not fully identifiable (Brownie et al. (1985:79)). In the one-age model the intermediate model with the constraint $S_i^{(0)} = S_i^{(1)}$ (the superscripts ν now refer to mark class) can be fitted and corresponds to model M_0 of Brownie et al. (1985). In the two-age case we make the constraints $S_i^{(0,0)} = S_i^{(0,1)}$ and $S_i^{(1,0)} = S_i^{(1,1)}$ leading to a model equivalent to H_2 . A complete age-dependence generalization of H_2 is obtained by making the constraint $S_i^{(\nu,0)} = S_i^{(\nu,1)}$ for all ν .

The key difference between the tag-resight and tag-recovery models is the fate of the animals when they are observed following release. In a tag-recovery study

Table 5.8: Probability structure for a $t = 4$ tag-resight study for animals tagged only as young and with observations obtained throughout the interval $i, i + 1$. Class 0 animals are young, class 1 animals are adult.

Young released following capture				
	$j = 1$	2	3	4
$i = 1$	$f_1^{(0)}$	$S_1^{(0)}\theta_1^{(0)}f_2^{(1)}$	$S_1^{(0)}\theta_1^{(0)}S_2^{(1)}\theta_2^{(1)}f_3^{(1)}$	$S_1^{(0)}\theta_1^{(0)}S_2^{(1)}\theta_2^{(1)}S_3^{(1)}\theta_3^{(1)}f_4^{(1)}$
2	-	$f_2^{(0)}$	$S_2^{(0)}\theta_2^{(0)}f_3^{(1)}$	$S_2^{(0)}\theta_2^{(0)}S_3^{(1)}\theta_3^{(1)}f_4^{(1)}$
3	-	-	$f_3^{(0)}$	$S_3^{(0)}\theta_3^{(0)}f_4^{(1)}$
4	-	-	-	$f_4^{(0)}$
Young released following observation				
$i = 1$	-	$\frac{(1-\theta_1^{(0)})}{f_1^{(0)}}S_1^{(0)}f_2^{(1)}$	$\frac{(1-\theta_1^{(0)})}{f_1^{(0)}}S_1^{(0)}S_2^{(1)}\theta_2^{(1)}f_3^{(1)}$	$\frac{(1-\theta_1^{(0)})}{f_1^{(0)}}S_1^{(0)}S_2^{(1)}\theta_2^{(1)}S_3^{(1)}\theta_3^{(1)}f_4^{(1)}$
2	-	-	$\frac{(1-\theta_2^{(0)})}{f_2^{(0)}}S_2^{(0)}f_3^{(1)}$	$\frac{(1-\theta_2^{(0)})}{f_2^{(0)}}S_2^{(0)}S_3^{(1)}\theta_3^{(1)}f_4^{(1)}$
3	-	-	-	$\frac{(1-\theta_3^{(0)})}{f_3^{(0)}}S_3^{(0)}f_4^{(1)}$
Adults released following capture				
	$j = 1$	2	3	4
$i = 1$	-	-	-	-
2	-	-	-	-
3	-	-	-	-
4	-	-	-	-
Adults released following observation				
$i = 1$	-	-	-	-
2	-	-	$\frac{(1-\theta_2^{(1)})}{f_2^{(1)}}S_2^{(1)}f_3^{(1)}$	$\frac{(1-\theta_2^{(1)})}{f_2^{(1)}}S_2^{(1)}S_3^{(1)}\theta_3^{(1)}f_4^{(1)}$
3	-	-	-	$\frac{(1-\theta_3^{(1)})}{f_3^{(1)}}S_3^{(1)}f_4^{(1)}$

the animals are removed from the population on observation and hence are not transferred to a new cohort. Ordinarily the observations are made by hunters or anglers returning or reporting tags from animals they have killed. In some cases the observations are obtained from members of the public reporting dead animals. These different types of tag-recovery do not effect the model, they just lead to different interpretations of the $f_i^{(\nu,k)}$ (Seber 1982:526). In either case the animals are not released following observation, thus we have no $C_{i,2}$ cohorts. In addition, the event “not observed in $i, i + 1$ given alive at $i + 1$ ” has probability one (i.e. $\theta_i^{(\nu,k)} = 1 \forall i$) thus the joint probability that an animal survives from i to $i + 1$ and is not observed in $i, i + 1$, is given simply by the survival rate $S_i^{(\nu,k)}$.

To facilitate comparison with Brownie et al. (1985) the relationship between our notation and their notation for the one-age model without marking effect is given in Table (5.9).

Table 5.9: Statistics used by Brownie et al. (1985) for the one-age model without a marking effect and the equivalent ancillary observations model statistics.

Statistic	Brownie et al. (1985)	Interpretation
$R_{i,1}$	R_i	total number of tags recovered from those released at i
O_i	C_i	total number of tag recoveries at time i
r_i	T_i	total tag recoveries from animals marked at or before i
Z_i	$T_i - C_i$	total tag recoveries at or after $i + 1$ from animals marked at or before i

Making the constraints $\theta_i^{(\nu)} = 1$ and $p_i^{(\nu)} = 0$ in the age-dependent model without a marking effect and noting that in a tag-recovery experiment we obtain only the observations $M_{i,j,1,2}^{(\nu)}$, $\nu = 0, \dots, l$ (and hence $C_i^{(\nu)} = 0 \forall i$), the reduction in dimensionality of the parameter space and the MSS is identical, hence the MLE's exist in closed form. We find that these correspond to 4.12 and 4.15, except for the survival rate estimator the term $\frac{R_{i,1}^{(\nu)} R_{i,2}^{(\nu)} L_{i,2}^{(\nu)}}{n_i^{(\nu)} N_i^{(\nu)} r_i^{(\nu)} T_{i+1}^{(\nu)}}$ reduces to zero. In the one-age

case the estimate of f_i is in fact identical to 4.12 (ignoring the superscript (ν) and the estimator for S_i reduces to

$$\hat{S}_i = \frac{R_{i,1} N_{i+1} Z_{i+1}}{N_i r_i R_{i+1,1}} .$$

as given by Brownie et al. (1985:16). In a similar manner we find that the 2-age survival and recovery rate estimators are equivalent to those given by Brownie et al. (1985:60). Explicit estimators under a temporary marking effect can be obtained from the estimators of section(4.4) however there are some restrictions on parameter estimability (see Brownie et al. 1985:30).

5.4 Models with Recaptures and 100% Losses on Observation

If all animals are lost on resighting, and in addition to resightings we have live-recaptures (i.e. $\rho_i^{(\nu,k)} = 0$ and $p_i^{(\nu,k)} > 0$) we obtain joint tag-recovery/recapture models. In the one age case with no marking effect and if emigration is random or permanent we obtain the set of models considered by Burnham (1993), with f_i interpreted as the tag recovery rate.

Because these models have only been recently developed, there is little published theory. Burnham (1993) noted that closed-form estimators do not appear to be possible under permanent emigration. The distribution of the MSS under random emigration and MLE's have been derived by Burnham (pers. comm.) for the one-age case without marking effect, although not published. For the general age-dependence and marking effect case the distribution of the MSS and hence the likelihood function and MLE's are easily derived directly from expression 4.20. Noting that there are no $C_{i,2}^{(\nu)}$ cohorts we simply omit terms involving $R_{i,2}^{(\nu)}$, and exclude any $M_{i,j,2,k}^{(\nu)}$ that appear in the the calculation of the statistics. Also, as in the tag-return model $\theta_i^{(\nu,k)} = 1 \forall i$. As an example, the likelihood for s study with $\nu = l$ (i.e. no resightings obtained after the interval $t, t + 1$, the likelihood under age- and temporary marking effect is given by

$$\begin{aligned}
\mathcal{L} = & \prod_{\nu=0}^l \left\{ \prod_{i=k+1}^t \prod_{k=0}^1 \left\{ \left(\begin{array}{c} N_i^{(\nu,k)} \\ R_{i,1}^{(\nu,k)} \end{array} \right) (\lambda_{i,1}^{(\nu,k)})^{R_{i,1}^{(\nu,k)}} (1 - \lambda_{i,1}^{(\nu,k)})^{N_i^{(\nu,k)} - R_{i,1}^{(\nu,k)}} \right\} \right. \\
& \times \prod_{k=1}^2 \prod_{i=k+1}^t \left\{ \left(\begin{array}{c} T_i^{(\nu+1,k)} \\ C_i^{(\nu+1,k)} \end{array} \right) (\tau_{i,1}^{(\nu+1,k)})^{C_i^{(\nu+1,k)}} (1 - \tau_{i,1}^{(\nu+1,k)})^{T_i^{(\nu+1,k)} - C_i^{(\nu+1,k)}} \right\} \\
& \times \prod_{i=k+1}^{t-1} \prod_{k=0}^1 \left\{ \left(\begin{array}{c} r_i^{(\nu,k)} \\ O_i^{(\nu,k)} \end{array} \right) (\tau_{i,2}^{(\nu,k)})^{O_i^{(\nu,k)}} (1 - \tau_{i,2}^{(\nu,k)})^{r_i^{(\nu,k)} - O_i^{(\nu,k)}} \right\} \left. \right\} \\
& \times \frac{\prod_{h=l-1}^l \left(\begin{array}{c} r_1^{(h,0)} - O_1^{(h,0)} - M_{1,2,p,1}^{(h,0)} \\ [M_{1,j,p,1}^{(h,0)}]_{j=3}^t [M_{1,j,p,2}^{(h,0)}]_{j=2}^t \end{array} \right) \left(\begin{array}{c} R_{2,1}^{(l,1)} \\ [M_{2,j,1,1}^{(l,1)}]_{j=3}^t [M_{2,j,1,2}^{(l,1)}]_{j=2}^t \end{array} \right)}{\left(\begin{array}{c} r_2^{(l,1)} \\ [M_{2,j,p,1}^{(l,1)}]_{j=3}^t [M_{2,j,p,2}^{(l,1)}]_{j=2}^t \end{array} \right)} \\
& \times \prod_{\nu=0}^{l-2} \left\{ \frac{\left(\begin{array}{c} r_1^{(\nu,0)} - O_1^{(\nu,0)} - M_{1,2,p,1}^{(\nu,0)} \\ [M_{1,j,p,1}^{(\nu,0)}]_{j=3}^t [M_{1,j,p,2}^{(\nu,0)}]_{j=2}^t \end{array} \right) \left(\begin{array}{c} R_{2,1}^{(\nu+1,1)} \\ [M_{2,j,1,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,1,2}^{(\nu+1,1)}]_{j=2}^t \end{array} \right)}{\left(\begin{array}{c} r_2^{(\nu+1,1)} \\ [M_{2,j,p,1}^{(\nu+1,1)}]_{j=3}^t [M_{2,j,p,2}^{(\nu+1,1)}]_{j=2}^t \end{array} \right)} \right\} \\
& \times \prod_{i=2}^{t-2} \left\{ \frac{\prod_{h=l-1}^i \prod_{k=0}^1 \left(\begin{array}{c} r_i^{(h,k)} - O_i^{(h,k)} - M_{i,i+1,p,1}^{(h,k)} \\ [M_{i,j,p,1}^{(h,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(h,k)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i+1,1}^{(l,1)} \\ [M_{i+1,j,1,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(l,1)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_{i+1}^{(l,1)} \\ [M_{i+1,j,p,1}^{(l,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(l,1)}]_{j=i+1}^t \end{array} \right)} \right. \\
& \left. \times \prod_{\nu=0}^{l-2} \left\{ \frac{\prod_{k=0}^1 \left(\begin{array}{c} r_i^{(\nu,k)} - O_i^{(\nu,k)} - M_{i,i+1,p,1}^{(\nu,k)} \\ [M_{i,j,p,1}^{(\nu,k)}]_{j=i+2}^t [M_{i,j,p,2}^{(\nu,k)}]_{j=i+1}^t \end{array} \right) \left(\begin{array}{c} R_{i+1,1}^{(\nu+1,1)} \\ [M_{i+1,j,1,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,1,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)}{\left(\begin{array}{c} r_i^{(\nu+1,1)} \\ [M_{i+1,j,p,1}^{(\nu+1,1)}]_{j=i+2}^t [M_{i+1,j,p,2}^{(\nu+1,1)}]_{j=i+1}^t \end{array} \right)} \right\} \right\}
\end{aligned}$$

The MLE's of $p_i^{*(\nu,k)}$, and $f_i^{(\nu,k)}$ are identical to those given in section (4.4).

Because the joint probability an animal survives from i to $i + 1$ and is not seen is given by $S_i^{(\nu,k)}$ in the tag-return model and not $S_i^{(\nu,k)} \theta_i^{(\nu,k)}$ we redefine

$$\alpha_{i,k}^{(\nu,k)} = \begin{cases} S_i^{(\nu,k)} F_i^{*(\nu,k)} p_{i+1}^{(\omega,1)} & k = 1 \\ f_i^{(\nu,k)} & k = 2 \end{cases}$$

and

$$\beta_i^{(\nu,k)} = S_i^{(\nu,k)} (1 - F_i^{(\nu,k)} p_{i+1}^{(\omega,1)})$$

leading to

$$\hat{S}_i^{(\nu,k)} = \left\{ \frac{R_{i,1}^{(\nu,k)}}{N_i^{(\nu,k)} r_i^{(\nu,k)}} \right\} \left\{ \frac{N_{i+1}^{(\omega,1)} Z_{i+1}^{(\nu+1,k+1)}}{R_{i+1,1}^{(\omega,1)}} + C_{i+1}^{(\nu+1,k+1)} \right\} \quad i = k + 1, \dots, t - 1,$$

with the exception of $S_i^{(0,1)}$ which does not appear in the model. Also, the relevant asymptotic variances are identical to those given in section 4.4 with the exception

$$\text{Var}(\hat{S}_i^{(\nu,k)}) = (S_i^{(\nu,k)})^2 \left\{ \frac{1}{E[R_{i,1}^{(\nu,k)}]} - \frac{1}{N_i^{(\nu,k)}} + \frac{1}{E[R_{i+1,1}^{(\omega,1)}]} - \frac{1}{N_{i+1}^{(\omega,1)}} \right. \\ \left. \frac{1}{r_i^{(\nu,k)} - E[O_i^{(\nu,k)}]} - \frac{1}{r_i^{(\nu,k)}} \right\}.$$

From the $P\tau(\text{MSS}|\text{Data})$ component of the likelihood, the overall goodness-of-fit test comprises only the second component of the test discussed in section 4.4 with terms corresponding to members of $C_{i,2}^{(\nu,k)}$ cohorts omitted.

Note that because of the live recaptures we can fit the joint age-dependence and temporary marking effect model of section 4.4 to the joint live-recapture/tag-recovery data without the constraint $S_i^{(\nu,0)} = S_i^{(\nu,1)}$. This represents a considerable improvement over the tag-return models which do not allow modelling a marking effect for both recovery and survival rates (Brownie et al. 1985:79).

Fitting the one-age model without marking effect is illustrated using the following example from a Wanganui paradise shelduck population tagged by the author between 1987 and 1991 (Table 5.10). Summary statistics are provided in Table 5.11 and parameter estimates in Table 5.12.

Table 5.10: Joint live-recapture and tag-recovery array for paradise shelduck tagged in the Wanganui area 1987-1991.

Year last released	No. released	Year recaptured				Year recovered				
		88	89	90	91	87	88	89	90	91
87	2330	468	49	33	19	76	59	18	19	7
88	2825		223	119	72		183	52	19	19
89	836			117	58			33	16	7
90	1018				120					33

Table 5.11: Summary statistics for Wanganui paradise shelduck tagging program 1987-1991.

Year	N_i	R_i	C_i	O_i	Z_i	T_i	r_i
87	2330	748		76			748
88	2825	687	468	242	204	672	891
89	836	231	272	103	377	649	608
90	1018	182	269	93	236	505	418
91	963	33	269	89	56	325	89

Table 5.12: Parameter estimates for the Wanganui paradise shelduck tagging data

Year	\hat{p}_i^*	$se(\hat{p}_i^*)$	\hat{f}_i	$se(\hat{f}_i)$	\hat{S}_i	$se(\hat{S}_i)$
87	-	-	.0326	.0037	.5609	.0261
88	.3581	.0207	.0661	.0042	.4466	.0271
89	.1662	.0135	.0468	.0050	.7222	.0617
90	.1693	.0157	.0398	.0045	.8140	.1550
91	.1413	.0274	.0343	.0059	-	-

The goodness-of-fit contingency table for members of r_{88} is given in Table 5.13. Cells are pooled to give the test of the random emigration hypothesis as suggested in section 3.6. This contingency table provides strong ($\chi^2_3 = 11.78, p = .008$) evidence

Table 5.13: 4×2 contingency table testing whether the probability that a member of r_{88} is ever captured or recovered is influenced by whether it was captured in 1988.

	Not captured 1988	Captured 1988	Member of r_{88}
Captured 1989	49	223	272
Captured after 1989	52	191	243
Not captured, recovered 1988	59	183	242
Not captured, recovered after 1988	44	90	134
	204	687	891

against the random emigration model for members of r_{88} . This may be because the random emigration hypothesis is inappropriate, however there may be other reasons for this lack of fit.

5.5 Fitting Less than Full Rank Models

In the previous sections of this chapter we considered a class of reduced parameter models that correspond to published mark-recapture models. These models are generally of full-rank, with well-known explicit estimators. Where the models are not of full rank explicit MLE's usually cannot be found and numerical procedures must be used (Brownie et al. 1985). Within the context of the live-recovery and tag-return models, important reduced parameter models have been considered in detail by Jolly (1982) and Brownie et al. (1986) for the live-recapture models and Brownie et al. (1985) for the tag-return models. In both cases software packages

are widely available that automatically fit these models.

The approach taken by Brownie et al. (1986) is to use the likelihood expressed in product binomial form such as (3.23), substitute the constrained parameters into the likelihood, then solve the likelihood equations numerically. In the method of scoring technique used by Brownie et al. (1985:216) each iteration requires computation of second-order partial derivatives of the likelihood to obtain corresponding elements of the estimated information matrix. Brownie et al. (1986) point out that this step can be simplified because of the binomial structure of the likelihood. If the random variable x is binomial (N, λ) , where λ is a function of the parameters $\theta_1, \dots, \theta_p$ then

$$-E \left[\frac{\partial^2 l}{\partial \theta_i \partial \theta_j} (x \ln(\lambda) + (N - x) \ln(1 - \lambda)) \right] = \frac{N}{\lambda(1 - \lambda)} \frac{\partial \lambda}{\partial \theta_i} \frac{\partial \lambda}{\partial \theta_j}.$$

Thus, at each iteration, only first-order partial derivatives need be computed.

Brownie et al. (1986) also point out that the product binomial form of the likelihood function means that tests between models have a simple form. If the likelihood comprises p binomial terms with indices N_1, \dots, N_p and corresponding parameters λ_i then

$$\chi_{BvA}^2 = \sum_{i=1}^p N_i \left[\frac{(\hat{\lambda}_{i,B} - \hat{\lambda}_{i,A})^2}{\hat{\lambda}_{i,B}} + \frac{(1 - \hat{\lambda}_{i,B} - 1 - \hat{\lambda}_{i,A})^2}{1 - \hat{\lambda}_{i,B}} \right]$$

has an asymptotic chi-square distribution where $\hat{\lambda}_{i,A}$ is the MLE of λ_i under the general model, model A, and $\hat{\lambda}_{i,B}$ the corresponding MLE under the reduced model, model B. Brownie et al. (1986) then show that overall goodness of fit tests for the reduced models can be constructed from the above test between models and the overall goodness-of-fit statistic for the general model. If χ_A^2 is the asymptotic chi-square statistic for the general goodness-of-fit test for model A obtained without pooling then

$$\chi_{BvA}^2 + \chi_A^2$$

is an asymptotic chi-square statistic under the null hypothesis that model B is correct.

If the likelihood cannot be expressed in a simple product binomial form the above procedures cannot be used. An alternative approach to numerical estimation is to use a general numerical optimization computer package. SURVIV (White 1983) is a software package designed for fitting mark-recapture type models that are based on the multinomial distribution. SURVIV is in fact a very general package and may be used for fitting any model based on a product multinomial likelihood. As input the user provides the size of each cohort, the observations in each multinomial cell, and the algebraic structure for the cell probabilities. SURVIV then fits the product multinomial likelihood numerically. Useful features of SURVIV are:

- (i) Constrained models can be fitted using a straight-forward CONSTRAINTS statement
- (ii) Goodness-of-fit tests with automatic pooling are provided
- (iii) The simple to use TEST procedure returns generalized likelihood ratio statistics for tests between models.

As originally developed the programme analyzes the data using a two cycle process. At the first cycle, the user supplied algebraic structure for the cell probabilities is used to generate FORTRAN source code for the log-likelihood, utilizing SURVIV's "front-end". The user then compiles this FORTRAN source code and links the compiled code to create the SURVIV executable programme. SURVIV is then run a second time and the analysis is performed utilizing the log-likelihood specified in the first cycle.

A limitation of the user-specified "front-end" is that space limitations restrict the complexity of the algebraic cell structure that may be written. For example do-loops cannot be used to compute the $\gamma_{i,j,k}^{(v)}$'s using the recursion relationships given in Chapters 3 and 4 for permanent and Markov emigration models.

SURVIV can be used for analyzing data requiring a more difficult log-likelihood functions by ignoring the first stage of the cycle in which SURVIV writes the FORTRAN source code for the log-likelihood. Instead the user can write the FORTRAN source code for the likelihood which is then compiled and linked with the

other programme object files to create the SURVIV executable code incorporating this log-likelihood. FORTRAN code for the age-dependent and temporary marking effects models under discussed in Chapters 3 and 4 is given in Section 5 of the Appendix for the random emigration case.

Chapter 6

Application - Lake Brunner

Trout Tagging 1987-1990

Between 1987 and 1990, 1,675 male and 1,718 female brown trout *Salmo trutta*, were tagged in spawning tributaries of Lake Brunner, Westland. Trapping was carried out in May each year and all fish were released alive after capture. During trapping, 188 recaptures of fish tagged in previous years were recorded, and by 1992, 285 tagged fish were reported killed by anglers and an additional 55 captured and released (not including fish captured and released twice within a year).

To be trapped and tagged a fish must have entered a spawning tributary and run up that tributary at least as far as the trap. Thus, at any trapping occasion the population was divided into two groups. Group 1 comprised those fish that had entered one of the spawning tributaries trapped during the study, at least as far as the trap, and hence were at risk of capture. The second group was those fish that were not at risk of capture because they (a) failed to enter any spawning stream, (b) entered a spawning stream that was not trapped, or (c) they entered one of the trapped spawning tributaries but did not run as far as the trap. The "population" is considered to be all fish which immediately prior to the trapping occasion were potentially at risk of capture. These include fish that had the opportunity to move into the segment of the population at risk of capture.

In this Chapter we use the lake Brunner brown trout data to illustrate applica-

tion of the models of Chapters 3 and 4 under random emigration. All models were fitted using the computer code given in the Appendix.

6.1 One-age Model with no Marking Effect

6.1.1 Females

Live recaptures (captures) and angler captures (observations) are summarized in Table 6.1 using the generalized m-array described in Chapter 3. Summary statistics and parameter estimates are given in Tables 6.2 and 6.3 respectively.

Table 6.1: Live-recapture and observation array for female brown trout tagged in Lake Brunner spawning tributaries, 1987-1990 and observed by angler captures 1987-1991.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Released following capture								
at spawning.								
87	15	6	4	11	3	1	2	0
88		60	17		21	7	6	4
89			41			36	18	7
90							22	15
Released following capture								
by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90							0	1

From the contingency tables, the overall fit of the model appeared adequate. Note that because the $R_{i,2}$ are all zero for $i=1,\dots,t-1$, there is no contribution from the first component of the goodness-of-fit test. The individual contingency

Table 6.2: Summary statistics for female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	n_i	$R_{i,1}$	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
87	115	0	42	0		11			42	11
88	515	0	115	0	15	24	16	31	131	24
89	719	6	102	0	66	44	41	107	143	38
90	512	10	37	1	62	48	37	99	74	38
91		6				27	27		27	21

Table 6.3: Parameter estimates for female brown trout under the one-age model with random emigration and no marking effect.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
87	-	0.0957	1.0000	0.7535	-
88	0.1731	0.0409	1.0000	0.6051	-
89	0.1859	0.0437	1.0000	0.5694	-
90	0.1080	0.0469	0.9630	-	-
91	-	-	-	-	0.0254

tables and associated test statistics making up the second component of the test are

6 60 4 17 3 21 1 7 2 6 0 4	which after pooling reduces to	6 60 4 17 6 38	with $\chi^2_2 = 1.60$, $p = 0.450$;	21 41 8 36 8 18 4 7
---	--------------------------------	----------------------	--	------------------------------

with $\chi^2_3 = 3.56$, $p = 0.313$; and $\begin{matrix} 26 & 22 \\ 11 & 15 \end{matrix}$ with $\chi^2_1 = 0.95$, $p = 0.411$.

6.1.2 Males

The raw data for the single age-class model are given in Table 6.4 and summary statistics in Table 6.5, with parameter estimates in Table 6.6.

Table 6.4: Live-recapture and observation array for male brown trout tagged in Lake Brunner spawning tributaries, 1987-1990 and observed by angler captures 1987-1991.

Cohort	Retrapped			Captured by angler				
$j = 88$	89	90	$j = 87$	88	89	90	91	
Released following capture								
at spawning.								
87	10	19	5	24	5	1	0	0
88		10	10		16	10	3	0
89			23			39	12	2
90							36	28
Released following capture								
by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90							0	4

Table 6.5: Summary statistics for male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	n_i	$R_{i,1}$	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
87	234	1	64	0		24			64	23
88	403	1	49	0	10	21	30	40	79	20
89	599	6	76	0	29	50	29	58	105	44
90	516	15	64	4	38	51	17	55	81	36
91		10				34	34		34	24

Table 6.6: Parameter estimates for male brown trout under the one-age model with no marking effect.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
87	-	0.1026	1.0000	1.0972	-
88	0.0390	0.0323	1.0000	0.3964	-
89	0.1126	0.0604	1.0000	0.2115	-
90	0.2171	0.0781	0.8824	-	-
91	-	-	-	-	0.0459

As with females, the $R_{i,2}$ ($i = 1, \dots, t-1$) are all zero, and there is no component 1 contribution to the overall goodness-of-fit test. For component 2, the 3 contingency

tables

19	10
5	10
5	16
1	10
0	3
0	0

, which after pooling gave

19	10
5	10
5	16
1	13

with $\chi_3^2 = 16.92$, $p = 0.001$;

15	23
11	39
3	12
0	2

, which after pooling reduced to

15	23
11	39
3	14

with $\chi_2^2 = 4.31$, $p = 0.116$; and

15	36
2	28

with $\chi_1^2 = 5.89$, $p < 0.001$ collectively provided strong evidence against the one-age random emigration model with no marking effect ($\chi_6^2 = 27.12$, $p < 0.0001$).

6.1.3 Comments on the one-age model with no marking effect

From the initial analysis, it appears that the random emigration model adequately represents the female data but for males there is evidence of lack of fit. If we examine the two contingency tables indicating significant lack of fit for males in more detail we note that of the marked animals in the population at the time of trapping in 1988, that were subsequently encountered, more of the animals that were most recently released in 1987 were captured in 1989 than those that were last released in 1988 (Table 6.7). Of the marked animals in the population at the time of trapping in 1990, that were subsequently encountered, more of the animals that were last released before 1990 were caught by anglers during 1990 than those that were most recently released in 1990 (Table 6.8).

One explanation for the result observed in Table 6.7 is the Markov movement model - animals spawning in 1988 were less likely to spawn in 1989, and hence less likely to have been recaptured, than marked animals not captured in 1988. An alternative explanation is that there is an initial marking response. The 1988 release

Table 6.7: Observed and expected values for the 1988 component 2 contingency table of the random emigration model goodness-of-fit test for males.

Next caught or seen	Last captured in 1987		Last captured in 1988	
	Observed	Expected	Observed	Expected
Recaptured 1989	19	11.01	10	17.99
Angler capture 1988	5	5.70	10	9.30
Angler capture 1989	5	7.97	16	13.03
Angler capture 1990 or 1991	1	5.32	13	8.68

Table 6.8: Observed and expected values for the 1990 component 2 contingency table of the random emigration goodness-of-fit test for males.

Next caught or seen	First captured before 1990		First captured in 1990	
	Observed	Expected	Observed	Expected
Angler capture 1990	15	10.70	36	40.30
Angler capture 1991	2	2.93	28	23.7

cohort is comprised mostly (393 of 403) of newly marked animals. The observed result may have arisen because newly marked animals in 1988 were less likely to be captured in 1989 than animals that were last released (and marked) in 1987. This explanation also accounts for the result observed in Table 6.8. A third possibility is the presence of age-effects. At time i the population can be partitioned into two groups (i) those animals who were in the population at time $i - 1$ and (ii) those animals recruited into the population between $i - 1$ and i . Because all animals are recruited unmarked the set of unmarked animals captured at i (i.e. “newly marked” at i) will on average tend to be younger than marked animals in the population immediately before i . Such an age-effect could also explain the results observed in Tables 6.7 and 6.8.

6.2 Age-Dependence and Marking Effect Models

To fit the age dependent model, trout were allocated to one of four age-classes at initial capture based on length (Table 6.9). Thus, the age-classes are in fact length classes and it is assumed that fish progress to the next length class at the end of each year.

Table 6.9: Length classes used to assign Lake Brunner brown trout to age-classes.

Age	Females	Males
3	$L < 410$	$L < 440$
4	$410 \leq L < 450$	$440 \leq L < 480$
5	$450 \leq L < 510$	$480 \leq L < 540$
≥ 6	$510 \leq L$	$540 \leq L$

6.2.1 Females

The reduced m-array required to fit the age-dependence and marking effect model to the female data is given in Tables 6.10 through 6.13. Summary statistics are given in Tables 6.14 through 6.17 and parameter estimates in Tables 6.18 through 6.21. Inestimable parameters are indicated by a dash. Because of the sparseness of some of the data arrays, many parameters that are identifiable under the model structure could not be estimated.

A valid goodness-of-fit test based on a chi-square approximation could not be computed. After the maximum possible pooling, cells with expected values less than 2 remained in all contingency tables. However as the restricted version (one-age model with no marking effect) fitted the data data adequately then the more general model must also provide an adequate fit.

Table 6.10: Age-class 0 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91.
Age 0, mark class 0 - released following capture at spawning.								
87	0	0	0	0	0	0	0	0
88		3	0		0	0	0	0
89			1			0	0	0
90							3	0
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90								0

Table 6.11: Age-class 1 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 1, mark class 0 - released following capture at spawning.								
87	2	2	0	2	0	0	0	0
88		13	4		2	0	1	0
89			7			4	2	1
90							5	1
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90								0
Age 1, mark class 1 - released following capture at spawning.								
87	-	-	-	-	-	-	-	-
88		0	0		0	0	0	0
89			0			0	0	0
90							0	0
Released following capture by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0			0	0	0
89			0				0	0
90								0

Table 6.12: Age-class 2 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 2, mark class 0 - released following capture at spawning.								
87	9	4	4	7	2	1	2	0
88		36	10		13	7	3	3
89			22			21	11	1
90							9	9
Released following capture by anglers.								
87	0	0	0	0	0	0	0	0
88		0	0		0	0	0	0
89			0			0	0	0
90							0	0
Age 2, mark class 1 - released following capture at spawning.								
87	-	-	-	-	-	-	-	-
88		2	0		0	0	0	0
89			0			0	0	1
90							0	0
Released following capture by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0			0	0	0
89			0				0	0
90								0

Table 6.13: Age-class 3 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 3, mark class 0 - released following capture at spawning.								
87	4	0	0	2	1	0	0	0
88		5	3		5	0	2	1
89			8			5	3	4
90							1	5
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90								0
Age 3, mark class 1 - released following capture at spawning.								
87	-	-	-	-	-	-	-	-
88		1	0		1	0	0	0
89			3			6	2	0
90							4	0
Released following capture by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0			0	0	0
89			0				0	0
90								1

Table 6.14: Summary statistics for age-class 0 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 0, mark class 0										
87	3	0	0	0	0	0	0	0	0	0
88	31	3	0	0	0	0	0	0	3	0
89	49	1	0	0	3	0	0	3	1	0
90	51	3	1	0	1	3	0	1	3	2

Table 6.15: Summary statistics for age-class 1 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 1, mark class 0										
87	16	6	0	0	0	2	0	0	6	2
88	119	20	0	0	2	2	2	4	20	2
89	168	14	0	0	13	4	5	18	14	4
90	128	6	1	0	7	5	3	10	6	4
Age-class 1, mark class 1										
87	-	-	-	-	-	-	-	-	-	-
88	0	0	0	0	0	0	0	0	0	0
89	3	0	0	0	0	0	0	0	0	0
90	1	0	0	0	0	0	0	0	0	0

Table 6.16: Summary statistics for age-class 2 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 2, mark class 0										
87	80	29	0	0	0	7	0	0	29	7
88	286	72	0	0	9	13	13	22	72	13
89	354	55	3	0	36	21	23	59	55	16
90	219	18	0	0	22	9	12	34	18	4
Age-class 2, mark class 1										
87	-	-	-	-	-	-	-	-	-	-
88	2	2	0	0	0	0	0	0	4	0
89	13	1	0	0	4	0	0	4	6	0
90	7	0	0	0	4	2	2	6	3	2

Table 6.17: Summary statistics for age-class 3 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 3, mark class 0										
87	16	7	0	0	0	2	0	0	7	2
88	64	16	0	0	4	5	1	5	16	5
89	82	20	1	0	5	5	6	11	20	4
90	52	6	0	0	8	1	7	15	6	1
Age-class 3, mark class 1										
87	0	0	0	0	0	0	0	0	0	0
88	13	2	0	0	0	4	0	0	16	4
89	50	11	2	0	5	14	7	12	47	12
90	54	4	8	1	20	28	13	33	38	20

Table 6.18: Parameter estimates for age class 0 females in the 4-age model with temporary marking effect under random emigration.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 0, mark class 0					
87	-	-	1.0000	-	-
88	-	0.0000	1.0000	-	-
89	-	0.0000	1.0000	-	-
90	-	0.0588	-	-	-
91	-	-	-	-	0.0000

Table 6.19: Parameter estimates for age class 1 females in the 4-age model with temporary marking effect under random emigration.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 1, mark class 0					
87	-	0.1250	1.0000	0.2500	-
88	0.5000	0.0168	1.0000	0.6555	-
89	0.1667	0.0238	1.0000	-	-
90	0.0000	0.0391	1.0000	-	-
91	-	-	-	-	0.0078
Age-class 1, mark class 1					
87	-	-	-	-	-
88	-	-	1.0000	-	-
89	-	-	1.0000	-	-
90	-	-	1.0000	-	-
91	-	-	-	-	0.0000

There was no evidence of a temporary marking effect, regardless of the presence of age-dependence (Table 6.23) but there was strong evidence of age-dependence ($p < 0.002$). Parameter estimates (including standard errors) from the 4-age model with no temporary marking effect are given in Table 6.22. Because the age-class 0 data were sparse, parameter estimates with standard errors were obtainable only for f_{90} ($\hat{f}_{90} = 0.0588$, $se = 0.0329$). The overall fit of the 4-age model with no temporary marking effect to the female data was adequate ($\chi_8^2 = 8.53$, $p = 0.383$).

6.2.2 Males

The reduced m-array required to fit the age-dependence and marking effect model to the male data is given in Tables 6.24 through 6.27. Summary statistics are given in Tables 6.28 through 6.31 and parameter estimates in Tables 6.32 through 6.35. Due to small expected values, the overall goodness-of-fit statistic based on a chi-square approximation was not computed. However, the intermediate model 2b (age-

Table 6.20: Parameter estimates for age class 2 females in the 4-age model with temporary marking effect under random emigration.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 2, mark class 0					
87	-	0.0875	1.0000	1.1687	-
88	0.0963	0.0455	1.0000	0.4914	-
89	0.2561	0.0593	1.0000	0.5198	-
90	0.1196	0.0411	1.0000	-	-
91	-	-	-	-	0.0411
Age-class 2, mark class 1					
87	-	-	-	-	-
88	-	0.0000	1.0000	1.0000	-
89	1.0000	0.0000	1.0000	0.3974	-
90	0.1290	0.0000	1.0000	-	-
91	-	-	-	-	0.0000

Table 6.21: Parameter estimates for age class 3 females in the 4-age model with temporary marking effect under random emigration.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 3, mark class 0					
87	-	0.1250	1.0000	0.6562	-
88	0.3810	0.0781	1.0000	0.5043	-
89	0.1549	0.0610	1.0000	1.2500	-
90	0.0780	0.0192	1.0000	-	-
91	-	-	-	-	0.0962
Age-class 3, mark class 1					
87	-	-	-	-	-
88	-	0.0385	1.0000	0.3540	-
89	0.1358	0.0655	1.0000	0.9151	-
90	0.1023	0.0546	0.9091	0.0000	-
91	-	-	-	-	0.0195

Table 6.22: Parameter estimates, standard errors in parentheses, for age classes 1,2, and 3 from the four age random emigration model with no temporary marking effect for female brown trout tagged in Lake Brunner 1987-1990

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{s}_i
Age-class 1				
87	-	0.1250 (0.0827)	1.0000 (0.0000)	0.6115 (0.2870)
88	0.2044 (0.1634)	0.0168 (0.0118)	1.0000 (0.0000)	0.3846 (0.1266)
89	0.2840 (0.1099)	0.0234 (0.0116)	1.0000 (0.0000)	0.2612 (0.1229)
90	0.1567 (0.0960)	0.0388 (0.0170)	1.0000 (0.0000)	-
$\hat{\xi}_{91} = 0.0078$				
Age-class 2				
87	-	0.0875 (0.0316)	1.0000 (0.0000)	0.8076 (0.2128)
88	0.1393 (0.0576)	0.0440 (0.0119)	1.0000 (0.0000)	0.4663 (0.0839)
89	0.2900 (0.0628)	0.0525 (0.0113)	1.0000 (0.0000)	0.4363 (0.1462)
90	0.1491 (0.0568)	0.0417 (0.0128)	1.0000 (0.0000)	-
$\hat{\xi}_{91} = 0.0379$				
Age-class 3				
87	-	0.1250 (0.0827)	1.0000 (0.0000)	0.5174 (0.2992)
88	0.4832 (0.2839)	0.0657 (0.0230)	1.0000 (0.0000)	0.4774 (0.1253)
89	0.1530 (0.0582)	0.0666 (0.0166)	1.0000 (0.0000)	0.8412 (0.2904)
90	0.1167 (0.0433)	0.0622 (0.0199)	0.9375 (0.0579)	-
$\hat{\xi}_{91} = 0.0322$				

Table 6.23: Results of contingency table tests for age- dependence and temporary marking effect. Model 1: no age-dependence and no marking effect; Model 2a marking effect but no age-dependence; Model 2b: age-dependence but no marking effect; Model 3: age-dependence and marking effect.

Null model	Alternative model		
	Model 2a	Model 2b	Model 3
Model 1	$\chi^2_8 = 5.03, p = 0.754$	$\chi^2_{22} = 47.03, p = 0.002$	-
Model 2a	-	-	$\chi^2_{24} = 50.12, p = 0.001$
Model 2b	-	-	$\chi^2_{10} = 12.76, p = 0.240$

dependence but no marking effect) appears to provide an adequate fit ($\chi^2_3 = 6.01, p = 0.11$), hence the more general model must also provide an adequate fit.

Table 6.24: Reduced m-array with temporary marking effect for age-class 0 male brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 0, mark class 0 - released following capture at spawning.								
87	0	0	0	1	1	0	0	0
88		1	0		0	1	0	0
89			4			2	0	1
90							3	0
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90								0

Table 6.25: Reduced m-array with temporary marking effect for age-class 1 male brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 1, mark class 0 - released following capture at spawning.								
87	2	3	2	2	1	0	0	0
88		2	4		2	4	2	0
89			5			6	2	0
90							8	2
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89			0				0	0
90								0
Age 1, mark class 1 - released following capture at spawning.								
87	-	-	-	-	-	-	-	-
88		0	0		0	0	0	0
89			0			0	0	0
90							0	1
Released following capture by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0			0	0	0
89			0				0	0
90								0

Table 6.26: Reduced m-array with temporary marking effect for age-class 2 male brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 2, mark class 0 - released following capture								
at spawning.								
87	4	12	2	14	2	0	0	0
88		6	5		11	3	1	0
89			7			21	8	0
90							15	11
Released following capture								
by anglers.								
87	0	0	0	0	0	0	0	0
88		0	0		0	0	0	0
89			0			0	0	0
90							0	3
Age 2, mark class 1 - released following capture								
at spawning.								
87	-	-	-	-	-	-	-	-
88		0	1		0	0	0	0
89			0			0	0	0
90							1	1
Released following capture								
by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0			0	0	0
89							0	0
90								0

Table 6.27: Reduced m-array with temporary marking effect for age-class 3 male brown trout tagged in Lake Brunner 1987 - 1990.

Cohort	Retrapped			Captured by angler				
	$j = 88$	89	90	$j = 87$	88	89	90	91
Age 3, mark class 0 - released following capture at spawning.								
87	4	4	1	7	1	1	0	0
88		1	0		2	1	0	0
89			4			9	2	0
90							5	11
Released following capture by anglers.								
87	0	0	0		0	0	0	0
88		0	0			0	0	0
89							0	0
90								1
Age 3, mark class 1 - released following capture at spawning.								
87	-	-	-	-	-	-	-	-
88		0	0		1	1	0	0
89			3			1	0	1
90							4	2
Released following capture by anglers.								
87	-	-	-	-	-	-	-	-
88		0	0		0	0	0	0
89			0			0	0	0
90							0	0

Table 6.28: Summary statistics for age-class 0 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 0, mark class 0										
87	6	2	0	0	0	1	0	0	2	1
88	31	2	0	0	0	0	1	1	2	0
89	67	7	0	0	1	2	1	2	7	2
90	56	3	0	0	4	3	1	5	3	3

Table 6.29: Summary statistics for age-class 1 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 1, mark class 0										
87	48	10	0	0	0	2	0	0	10	2
88	108	14	0	0	2	2	6	8	14	2
89	114	13	0	0	2	6	10	12	13	6
90	86	10	2	0	5	8	2	7	10	6
Age-class 1, mark class 1										
87	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	1	0	0	1	1
89	1	0	0	0	0	1	0	0	1	1
90	4	1	0	0	0	0	0	0	2	0

Table 6.30: Summary statistics for age-class 2 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 2, mark class 0										
87	119	34	1	0	0	14	0	0	34	13
88	205	26	1	0	4	11	16	20	26	10
89	303	36	1	0	6	21	9	15	36	20
90	256	26	7	3	7	15	8	15	26	8
Age-class 2, mark class 1										
87	0	0	0	0	0	0	0	0	0	0
88	2	1	0	0	0	1	0	0	7	1
89	2	0	1	0	3	4	3	6	10	3
90	5	2	0	0	4	3	2	6	4	3

Table 6.31: Summary statistics for age-class 3 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.

year	N_i	$R_{i,1}$	n_i	$R_{i,2}$	C_i	O_i	Z_i	T_i	r_i	L_i
Age-class 3, mark class 0										
87	61	18	0	0	0	7	0	0	18	7
88	49	4	0	0	4	2	7	11	4	2
89	86	15	3	0	1	9	1	2	15	6
90	80	16	3	1	4	5	2	6	16	2
Age-class 3, mark class 1										
87	0	0	0	0	0	0	0	0	0	0
88	8	2	0	0	0	4	0	0	25	4
89	26	5	1	0	16	7	5	21	23	6
90	29	6	3	0	14	17	2	16	20	14

Table 6.32: Parameter estimates for age-class 0 males under the 4-age model with temporary marking effect under random emigration fitted to the male data.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 0, mark class 0					
87	-	0.1667	1.0000	-	-
88	-	0.0000	1.0000	-	-
89	0.0000	0.0299	1.0000	0.1194	-
90	0.5000	0.0536	1.0000	-	-
91	-	-	-	-	0.0000

Table 6.33: Parameter estimates for age-class 1 males under the 4-age model with temporary marking effect under random emigration fitted to the male data.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 1, mark class 0					
87	-	0.0417	1.0000	0.2917	-
88	0.1429	0.0185	1.0000	-	-
89	0.0000	0.0526	1.0000	0.0877	-
90	0.5000	0.0930	1.0000	-	-
91	-	-	-	-	0.0233
Age-class 1, mark class 1					
87	-	-	-	-	-
88	-	-	1.0000	-	-
89	-	0.0000	1.0000	0.0000	-
90	-	0.0000	1.0000	-	-
91	-	-	-	-	0.2500

Table 6.34: Parameter estimates for age-class 2 males under the 4-age model with temporary marking effect under random emigration fitted to the male data.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 2, mark class 0					
87	-	0.1176	1.0000	0.5714	-
88	0.0588	0.0537	1.0000	0.2576	-
89	0.1136	0.0693	1.0000	0.1507	-
90	0.1533	0.0586	0.7857	-	-
91	-	-	-	-	0.0430
Age-class 2, mark class 1					
87	-	-	-	-	-
88	-	0.0714	1.0000	1.3286	-
89	0.1613	0.0000	1.0000	0.0000	-
90	0.2927	0.3000	1.0000	-	-
91	-	-	-	-	0.1000

There was evidence of a temporary marking effect ($p < 0.025$) but only weak ($0.05 < p < 0.1$ evidence of age-dependence (Table 6.36).

The age-independent random emigration model with temporary marking effect was fitted to the male data set. Tests for a marking effect in the capture probabilities, survival rates, and unconditional observation probabilities indicated that the temporary marking effect was manifest through the capture probabilities ($\chi^2_2 = 12.47$, $p = .002$) but not the survival rates ($\chi^2_2 = 0.85$, $p = .655$). There was weak evidence of a temporary marking effect in the f_i 's ($\chi_3 = 6.48$, $p = .090$). There were insufficient data to test for a marking effect in the θ_i 's. Parameter estimates for the age-independent random emigration model with temporary trap response in just the capture probabilities is given in Table 6.37. This model provides an adequate fit to the data $\chi^2_{11} = 14.05$, $p = 0.232$.

Table 6.35: Parameter estimates for age-class 3 males under the 4-age model with temporary marking effect under random emigration fitted to the male data.

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{S}_i	$\hat{\xi}_i$
Age-class 3, mark class 0					
87	-	0.1148	1.0000	0.5246	-
88	0.1250	0.0408	1.0000	0.1265	-
89	0.1613	0.1047	1.0000	0.1589	-
90	0.2927	0.0625	0.9167	-	-
91	-	-	-	-	0.1375
Age-class 3, mark class 1					
87	-	-	-	-	-
88	-	0.0400	1.0000	0.4200	-
89	0.3810	0.0585	1.0000	0.1979	-
90	0.5915	0.1759	1.0000	-	-
91	-	-	-	-	0.0310

Table 6.36: Results of contingency table tests for age- dependence and temporary marking effect for males. Model 1: no age- dependence and no marking effect; Model 2a marking effect but no age-dependence; Model 2b: age-dependence but no marking effect; Model 3: age-dependence and marking effect.

	Alternative model		
	Model 2a	Model 2b	Model 3
Null model			
Model 1	$\chi^2_7 = 24.85, p = 0.001$	$\chi^2_{26} = 37.96, p = 0.061$	-
Model 2a	-	-	$\chi^2_{26} = 35.97, p = 0.092$
Model 2b	-	-	$\chi^2_8 = 17.91, p = 0.021$

Table 6.37: Parameter estimates, standard errors in parentheses, for the age-independent random emigration model with temporary marking effect in capture probabilities for male brown trout tagged in Lake Brunner 1987-1990

Year	\hat{p}_i	\hat{f}_i	$\hat{\theta}_i$	\hat{s}_i
Trap-class 0				
87	-	0.1026 (0.0198)	1.0000 (0.0000)	0.7119 (0.1740)
88	0.0600 (0.0234)	0.0375 (0.0085)	1.0000 (0.0000)	0.3561 (0.0834)
89	0.0720 (0.0273)	0.0650 (0.0095)	1.0000 (0.0000)	0.2586 (0.0676)
90	0.1363 (0.0446)	0.0753 (0.0115)	0.8363 (0.0662)	-
$\hat{\xi}_{91} = 0.0496(0.0099)$				
Trap-class 1				
87	-			
88	-			
89	0.3146 (0.0975)			
90	0.3446 (0.1178)			
$\hat{\xi}_{91} = 0.0310(0.0146)$				

6.3 Discussion

Overall, the age-dependent random emigration model with no temporary marking effect seems to provide the best representation of the data set for females. In contrast, the results for males indicate that a model with a temporary marking effect but no age-dependence best fits the data. However an alternative explanation that should be examined is that there is Markovian movement of males between spawnings.

The implication of the random emigration model with temporary marking effect is that males avoid the trap in the second year following initial capture but not in subsequent years. Moreover, behaviour is not altered by subsequent encounters with the trap. Given that the animals are only marked on their first encounter with the trap, and that marking involves application of a plastic tag through the flesh via a needle the first trapping occasion does provide the fish with a potentially unpleasant experience. Thus a temporary marking effect induced at the first capture occasion provides a plausible explanation for the observed data. A weakness with this explanation is that since both sexes are treated alike, there should be a similar response for females, however there was no evidence of a similar response for females. Indeed, if the temporary marking effect model is correct, then there needs to be some explanation for the lack of evidence of a temporary marking effect for females.

In the absence of a clear biological explanation for this result a reasonable conclusion for males is that there is some process affecting capture probabilities but it is unclear whether this is a consequence of animal movement patterns or whether the underlying behaviour is induced by the experiment.

The biological interpretation of the Markov emigration model is that brown trout spawning in year i are less likely to spawn in year $i + 1$ than those trout that do not spawn in year i . Again, if this is the correct model we need a reasonable explanation as to why this is the case for males but not for females. Given the different roles of males and females in the spawning process such an asymmetry

in spawning behaviour between the sexes may be a reasonable explanation for the observed results. If the Markov movement model is correct, and if in fact males and females are utilizing different reproductive strategies, then there are some interesting possibilities. For example, if we denote spawning in year i , not in $i + 1$ and then spawning in year $i + 2$ as the 101 strategy and spawning in each of the years $i, i + 1, i + 2$ as the 111 strategy, then the 101 strategy provides a longer recuperation period between spawnings with a potential benefit in terms of resources that can be put into each reproductive effort, but it involves a greater exposure to mortality factors between spawnings. Thus depending on values for key parameters a 101 strategy may lead to greater expected lifetime reproductive output than the 111 strategy.

A satisfactory way to resolve this question may be to carry out some sort of experiment designed to discriminate between the different possibilities. One approach would be to obtain observations of marked fish in the spawning stream above the trap following trapping. If there is no marking effect, then of those fish marked before i observed in the spawning stream after trapping between i and $i + 1$, the proportion that were also trapped at i should not depend on whether the fish were first marked at $i + 1$.

Chapter 7

Discussion

7.1 Benefits of the New Models and Implications for Existing Methods

The extension of the Jolly-Seber model to incorporate observations of animals between capture periods unites mark-recapture, mark-resight and tag-recovery models in a common framework and allows simultaneous estimation of parameters when data are gathered in all three ways. An important advantage is that all data can be used in an efficient manner with potentially large reductions in variances of key parameter estimates such as survival rates. We considered gains in precision only under random emigration. Under permanent emigration, the gains may be even greater due to the fact that once an animal has emigrated, it can never be available for recapture again (K. P. Burnham, pers. comm.). Under random emigration this loss of animals need only be temporary.

In addition to gains in precision, the inclusion of ancillary observations allows separation of the parameters S_{t-1} and p_t which in the Jolly-Seber model are confounded. It also allows separate fitting of the model under different assumptions about movement of animals in and out of the study area. In addition we have shown how the assumption of a negligible sampling period can be relaxed in a tag-resight study, and we have shown how to include losses on observation.

The introduction of ancillary observations into the analysis and the differing means of representing the movement of animals into and out of the component of the population that is at risk of capture leads to a very large class of models that can be fitted to any given data set. As illustrated by the west coast trout tagging example, the models to be fitted may have a very large number of parameters and the data set needed to fit the fullest models may be sparse. While this proliferation of potential models may appear to cause some model fitting and selection difficulties, it is generally better to have a large set of potential models to choose from than a restricted class of models.

The focus of our treatment has been the estimation of capture probabilities, survival rates, and observation rates. As in the Jolly-Seber model estimation of population size using ancillary observations in addition to recaptures involves first specifying a model for captures of unmarked animals. The usual assumption, (i.e. as in the Jolly-Seber model) is that unmarked and marked animals are captured at i with the same probability p_i . Under the assumption of permanent emigration the expected number of animals captured at i in the one-age model without marking effect is given by

$$\begin{aligned} E[n_i] &= N_{i-1}S_{i-1}F_{i-1}p_i + B_{i-1}p_i \\ &= N_i p_i, \end{aligned}$$

where N_i is the total number of animals in the at-risk-of-capture segment of the population at i and B_i is the number of new animals recruited into the population between $i - 1$ and i who are in the at risk of capture segment of the population at i . The obvious population size estimator under permanent emigration is then the Jolly-Seber MLE

$$\hat{N}_i = \frac{n_i}{\hat{p}_i}. \quad (7.1)$$

Under Markov emigration we must also specify the probability that the recruits are at risk of capture which we denote F'_i . Hence

$$\begin{aligned} E[n_i] &= N_{i-1,A}S_{i-1}\psi_{i-1,1,1}p_i + N_{i-1,N}S_{i-1}\psi_{i-1,2,1}p_i + B_{i-1}F'_i p_i \\ &= N_{i,A} p_i, \end{aligned}$$

where $N_{i,A}$ is the total number of animals at risk of capture at i and $N_{i,N}$ the total number not at risk of capture at i . Hence (7.1) will be an estimate of the size of $N_{i,A}$. To obtain MLE's of population size under either permanent or Markov emigration a component corresponding to unmarked animals can be included in the likelihood as described in Section 1.3.3 for the Jolly-Seber model.

Under random emigration

$$E[n_i] = N_{i-1,A} S_{i-1} F_{i-1} p_i + N_{i-1,N} S_{i-1} F_{i-1} p_i + B_{i-1} F'_i p_i .$$

Unlike the permanent emigration or Markov emigration models, under random emigration we cannot estimate p_i , just the product $F_{i-1} p_i$. Hence if B_{i-1} does not equal zero, we cannot estimate the size of the population (either total or at risk of capture) without a further restriction on F'_i . For example if we assume $F'_i = F_i$ then the Jolly-Seber MLE is an estimate of the total population size at i , however this assumption is unreasonable unless animals are recruited exactly at i . Thus, under random emigration we do not appear to be able to estimate population size without restrictive assumptions about the movement of recruits or without additional information. For example, under Pollock's (1981) "robust" design, population size is estimated using the closed population models described in section 1.1. Hence population size can be estimated regardless of the assumption about movement of animals between primary capture periods (Nichols et al. unpubl. manusc.)

The situation that we have described applies equally to the Jolly-Seber model (i.e. without ancillary observations). This is even more unsatisfying as without ancillary observations the two movement assumptions lead to identical expected recaptures and we cannot distinguish between the models. Moreover, the goodness-of-fit statistics for the Jolly-Seber model test only the fit of the model to the recaptures of marked animals. Thus we have two equally valid models for marked animals, no means of distinguishing between them, and we only have a valid population size estimator under permanent emigration. In addition, in the Jolly-Seber model we are unable to determine whether the Jolly-Seber survival rate estimator ϕ_i is a true survival rate S_i (i.e random emigration) or $S_i F_i$, the joint probability that

an animal has survived and not emigrated (i.e permanent emigration). This result reinforces the importance of obtaining additional information that allows separate modelling of the different types of emigration.

7.2 Implication for the Design of New Studies

There are many situations in which mark-recapture data with ancillary observations may arise. The “ancillary” observations may in fact be the focus of the recapture effort as in the case of a tag-resight or a tag-return study. In such a study the new aspect of the analysis introduced by the models presented in this thesis is the inclusion of the live-recaptures as well as relaxation of the assumption that resightings are carried out over a negligible time period. As methods of data acquisition become more sophisticated (e.g. the use of passive integrated transponder tags or satellite telemetry) it may become increasingly easy to obtain observations on animals between capture periods and we may see increasing collection of resight data to be used in conjunction with recapture data.

In many studies the focus of the study may indeed be a live-recapture experiment but where sightings of marked animals are reported by members of the public. In the situation envisaged by Jolly (1965) the experimenter may deliberately seek such ancillary sightings. An interesting point arises in the situation considered by Jolly (1965) if the resources put into observations of animals between capture periods compete with the resources available for live-recapture and marking. An interesting follow-up study would be to consider the optimal allocation of resources from the point of view of estimation of S_1, \dots, S_{t-2} , say. In the case of S_{t-1} the design with ancillary observations is superior as an estimate is not otherwise possible.

The inclusion of resightings in the model and the associated parameters f_i and θ_i raise the possibility of studies where these parameters are of specific interest. There are many examples in fisheries and wildlife management where animal counts with unknown observation probabilities are used as indices of abundance (i.e. as indicators of population change). A feature of all such trend monitoring methods is

that they assume that the observation probabilities remain constant through time, and possibly space, or that they can be modelled in some simple way. In a case where the index method yields observations of marked animals an interesting analysis would be to explicitly estimate time and geographic effects on the observation probabilities.

7.3 Future Research

7.3.1 Direct modelling of capture histories

In this thesis, the primary effort has been in developing a model under random emigration after first summarizing the data using an m-array. As is needed for the permanent emigration and Markov emigration model, an alternative is to model the individual capture histories directly. An advantage to this approach is that it allows the model to be generalized to include individual covariates.

It has also been pointed out (K. P. Burnham pers. comm.) that the goodness of fit tests reported in this thesis will not be fully efficient as there is some information lost in summarizing the capture history data using the m-array. Each of the release cohorts in the m-array (i.e. the $C_{i,k}$'s) can be partitioned according to the time at which the animal was first captured. Utilizing this partitioning into "subcohorts", contingency tables contributing information on goodness of fit of the random emigration model can be constructed leading to a test similar in form to TEST 3 of Burnham et al. (1987:74-77). Under permanent and Markov emigration information needed for parameter estimation is lost in the $M_{i,j,2,k}$ summary of recaptures/resightings for animals last released following observation. Therefore the TEST 3 component will be sensitive to departures from the random emigration model caused by Markovian movement.

7.3.2 Alternative handling effect models

The marking effect models of section 4.3 are appropriate in the case when capture lowers the probability of capture or observation in the period immediately following initial capture. However, it is possible to envisage a situation where a similar effect occurs after any capture, not just the first one, but as in the temporary marking effect model, we may be prepared to assume this effect “wears off” after one time period. Under the Jolly-Seber model Burnham et al. (1987:218-221) show that a handling effect on survival rates that occurs at each capture leads to a model structure that has an MSS identical to that of the Jolly-Seber model. Therefore the handling effect model cannot be distinguished from the Jolly-Seber model. The difficulty arises when all information following release is provided by recaptures, because recaptures necessarily involve handling.

It is possible that where some information comes from resightings in addition to recaptures identifiable handling effects models might be constructed. For simplicity, we just consider the case of a single age-class. If we let class 0 animals at time i be those animals captured at i , and class 1 those animals not captured at i , and if we write the probability structure for the model out, we find that it leads to an identical structure to the model of section 4.3, but where there are no $C_{i,1}^{(1)}$ animals since all animals captured at i are released in a $C_{i,1}^{(0)}$ cohort. Because the $C_{i,1}^{(1)}$ are required to estimate $\lambda_{i,1}^{(1)}$ this model will not be fully identifiable (i.e. the dimension of the MSS is lower than the dimension of the parameter space), and some constraints will be required. In particular we are unable to estimate the $\delta_i^{(1)}$. In certain cases it may be reasonable to assume that the handling effects do not influence the probability an animal is observed. This allows us to make the constraint $\delta_i^{(1)} = \delta_i^{(0)}$ and the model may become identifiable.

We may be able to further generalize this model and allow separate tagging and handling effects. Thus an animal which is both handled and tagged at i can have different survival and or capture and or observation probabilities than animals which are just handled, or not handled at all. In our brown trout example considered in Chapter 6 the fish received a physical insult at tagging but not on later recaptures.

Thus, the response to initial capture might be stronger than the response to later captures.

7.3.3 General multi-strata movement model

In Chapter 4 we discussed special cases of multi-strata models where movement was highly structured in that it was deterministic and one-way. Schwarz et al. (1991) and Brownie et al. (1993) have demonstrated how the Jolly-Seber model and tag-return models can be generalized to permit two-way movement between strata. Schwarz et al (1993) assumed that movement could be described by a Markov chain, and Brownie et al. (1993) generalized this to allow “memory”, where the dependence extends for more than one time period.

Except in the case of joint live-recovery and tag-return models the theory we have described in Chapter 3 and the current Chapter does not appear to fully generalize to the multi-strata case with Markovian movement between strata because of the re-release of animals following observation. In the case of tag-return models the animals are not re-released, simplifying the problem.

The difficulty arises because in the general multi-strata Jolly-Seber and tag-return models stratification is defined with respect to the capture process. Thus we model the manner in which animals are in stratum k at capture time i , and at stratum l at capture time $i + 1$ and are able to avoid making an assumption about how the animals move between time periods. This movement may follow some clear pattern or it may be chaotic. It does not matter as far as the model is concerned. To make use of observations between i and $i + 1$ in a manner analogous to the single-stratum case we need to determine the probability that an animal alive at time i in location k is alive at time $i + 1$ and in location l given that it was observed between times i and $i + 1$ at location m (or even several different locations). In the unconstrained case we make no assumption about the mechanism by which animals at location k at i move through location m some time between i and $i + 1$, then appear at location l at time $i + 1$. In the absence of simplifying assumptions, we require additional parameters to describe this movement and the

model becomes over-parameterized. These parameters are required in order to link the strata occupied at time of observation in $i, i + 1$ to the strata occupied at time i and $i + 1$.

A useful solution might be to completely ignore the stratum occupied on observation. In such a case we utilize the fact that the animals were observed somewhere to contribute information on the survival process. To illustrate the basic form of this model we consider a one-age model in the absence of a marking effect with t years of capture and observation. For a study with s strata we generalize the notation of Chapter 3 so that:

Statistics

$M_{i,j,k,1}$ is an $s \times s$ matrix with g, h th element $M_{i,j,k,1,g,h}$ the number of animals last released at time i following encounter by method k ($k = 1, 2$) in stratum g that are next encountered by capture at j in stratum h .

$\underline{M}_{i,j,k,1}$ is an $s \times 1$ vector with g th element $M_{i,j,k,2,g}$ the number of animals last released at time i following encounter by method k ($k = 1, 2$), and that were last *captured* in stratum g , that are next encountered by observation between j and $j + 1$ in any stratum.

Parameters

S_i = the $s \times s$ matrix with g, h th element $S_{i,g,h}$, the probability an animal alive and in stratum g at time i is alive and in stratum h at $i + 1$.

$\underline{\theta}_i$ = an $s \times 1$ vector with g th element $\theta_{i,g}$, the probability an animal alive and in stratum g at time i is not observed between i and $i + 1$ given that it is alive at $i + 1$.

\underline{f}_i = an $s \times 1$ vector with g th element $f_{i,g}$, the probability an animal alive and in stratum g at time i is observed between i and $i + 1$.

p_i the $s \times s$ matrix with g, h th element $p_{i,g,h}$, the probability an animal in stratum g at $i - 1$ and alive at i is captured in stratum h at i .

Ψ_i = the $s \times s$ matrix with g, h th element $\psi_{i,g,h}$, the probability an animal alive and in stratum g at time i is in stratum h given it is also alive at $i + 1$.

$\underline{\rho}_i$ = an $s \times 1$ vector with g th element $\rho_{i,g}$, the probability an animal observed in stratum g at time i is released.

Note in particular that the elements of the vector $\underline{M}_{i,j,k,1}$ are indexed by where the animals were last captured, not the stratum in which they were observed between i and $i + 1$. In this way the strata are identified only by capture location.

Let $D(x)$ be the diagonal matrix with j, j th element given by the j th element of the vector x , and $A \cdot B$ represent element-by-element multiplication of the conformable matrices A and B and the matrix $1 - A$ be the matrix with i, j th element given by $1 - A_{i,j}$. We also define the working parameter matrices

$$q_i = 1 - p_i$$

$$\Phi_i = D(\underline{\theta}_i)S_i \cdot \Psi_i$$

and

$$\Delta_i = D^{-1}(\underline{f}_i)D^{-1}(\underline{\rho}_i)D(1 - \underline{\theta}_i)D^{-1}(\underline{\theta}_i)$$

To develop the probability structure of the model we first arrange the data in the form of the multivariate m-array illustrated in Table 7.1.

Table 7.1: Multivariate reduced m-array for a mark-recapture study beginning at time 1 with t capture periods and ancillary observations of marked animals obtained during the interval $1, t + 1$.

Cohort	Next encountered by capture				Next encountered by observation				
	$j = 2$	3	...	t	$j = 1$	2	...	$t - 1$	t
$C_{i,1}$ - last released following capture									
$i=1$	$M_{1,2,1,1}$	$M_{1,3,1,1}$...	$M_{1,t,1,1}$	$\underline{M}_{1,1,1,2}$	$\underline{M}_{1,2,1,2}$...	$\underline{M}_{1,t-1,1,2}$	$\underline{M}_{1,t,1,2}$
2		$M_{2,3,1,1}$...	$M_{2,t,1,1}$		$\underline{M}_{2,2,1,2}$...	$\underline{M}_{2,t-1,1,2}$	$\underline{M}_{2,t,1,2}$
$t - 1$...	$M_{t-1,t,1,1}$...	$\underline{M}_{t-1,t-1,1,2}$	$\underline{M}_{t-1,t,1,2}$
t			...					$\underline{M}_{t,t,1,2}$	
$C_{i,2}$ - last released following observation									
$i=1$	$M_{1,2,2,1}$	$M_{1,3,2,1}$...	$M_{1,t,2,1}$		$\underline{M}_{1,2,2,2}$...	$\underline{M}_{1,t-1,2,2}$	$\underline{M}_{1,t,2,2}$
2		$M_{2,3,2,1}$...	$M_{2,t,2,1}$...	$\underline{M}_{2,t-1,2,2}$	$\underline{M}_{2,t,2,2}$
$t - 1$...	$M_{t-1,t,2,1}$...		$\underline{M}_{t-1,t,2,2}$

If we let $\Pi_{i,j,m,n} =$ the multinomial cell probability for the $M_{i,j,m,n}$ conditional on the releases then the corresponding multivariate "cell" probabilities are given by

$$\Pi_{i,j,1,1} = \Phi_{i,q_{i+1}} \Phi_{i+1,q_{i+2}} \cdots \Phi_{j-2,q_{j-1}} \Phi_{j-1,p_j},$$

$$\Pi_{i,j,2,1} = \Delta_i \Pi_{i,j,1,1},$$

$$\Pi_{i,j,1,2} = D(\underline{f}_j) \Phi_{i,q_{i+1}} \Phi_{i+1,q_{i+2}} \cdots \Phi_{j-2,q_{j-1}} \Phi_{j-1,q_j},$$

$$\Pi_{i,j,2,2} = D(\underline{f}_j, \Delta_i \{ \Phi_{i,q_{i+1}} \Phi_{i+1,q_{i+2}} \cdots \Phi_{j-2,q_{j-1}} \Phi_{j-1,q_j} \}).$$

The final multivariate “cell” vector corresponding to animals that were never captured or seen again following release has probability

$$\underline{1} - \left[\sum_{j=i+1}^t \Pi_{i,j,1,1} + \sum_{j=i}^t \Pi_{i,j,1,2} \right]$$

for animals last released following capture and

$$\underline{1} - \left[\sum_{j=i+1}^t \Pi_{i,j,2,1} + \sum_{j=i+1}^t \Pi_{i,j,2,2} \right]$$

for animals last released following observation.

This representation of a multi-state mark-recapture model with captures augmented by observations between capture periods represents a generalization of model JMV described by Brownie et al. (1993). Numerical procedures can be used to find MLE's subject to appropriate identifiability constraints similar to those imposed by Schwarz et al. (1993) and Brownie et al. (1993). As an alternative to MLE's, we might be able to find moment estimators that are matrix analogues of the Chapter 3 estimators as reported by Brownie et al. (1993) for their model JMV.

An alternative to the above approach of ignoring stratum occupied on observation is to impose some constraint on the movement process as we have done in the age-dependent and temporary marking effect models. Because of the potential complexity of the models it is likely that in different experimental situations different constraints on movement will be relevant. Thus a general model relevant to most experimental situations will be unlikely to exist.

Possible constraints on movement may include modelling movement via diffusion models. In such a model the exact time at which the animal was observed between i and $i+1$ would be relevant, and we would make use of multiple observations between capture occasions. In some cases the problem may be simplified by movement occurring at some exact time in the interval $i, i+1$ which is common to all such intervals. For example in migratory species there may be a clearly defined pattern of movement that can be exploited in simplifying the model. In other cases the observations may be gathered over a short period at the same time in each between-capture interval, thus we could have one set of movement parameters for the two

sets of movements between capture periods. Regardless of the modelling approach we also need to consider how we model the process by which animals are at risk of capture within a stratum. For example, animals may be at risk of capture throughout each stratum or they may be at risk of capture only in a portion of the stratum.

7.3.4 Models with different resighting assumptions

In the models discussed in this thesis, we assume that animals are available for resighting throughout their geographic range, but otherwise there are no restrictions on the sampling process. An obvious restriction that can be incorporated in any new models is where resighting occur over a restricted range. If resightings can only occur over the same area where animals are at risk of capture then we are in the situation faced by the Jolly-Seber model where we can have either random or permanent emigration, but we are unable to tell which. If we have permanent emigration, then the survival rate parameter would need to be reinterpreted as the product $F_i S_i$. Note that if we have stationary Markov emigration, we may still be able to fit the model.

In the intermediate case, where resightings occur over a larger but not all-encompassing range, we may be able to fit all three models, but the parameter definitions would require appropriate redefinition. For example, if the movement in and out of the resighting area were random then we would still have S_i as a true survival rate, but f_i and θ_i would be redefined as joint movement and resighting probabilities. If movement from the resighting area was permanent, then S_i would require redefinition as the probability the animal remains in the resighting area between i and $i + 1$ and survives.

In some studies it may be possible to determine the at-risk-of-capture status for an animal at time i for animals resighted between i and $i + 1$. If this information is available, then we have a special case of the general multi-strata problem but where recapture can only occur in the at-risk-of-capture stratum. The advantage of a model developed to allow this possibility would be that discrimination between

the three types of movement model discussed in this thesis would likely be improved.

Reliable determination of whether an animal resighted in $i, i + 1$ was also at risk of capture may be difficult for two reasons. First, if the period between captures is long, there may be considerable movement of animals with respect to the trapping site making identification of the position of the animal at i difficult. Second, the definition of the population of animals at risk of capture in a mark recapture study is often vague. All we know is that it is the animals that were vulnerable to our capture technique at the time of captures. The area within which these animals occur may be poorly delimited. One possible exception might be where it is breeding animals that are at risk of capture, and that during the interval $i, i + 1$ we can determine the breeding status of an animal at time i .

7.3.5 Investigations concerning underlying assumptions

Ultimately, the usefulness of any model(s) depends on the extent to which key assumptions are violated. As noted by McCullagh and Nelder (1989) "...all models are wrong; some though, are better than others...". In Chapter 5 we briefly considered the extent to which heterogeneous capture probabilities might bias estimates produced for the models described in this thesis. Because with real data some, and possibly all, the assumptions of the model may be violated to a certain extent it is important to consider the effect of these violation on the estimators. Further investigations of this nature would be of interest.

A particularly important assumption is that animals do not lose their tags. The effect of tag loss on the Jolly-Seber and tag-return estimators is well known (Arnason and Mills 1981, Nelson et al. 1980, Pollock 1981a). Intuitively, the loss of tags acts in a similar manner to mortality and in the absence of additional information tag loss parameters will be confounded with survival rate parameters. In many studies incorporating resightings, the animals are marked with large, easy to read tags. In some studies these tags are known to have a non-negligible rate of loss, and animals are also marked with a smaller, permanent tag that can only be read when the animal is recaptured. Such double tagging permits estimation of

the rates of tag loss. If the rate of tag loss depends only on i and not on the time since tagging, then estimation in such double tagging schemes is straight forward (Arnason and Mills 1981, Pollock 1981). If S_i is the survival rate computed using the mark-recapture or mark-resight model and if θ_i is the tag loss rate between i and $i + 1$ then the corrected survival rate estimator is simply

$$\hat{S}_i^c = \frac{\hat{S}_i}{\hat{\theta}_i}.$$

In many situations it is not reasonable to assume that the rate of tag loss depends only on i . Samuel et al. (1990) (Canada geese) and Nichols et al. (1992) (tundra swan) found evidence that the annual neckband retention probability decreased with increasing time since application.

Kremers (1988) and Nichols et al. (1992) showed that in a double tagging study where animals are recaptured as well as resighted it is possible to develop a joint likelihood incorporating both recapture and resighting data. The model of Kremers requires the restrictive assumption that one of the tags is permanent and that the period between recaptures and resighting is negligible. Also, the models of Kremers (1988) use only the final observation of the animal. The model of Nichols et al. (1992) utilized recapture data only as a source of information about tag-retention rate and not recapture and survival probabilities and ignored intermediate captures. However, an important advantage of the models of Nichols et al. (1992) is that they do not assume that one tag is permanent. An important area of future research might be to consider the extension of the models discussed in this thesis to allow for double tagging. This may lead to the development of more efficient models that make full use of recapture and observation data and permit simultaneous estimation of tag-retention and survival probabilities.

7.4 Concluding Remarks

By including observations on marked animals from different sources the experimenter has a potentially richer class of models from which to choose a suitable

model. Particularly important is the ability to distinguish between different possible types of emigration, provided at least one type of data includes observations on animals from throughout their geographic range. Mark-recapture studies have for the most part been based on one type of "recapture" data, and studies based on more than one source of recapture data are unusual. We concur with Nichols and Hines (1993) who recommended that the designs of resighting studies include efforts to recapture animals. In addition we recommend that a similar effort to catch marked animals is made in tag-recovery studies, and in live-recapture studies, that an effort is made to obtain observations on animals throughout the range of the study population. A particularly important issue is the allocation of resources to the different aspects of the study. As noted by Nichols and Hines (1993), knowledge of the relationship between effort and both recapture and observation probabilities will allow consideration of the optimal allocation of resources in future studies.

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Appendix

Programme JOLLYOBS and SURVIV sub-routines

Programme JOLLYOBS fits the random emigration age-and trap-dependent mark-recapture models when recapture data are augmented by observations of animals between capture periods. In addition to fitting the full model, reduced models assuming age-independence and trap independence are fitted where appropriate. Maximum likelihood estimates with asymptotic standard errors are returned as well as goodness-of-fit tests and tests between reduced models.

The data must first be summarized in the form of a reduced m-array. However if the data are in the form of a capture history, programme CAPHIS can be used to create the reduced m-array required as input for JOLLYOBS. A description of CAPHIS is given following description of JOLLYOBS.

1. Programme input

In the input file the m-array is preceded by two lines of input. The first line provides a title for the data and the second line information on the structure of the data. In line two of input the first character (columns 1-3) provides t , the number of years of capture. The second character (columns 4-6) provides v , the number of years of recovery. The third character (columns 7-9) provides $l + 1$, the number of age-classes. the final character (columns 10-12) takes the value 0 if there is no trap dependence and 1 if trap-dependence is to be fitted. An example for a two age-class study with trap dependence is provided in Table . The reduced m-array follows the form described in section 3.2.3 with the recapture/observation array given first for age-class 0, trap-class 0, then age-class 0, trap class 1, then age-class 1, trap class 0 etc. If there is more than one age-class, then all entries for age-class 0 and trap-class 0 are zero.

Table 7.2: Programme JOLLYOBS Data input for a study of a 2-age population with temporary trap response where there are 4 years of capture and 4 years of recovery.

FAKE 2-AGE DATA WITH TRAP-RESPONSE USED TO ILLUSTRATE JOLLYOBS

```

4 4 2 1
1000 1000 1000 1000
400 500 450
21 4 1 400 50 4 0
    35 7 500 58 5
        54 450 63
            400
49 9 1 118 9 1
    65 13 107 10
        81 95
            0 0 0 0
            0 0 0 0
0 0 0 0 0 0 0
    0 0 0 0 0
        0 0 0
            0
0 0 0 0 0 0
    0 0 0 0
        0
1000 795 620 560
500 477 341
27 3 0 500 38 3 0
    35 4 477 36 3
        41 341 31
            280
108 11 1 151 11 1
    104 13 107 10
        95 72
            0 205 380 440
            0 480 660

```

```

0 0 0 0 0 0 0
  9 1 123 9 1
    25 209 19
      220
0 0 0 0 0 0
  105 13 107 10
    185 139

```

2. Programme output

The output from programme JOLLYOBS is written to the file jollyobs.out. Output for the data set of Table 3.5 follows.

ONE AGE CLASS WITH NO TRAP DEPENDENCE

```

-----
N(I) R(I,1) N(I) R(I,2) C(I) O(I)
-----
1000 264 108 30 0 108
1000 237 150 35 63 150
1000 203 189 20 81 189
1000 107 0 0 97 208
-----

```

```

-----
Z(I) T(I) R(I) L(I)
  0 0 264 0
123 186 360 0
164 245 367 0
101 198 208 208
-----

```

PARAMETER ESTIMATES

```

-----
P SE F SE THETA SE S SE
0.0000 0.0000 0.1080 0.0098 0.8387 0.0270 0.5820 0.0544
0.1082 0.0159 0.0988 0.0083 0.8571 0.0224 0.5852 0.0557
0.0911 0.0124 0.1045 0.0084 0.8990 0.0214 0.5758 0.0740
-----

```

0.0932 0.0143 0.1070 0.0098 0.0000 0.0000 0.0000 0.0000

OVERALL GOODNESS-OF-FIT

(A) T(I+1) // C(I+1)

YEAR 1

OBSERVED VALUES

12 51

18 105

EXPECTED VALUES

10.16 52.84

19.84 103.16

CHISQ = 0.5999 DF = 1 P =0.4386

YEAR 2

OBSERVED VALUES

13 68

22 142

EXPECTED VALUES

11.57 69.43

23.43 140.57

CHISQ = 0.3074 DF = 1 P =0.5793

YEAR 3

OBSERVED VALUES

9 88
11 90

EXPECTED VALUES

9.80 87.20
10.20 90.80

CHISQ = 0.1417 DF = 1 P =0.7066

(B) R(I+1) // MP(I,J,K,NU,OMEGA)

AGE 1 YEAR 1

OBSERVED VALUES

29 5 69
48 8 94
28 5 74

EXPECTED VALUES

30.04 5.15 67.81
43.75 7.50 98.75
31.21 5.35 70.44

CHISQ = 1.2686 DF = 4 P =0.8667

AGE 1 YEAR 2

OBSERVED VALUES

35 5 48
76 12 101
31 5 54

EXPECTED VALUES

34.05 5.28 48.68

73.13 11.33 104.54
34.82 5.40 49.78

CHISQ = 1.1288 DF = 4 P =0.8897

TEST STATISTIC FOR OVERALL GOODNESS-OF-FIT

CHISQ = 3.4463 DF = 11 P =0.9834

LOG-LIKELIHOOD: -70.3316

NO. PARAMETERS IN MODEL: 13

MULTINOMIAL NORMALIZING CONSTANT FOR MOST GENERAL MODEL

3197.407327

3. FORTRAN source code

JOLLYOBS was written using the FORTRAN programming language and comprises 18 object modules. Each module is compiled and then linked to form the executable code.

MPAR - parameter declarations

```
PARAMETER (MXAGE=5,MXCOL=9,MXCLAS=10,MXCOHT=10)
```

```
INTEGER MXAGE,MXCOL,MAXCHOT,MXCLAS
```

```
INTEGER M(MXCLAS,MXCLAS,2,2,MXAGE,2),IAGES,INCLASS,INCOHT,  
&N(MXCLAS,MXCLAS,2),NN(MXCLAS,MXCLAS,2),NKILL(MXCLAS,MXCLAS,2),  
&RI1(MXCLAS,MXAGE,2),RI2(MXCLAS,MXAGE,2),CI(MXCLAS,MXAGE,2),  
&OI(MXCLAS,MXAGE,2),NSUM(MXCOHT,2),R1(MXCLAS,2),NNSUM(MXCLAS,2),  
&R2(MXCLAS,2),CSUM(MXCLAS,2),OSUM(MXCLAS,2),Z(MXCLAS,MXAGE,2),  
&ZSUM(MXCLAS,2),MP(MXCOHT,MXCLAS,2,MXAGE,2),  
&R(MXCLAS,MXAGE,2),RSUM(MXCLAS,2),T(MXCLAS,MXAGE,2),  
&TSUM(MXCLAS,2),OBSERV(MXCLAS*2,MXCOL),OMEGA,L2(MXCLAS,MXAGE,2),  
&M1(MXCLAS,MXCLAS,2,2,MXAGE,2),N1(MXCLAS,MXCLAS,2),NN1(MXCLAS,  
&MXCLAS,2)
```

```

DOUBLE PRECISION EXPECT(MXCLAS*2, MXCOL), FHAT(MXCLAS, MXAGE, 2),
&PHAT(MXCOHT, MXAGE, 2), THETAHAT(MXCLAS, MXAGE, 2),
&SHAT(MXCOHT, MXAGE, 2), MHAT(MXCLAS, MXAGE, 2), XI(MXCLAS, MXAGE, 2),
&ZETA(MXCOHT, MXCLAS, MXAGE, 2), VFHAT(MXCLAS, MXAGE, 2),
&VPHAT(MXCLAS, MXAGE, 2), VSHAT(MXCLAS, MXAGE, 2), VTHAT(MXCLAS, MXAGE, 2)

```

JOLLYOBS

```

PROGRAM JOLLYOBS
C
C MAX NO. YEARS=20
C
IMPLICIT DOUBLE PRECISION (A-H,O-Z)
INCLUDE 'MPAR'
C
C LOCAL VARIABLES
C
CHARACTER BANNER
CHARACTER*12 FNAME

PRINT*, 'INPUT FILE? '
READ8, FNAME
OPEN(1, FILE=FNAME)
OPEN(2, FILE='JOLLYOBS.OUT')
1 FORMAT(5I3)
2 FORMAT(20I6)
3 FORMAT(40I4)
4 FORMAT(8(1X,F8.4))
5 FORMAT(A16,F14.4)
6 FORMAT(A25,I3)
7 FORMAT(A80)
8 FORMAT(A12)
READ(1,7) BANNER
READ(1,1) INCOHT, INCLASS, IAGES, IFTRAP, ICPOOL

DO 20 NU=1, IAGES
DO 20 OMEGA=1, IFTRAP+1

```

```

      READ(1,2)(N(I,NU,OMEGA),I=1,INCOHT)
      READ(1,2)(NN(I,NU,OMEGA),I=1,INCLASS-1)
      DO 10 I=1,INCOHT
10      READ(1,3)(M(I,J+1,1,1,NU,OMEGA),J=1,INCOHT-1),
      &          (M(I,J,1,2,NU,OMEGA),J=1,INCLASS)
      IMAX=INCOHT-1
      IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1
      DO 20 I=1,INCLASS-1
20      READ(1,3)(M(I,J+1,2,1,NU,OMEGA),J=1,INCOHT-1),
      &          (M(I,J,2,2,NU,OMEGA),J=1,INCLASS)

      CLOSE(1)

C
C FIRST FIT THE MODEL WITH NO AGE OR TRAP EFFECTS UNLESS THE DATA ARE
C FOR JUST ONE AGE CLASS WITH NO TRAP RESPONSE
C
      IF(IAGES.EQ.1 .AND. IFTRAP.EQ.0) GOTO 265

      DO 22 I=1,INCLASS
22      NN1(I,1,1)=0

      DO 29 NU=1,IAGES
      DO 29 KK=1,IFTRAP+1
      DO 26 I=1,INCOHT
      N1(I,1,1)=N1(I,1,1)+N(I,NU,KK)
      DO 25 J=2,INCOHT
25      M1(I,J,1,1,1,1)=M1(I,J,1,1,1,1)+M(I,J,1,1,NU,KK)
      DO 26 J=1,INCLASS
26      M1(I,J,1,2,1,1)=M1(I,J,1,2,1,1)+M(I,J,1,2,NU,KK)
      DO 28 I=1,INCLASS-1
      NN1(I,1,1)=NN1(I,1,1)+NN(I,NU,KK)
      DO 27 J=2,INCOHT
27      M1(I,J,2,1,1,1)=M1(I,J,2,1,1,1)+M(I,J,2,1,NU,KK)
      DO 28J=1,INCLASS
28      M1(I,J,2,2,1,1)=M1(I,J,2,2,1,1)+M(I,J,2,2,NU,KK)
29 CONTINUE

```

```

WRITE(2,*)'MODEL 1 - SINGLE AGE-CLASS WITH NO TRAP RESPONSE'
WRITE(2,*)' '
WRITE(2,2)(N1(I,1,1),I=1,INCOHT)
WRITE(2,2)(NN1(I,1,1),I=1,INCLASS-1)
DO 30 I=1,INCOHT
30 WRITE(2,3)(M1(I,J,1,1,1,1),J=2,INCOHT),
&(M1(I,J,1,2,1,1),J=1,INCLASS)
WRITE(2,*)' '
DO 31 I=1,INCLASS-1
31 WRITE(2,3)(M1(I,J,2,1,1,1),J=2,INCOHT),
&(M1(I,J,2,2,1,1),J=1,INCLASS)
32 CONTINUE

33 CONTINUE

```

```

CALL SUMMARY(INCOHT,INCLASS,1,0,M1,RI1,RI2,CI,OI,R1,
&R2,NSUM,NNSUM,R1SUM,R2SUM,CSUM,OSUM,Z,ZSUM,T,R,TSUM,RSUM)

```

C

C PRINT OUT SUMMARY STATISTICS

C

```

WRITE(2,*)' '

WRITE(2,*)'-----'
WRITE(2,*)' N(I) R(I,1) N(I) R(I,2) C(I) O(I)'
WRITE(2,*)'-----'

IMAX=INCOHT
IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1
DO 40 I=1,IMAX
40 WRITE(2,2)N1(I,1,1),RI1(I,1,1),NN1(I,1,1),RI2(I,1,1),
&CI(I,2,1),OI(I,1,1)
WRITE(2,*)'-----'
WRITE(2,*)' '
WRITE(2,*)'-----'
WRITE(2,*)' Z(I) T(I) R(I) L(I)'

```

```

DO 50 I=1,INCOHT
50  WRITE(2,2)Z(I,2,1),T(I,2,1),R(I,1,1),OI(I,1,1)-NN1(I,1,1)
    WRITE(2,*)'-----'

    CALL PAREST(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,1,
&O,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)
    CALL VAR(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,1,
&O,VFHAT,VPHAT,VTHAT,VSHAT)

    WRITE(2,*)'PARAMETER ESTIMATES'
    WRITE(2,*)'-----'
&-----'
    WRITE(2,*)'      P          SE          F          SE          THETA          SE
&      S          SE'
    DO 52 I=1,INCOHT
52  WRITE(2,4)PHAT(I,1,1),SQRT(VPHAT(I,1,1)),FHAT(I,1,1),
&SQRT(VFHAT(I,1,1)),THETAHAT(I,1,1),SQRT(VTHAT(I,1,1)),SHAT(I,1,1)
&,SQRT(VSHAT(I,1,1))
    WRITE(2,*)'      '
    IF(INCLASS.EQ.INCOHT)GOTO 55
    WRITE(2,*)'XI'
    WRITE(2,4)(XI(J,1,1),J=INCOHT+1,INCLASS)
    IF(INCLASS-INCOHT .LT. 2) GOTO 55
    WRITE(2,*)'      '
    WRITE(2,*)'ZETA'
    DO 54 I=INCOHT+1,INCLASS-1
54  WRITE(2,4)(ZETA(I,J,1,1),J=I+1,INCLASS)
55  CONTINUE
    WRITE(2,*)'-----'
&-----'
    WRITE(2,*)'      '
    CALL PRMSS(M1,N1,NN1,RI1,RI2,CI,OI,T,R,Z,1,INCOHT,INCLASS,0,
&XLL1)
    CALL PRDATA(M1,RI1,RI2,CI,OI,T,R,1,INCOHT,INCLASS,0,XLL2)
    WRITE(2,*)'      '
    WRITE(2,5)'LOG-LIKELIHOOD: ',XLL1+XLL2

```



```

DO 136 J=1,INCLASS
136      M1(I,J,1,2,1,KK)=M1(I,J,1,2,1,KK)+M(I,J,1,2,NU,KK)
DO 139 I=1,INCLASS-1
      NN1(I,1,KK)=NN1(I,1,KK)+NN(I,NU,KK)
DO 138 J=2,INCOHT
138      M1(I,J,2,1,1,KK)=M1(I,J,2,1,1,KK)+M(I,J,2,1,NU,KK)
DO 139J=1,INCLASS
139      M1(I,J,2,2,1,KK)=M1(I,J,2,2,1,KK)+M(I,J,2,2,NU,KK)
142 CONTINUE

      CALL SUMMARY(INCOHT,INCLASS,1,1,M1,RI1,RI2,CI,OI,R1,
&R2,NSUM,NNSUM,R1SUM,R2SUM,CSUM,OSUM,Z,ZSUM,T,R,TSUM,RSUM)
      CALL PAREST(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,1,
&1,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)
      CALL VAR(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,1,
&1,VFHAT,VPHAT,VTHAT,VSHAT)
      IF(IFTRAP.EQ.0) THEN
        WRITE(2,*)'MODEL 2A - NO AGE-EFFECT'
      ELSE
        WRITE(2,*)'MODEL 2A - TEMPORARY TRAP RESPONSE BUT NO AGE-EFFECT'
      ENDIF
      WRITE(2,*)' '
      DO 190 KK=1,IFTRAP+1
        IF(IFTRAP.EQ.1.AND.KK.EQ.1)WRITE(2,*)'TRAP-CLASS 0'
        IF(IFTRAP.EQ.1.AND.KK.EQ.2)WRITE(2,*)'TRAP-CLASS 1'
        WRITE(2,2)(N1(I,1,KK),I=1,INCOHT)
        WRITE(2,2)(NN1(I,1,KK),I=1,INCLASS-1)
        DO 145 I=1,INCOHT
145          WRITE(2,3)(M1(I,J,1,1,1,KK),J=2,INCOHT),
&(M1(I,J,1,2,1,KK),J=1,INCLASS)
          WRITE(2,*)' . '
          DO 146 I=1,INCLASS-1
146          WRITE(2,3)(M1(I,J,2,1,1,KK),J=2,INCOHT),
&(M1(I,J,2,2,1,KK),J=1,INCLASS)
147 CONTINUE

```

C

C PRINT OUT SUMMARY STATISTICS

C

```
WRITE(2,*)'  '
WRITE(2,*)'-----'
WRITE(2,*)' N(I) R(I,1) N(I) R(I,2) C(I) O(I)'
WRITE(2,*)'-----'
IMAX=INCOHT
IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1
DO 140 I=1,IMAX
140  WRITE(2,2)N1(I,1,KK),RI1(I,1,KK),NN1(I,1,KK),RI2(I,1,KK),
    &CI(I,2,KK),OI(I,1,KK)
    WRITE(2,*)'-----'
    WRITE(2,*)'  '
    WRITE(2,*)'-----'
    WRITE(2,*)' Z(I) T(I) R(I) L(I)'
    DO 150 I=1,INCOHT
150  WRITE(2,2)Z(I,2,KK),T(I,2,KK),R(I,1,KK),OI(I,1,KK)-NN1(I,1,KK)
    WRITE(2,*)'-----'
160  CONTINUE

WRITE(2,*)'PARAMETER ESTIMATES'
WRITE(2,*)'-----'
&-----'
WRITE(2,*)'      P      SE      F      SE      THETA      SE
&  S      SE'
    DO 170 I=1,INCOHT
170  WRITE(2,4)PHAT(I,1,KK),SQRT(VPHAT(I,1,KK)),FHAT(I,1,KK),
    &SQRT(VFHAT(I,1,KK)),THETAHAT(I,1,KK),SQRT(VTHAT(I,1,KK)),
    &SHAT(I,1,KK),SQRT(VSHAT(I,1,KK))
    WRITE(2,*)'      '
    IF(INCLASS.EQ.INCOHT)GOTO 180
    WRITE(2,*)'XI'
    WRITE(2,4)(XI(J,1,KK),J=INCOHT+1,INCLASS)
    IF(INCLASS-INCOHT.LT. 2) GOTO 180
    WRITE(2,*)'      '
    WRITE(2,*)'ZETA'
```

```

DO 175 I=INCOHT+1,INCLASS-1
175  WRITE(2,4)(ZETA(I,J,1,KK),J=I+1,INCLASS)
180  CONTINUE
      WRITE(2,*)'-----'
      &-----'
190  WRITE(2,*)'      '

      CALL PRMSS(M1,N1,NN1,RI1,RI2,CI,OI,T,R,Z,1,INCOHT,INCLASS,1,
&XLL1)
      CALL PRDATA(M1,RI1,RI2,CI,OI,T,R,1,INCOHT,INCLASS,1,XLL2)
      WRITE(2,*)'      '
      WRITE(2,5)'LOG-LIKELIHOOD: ',XLL1+XLL2
      CALL NPARAM(INCOHT,INCLASS,1,1,NPAR)
      WRITE(2,6)'NO. PARAMETERS IN MODEL: ',NPAR
      WRITE(2,*)'      '
      CALL GOF(M1,RI1,RI2,CI,OI,T,R,1,INCOHT,INCLASS,1,
&CHISQ,IDF,ICPOOL)

      CALL TRAPTEST(M1,N1,NN1,RI1,RI2,CI,OI,T,R,1,INCOHT,INCLASS,
&IFTRAP)

      WRITE(2,*)'-----'
200  CONTINUE
C
C SECOND, IF IFTRAP = 1 FIT THE MODEL WITH NO TRAP RESPONSE BUT WITH AGE
C EFFECTS
C
C
C RESET N,NN1, AND M1 TO ZERO
C
      DO 220 K=1,IFTRAP+1
      DO 220 NU=1,IAGES
      DO 220 I=1,INCLASS
      N1(I,NU,K)=0

```

```

      NN1(I,NU,K)=0
      DO 220 J=1,INCLASS
        DO 220 IL=1,2
          DO 220 IM=1,2
220          M1(I,J,IL,IM,NU,K)=0

      DO 230 NU=1,IAGES
        DO 230 KK=1,IFTRAP+1
          DO 224 I=1,INCOHT
            N1(I,NU,1)=N1(I,NU,1)+N(I,NU,KK)
            DO 223 J=2,INCOHT
223              M1(I,J,1,1,NU,1)=M1(I,J,1,1,NU,1)+M(I,J,1,1,NU,KK)
            DO 224 J=1,INCLASS
224              M1(I,J,1,2,NU,1)=M1(I,J,1,2,NU,1)+M(I,J,1,2,NU,KK)
            DO 227 I=1,INCLASS-1
              NN1(I,NU,1)=NN1(I,NU,1)+NN(I,NU,KK)
              DO 226 J=2,INCOHT
226                M1(I,J,2,1,NU,1)=M1(I,J,2,1,NU,1)+M(I,J,2,1,NU,KK)
              DO 227J=1,INCLASS
227                M1(I,J,2,2,NU,1)=M1(I,J,2,2,NU,1)+M(I,J,2,2,NU,KK)
230 CONTINUE

      CALL SUMMARY(INCOHT,INCLASS,IAGES,0,M1,RI1,RI2,CI,OI,R1,
&R2,NSUM,NNSUM,R1SUM,R2SUM,CSUM,OSUM,Z,ZSUM,T,R,TSUM,RSUM)
      CALL PAREST(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,IAGES,
&O,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)
      CALL VAR(M1,N1,NN1,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,IAGES,
&O,VFHAT,VPHAT,VTHAT,VSHAT)

      IF (IAGES.EQ.1)THEN
        WRITE(2,*)'MODEL 2B - NO TEMPORARY TRAP RESPONSE'
      ELSE
        WRITE(2,*)'MODEL 2B - AGE-EFFECT BUT NO TEMPORARY TRAP RESPONSE'
      ENDIF
      WRITE(2,*)' '
      DO 260 NU=1,IAGES
        IF(IAGES.GT.1)WRITE(2,*)'AGE-CLASS',NU

```

```

WRITE(2,2)(N1(I,NU,1),I=1,INCOHT)
WRITE(2,2)(NN1(I,NU,1),I=1,INCLASS-1)
DO 234 I=1,INCOHT
234   WRITE(2,3)(M1(I,J,1,1,NU,1),J=2,INCOHT),
      &(M1(I,J,1,2,NU,1),J=1,INCLASS)
      WRITE(2,*)'      '
      DO 236 I=1,INCLASS-1
236   WRITE(2,3)(M1(I,J,2,1,NU,1),J=2,INCOHT),
      &(M1(I,J,2,2,NU,1),J=1,INCLASS)
      WRITE(2,*)'      '
C
C PRINT OUT SUMMARY STATISTICS
C
      WRITE(2,*)'      '
      WRITE(2,*)'-----'
      WRITE(2,*)' N(I) R(I,1) N(I) R(I,2) C(I) O(I)'
      WRITE(2,*)'-----'
      IMAX=INCOHT
      IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1
      DO 240 I=1,IMAX
240   WRITE(2,2)N1(I,NU,1),RI1(I,NU,1),NN1(I,NU,1),RI2(I,NU,1),
      &CI(I,NU+1,1),OI(I,NU,1)
      WRITE(2,*)'-----'
      WRITE(2,*)'      '
      WRITE(2,*)'-----'
      WRITE(2,*)' Z(I) T(I) R(I) L(I)'
      DO 250 I=1,INCOHT
250   WRITE(2,2)Z(I,NU+1,1),T(I,NU+1,1),R(I,NU,1),OI(I,NU,1)-
      &NN1(I,NU,1)
      WRITE(2,*)'-----'

      WRITE(2,*)'PARAMETER ESTIMATES'
      WRITE(2,*)'-----'
      &-----'
      WRITE(2,*)'      P      SE      F      SE      THETA      SE
      &      S      SE'

```

```

DO 252 I=1,INCOHT
252  WRITE(2,4)PHAT(I,NU,1),SQRT(VPHAT(I,NU,1)),FHAT(I,NU,1),
    &SQRT(VFHAT(I,NU,1)),THETAHAT(I,NU,1),SQRT(VTHAT(I,NU,1)),
    &SHAT(I,NU,1),SQRT(VSHAT(I,NU,1))
    WRITE(2,*)'      '
    IF(INCLASS.EQ.INCOHT)GOTO 255
    WRITE(2,*)'XI'
    WRITE(2,4)(XI(J,NU,1),J=INCOHT+1,INCLASS)
    IF(INCLASS-INCOHT .LT. 2) GOTO 255
    WRITE(2,*)'      '
    WRITE(2,*)'ZETA'
    DO 254 I=INCOHT+1,INCLASS-1
254  WRITE(2,4)(ZETA(I,J,NU,1),J=I+1,INCLASS)
255  CONTINUE
    WRITE(2,*)'-----'
    &-----'
    WRITE(2,*)'      '

260 CONTINUE

    CALL PRMSS(M1,N1,NN1,RI1,RI2,CI,OI,T,R,Z,IAGES,INCOHT,INCLASS,0,
    &XLL1)
    CALL PRDATA(M1,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,0,XLL2)
    WRITE(2,*)'      '
    WRITE(2,5)'LOG-LIKELIHOOD: ',XLL1+XLL2
    CALL NPARAM(INCOHT,INCLASS,IAGES,0,NPAR)
    WRITE(2,6)'NO. PARAMETERS IN MODEL: ',NPAR
    CALL GOF(M1,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,0,
    &CHISQ,IDF,ICPOOL)

C
C CARRY OUT AGE-DEPENDENCE TEST (HO: ONE-AGE MODEL WITH NO TRAP DEPENDENCE)
C
    CALL AGETEST(M1,N1,NN1,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,
    &INCLASS,0)
    WRITE(2,*)'-----'

```

265 CONTINUE

C

C FINALLY FIT THE MOST GENERAL MODEL

C

```
WRITE(2,*) ' '
IF(IAGES.EQ.1 .AND. IFTRAP.EQ.0)THEN
  WRITE(2,*) 'ONE AGE CLASS WITH NO TRAP DEPENDENCE'
ELSEIF(IAGES.NE.1 .AND. IFTRAP.EQ.0)THEN
  WRITE(2,*) 'GENERAL MODEL - AGE DEPENDENCE'
ELSEIF(IAGES.EQ.1 .AND. IFTRAP.EQ.1)THEN
  WRITE(2,*) 'GENERAL MODEL - TRAP DEPENDENCE'
ELSE
  WRITE(2,*) 'GENERAL MODEL - AGE + TRAP DEPENDENCE'
ENDIF
CALL SUMMARY(INCOHT, INCLASS, IAGES, IFTRAP, M, RI1, RI2, CI, OI, R1,
&R2, NSUM, NNSUM, R1SUM, R2SUM, CSUM, OSUM, Z, ZSUM, T, R, TSUM, RSUM)
```

C

C PRINT OUT SUMMARY STATISTICS

C

```
DO 290 KK=1, IFTRAP+1
  DO 290 NU=1, IAGES
    IF(IAGES.NE.1)WRITE(2,*) 'AGE-CLASS ', NU
    IF(IFTRAP.EQ.1)WRITE(2,*) 'TRAP-CLASS ', KK-1
    WRITE(2,*) ' '
    WRITE(2,*) '-----'
    WRITE(2,*) ' N(I) R(I,1) N(I) R(I,2) C(I) O(I)'
    WRITE(2,*) '-----'
    IMAX=INCOHT
    IF(INCLASS.GT. INCOHT)IMAX=INCLASS-1
    DO 270 I=1, IMAX
270      WRITE(2,2)N(I, NU, KK), RI1(I, NU, KK), NN(I, NU, KK),
&RI2(I, NU, KK), CI(I, NU+1, KK), OI(I, NU, KK)
    WRITE(2,*) '-----'
    WRITE(2,*) ' '
    WRITE(2,*) '-----'
```

```

        WRITE(2,*)' Z(I) T(I) R(I) L(I)'
        DO 280 I=1,INCOHT
280      WRITE(2,2)Z(I,NU+1,KK),T(I,NU+1,KK),R(I,NU,KK),OI(I,NU,KK)-
        &NN(I,NU,KK)
        WRITE(2,*)'-----'
290 CONTINUE

C
C OBTAIN PARAMETER ESTIMATES FOR MOST GENERAL MODEL
C

        CALL PAREST(M,N,NN,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,IAGES,
        &IFTRAP,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)
        CALL VAR(M,N,NN,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,IAGES,
        &IFTRAP,VFHAT,VPHAT,VTHAT,VSHAT)

349 FORMAT(4(1X,F8.4))
        DO 352 NU=1,IAGES
        DO 352 K=1,IFTRAP+1
        IF(IAGES.NE.1 .AND. IFTRAP.EQ.1)THEN
            WRITE(2,*)'AGE-CLASS',NU-1,' TRAP-CLASS',K-1
        ELSEIF(IAGES.NE.1 .AND. IFTRAP.EQ.0)THEN
            WRITE(2,*)'AGE-CLASS',NU-1
        ELSEIF(IAGES.EQ.1 .AND. IFTRAP.EQ.1)THEN
            WRITE(2,*)'TRAP-CLASS',K-1
        ENDIF
        WRITE(2,*)'PARAMETER ESTIMATES'
        WRITE(2,*)'-----'
        &-----'
        WRITE(2,*)'      P      SE      F      SE      THETA      SE
        &      S      SE'
        DO 350 I=1,INCOHT
350      WRITE(2,4)PHAT(I,NU,K),SQRT(VPHAT(I,NU,K)),FHAT(I,NU,K),
        &SQRT(VFHAT(I,NU,K)),THETAHAT(I,NU,K),SQRT(VTHAT(I,NU,K)),
        &SHAT(I,NU,K),SQRT(VSHAT(I,NU,K))
        WRITE(2,*)'      '

```

```

        IF(INCLASS.EQ.INCOHT)GOTO 352
        WRITE(2,*)'XIHAT '
        WRITE(2,349)(XI(J,NU,K),J=INCOHT+1,INCLASS)
        IF(INCLASS-INCOHT .LT. 2) GOTO 352
        WRITE(2,*)'ZETAHAT'
        DO 351 I=INCOHT+1,INCLASS-1
351  WRITE(2,349)(ZETA(I,J,NU,K),J=I+1,INCLASS)
352  CONTINUE

        WRITE(2,*)'-----'
        &'-----'
        WRITE(2,*)'      '

C
C OBTAIN GOODNESS-OF-FIT STATISTICS
C
        CALL GOF(M,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,IFTRAP,
        &CHISQ,IDF,ICPOOL)
C
C OBTAIN LOG-LIKELIHOOD FOR MOST GENERAL MODEL
C

        CALL PRMSS(M,N,NN,RI1,RI2,CI,OI,T,R,Z,IAGES,INCOHT,INCLASS,IFTRAP,
        &XLL1)

        PRINT*,'PR(MSS) = ',XLL1

        CALL PRDATA(M,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,IFTRAP,XLL2)

        PRINT*,'PR(DATA|MSS) = ',XLL2
        PRINT*,'LOG-LIKE = ',XLL1+XLL2
360 FORMAT(A16,F14.4)
        WRITE(2,*)'      '
        WRITE(2,360)'LOG-LIKELIHOOD: ',XLL1+XLL2
        CALL NPARM(INCOHT,INCLASS,IAGES,IFTRAP,NPAR)
        WRITE(2,6)'NO. PARAMETERS IN MODEL: ',NPAR

```

```

WRITE(2,*)'
WRITE(2,*)'MULTINOMIAL NORMALIZING CONSTANT FOR MOST GENERAL MODEL
&'
CALL CONSTANT(M,N,NN,RI1,RI2,IAGES,INCOHT,INCLASS,IFTRAP,CONST)
WRITE(2,FMT='(F12.6)')CONST
C
C CARRY OUT THE GENERAL MODEL SPECIFIC TRAP AND AGE-DEPENDENCE TESTS
C
IF(IAGES.NE.1) CALL AGETEST(M,N,NN,RI1,RI2,CI,OI,T,R,IAGES,
&INCOHT,INCLASS,IFTRAP)

IF(IFTRAP.EQ.1) CALL TRAPTEST(M,N,NN,RI1,RI2,CI,OI,T,R,IAGES,
&INCOHT,INCLASS,IFTRAP)

C
C CARRY OUT THE GENERAL AGE-DEPENDENCE TEST, MAKING NO ASSUMPTION ABOUT
C TYPE OF MOVEMENT
C
IF(IAGES.EQ.1)GOTO 390
X2=0.
NDF=0
399 FORMAT(A14,1X,I2,A12,1X,I2)
WRITE(2,*)'
WRITE(2,*)'OMNIBUS AGE-DEPENDENCE TEST'
WRITE(2,*)'-----'
WRITE(2,*)'(A) C(I,1) COHORTS'
WRITE(2,*)'
ICOL=IAGES
DO 320 KK=1,IFTRAP+1
DO 320 I=KK,INCOHT
IRO=INCOHT-I+INCLASS-I+2
IF(IFTRAP.EQ.0)WRITE(2,399)'TEST FOR TIME ',I
IF(IFTRAP.EQ.1)WRITE(2,399)'TEST FOR TIME ',I,' TRAP CLASS',
&KK-1
DO 307 NU=1,IAGES
ISUM=0

```

```

DO 300 J=I+1,INCOHT
      K=J-I
      OBSERV(K,NU)=M(I,J,1,1,NU,KK)
300   ISUM=ISUM+OBSERV(K,NU)
      DO 305 J=I,INCLASS
      K=INCOHT-I+J-I+1
      OBSERV(K,NU)=M(I,J,1,2,NU,KK)
305   ISUM=ISUM+OBSERV(K,NU)
307   OBSERV(IRO,NU)=N(I,NU,KK)-ISUM
      CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
      NDF=NDF+IDF
320   X2=X2+CHISQ
      WRITE(2,*)'(B) C(I,2) COHORTS '
      WRITE(2,*)'
      ICOL=IAGES
      DO 340 KK=1,IFTRAP+1
      DO 340 I=KK,INCLASS-1
      IRO=INCOHT-I+INCLASS-I+1
      IF(IFTRAP.EQ.0)WRITE(2,399)'TEST FOR TIME ',I
      IF(IFTRAP.EQ.1)WRITE(2,399)'TEST FOR TIME ',I,' TRAP CLASS',
&KK-1
      DO 337 NU=1,IAGES
      ISUM=0
      DO 330 J=I+1,INCOHT
      K=J-I
      OBSERV(K,NU)=M(I,J,2,1,NU,KK)
330   ISUM=ISUM+OBSERV(K,NU)
      DO 335 J=I+1,INCLASS
      K=INCOHT-I+J-I
      OBSERV(K,NU)=M(I,J,2,2,NU,KK)
335   ISUM=ISUM+OBSERV(K,NU)
337   OBSERV(IRO,NU)=NN(I,NU,KK)-ISUM
      CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
      NDF=NDF+IDF
340   X2=X2+CHISQ
      CALL CDTR(X2,NDF,SVALUE,IERR2)

```

```

PVALUE=1-SVALUE
WRITE(2,*)'OMNIBUS AGE-DEPENDENCE TEST'
WRITE(UNIT=2,FMT='(A8,F8.4,3X,A5,I3,3X,A4,F6.4)')
&'CHISQ = ',X2,'DF = ',NDF,'P = ',PVALUE
WRITE(UNIT=2,FMT='(A5)')'

390 CONTINUE
C
C CARRY OUT OMNIBUS TRAP-DEPENDENCE TEST
C

IF(IFTRAP.EQ.0) GOTO 450
X2=0.
NDF=0
499 FORMAT(A14,1X,I2,A4,1X,I2)
WRITE(2,*)'
WRITE(2,*)'OMNIBUS TRAP-DEPENDENCE TEST'
WRITE(2,*)'-----'
WRITE(2,*)'(A) C(I,1) COHORTS'
WRITE(2,*)'
ICOL=2
DO 420 NU=1,IAGES
DO 420 I=2,INCOHT
IRO=INCOHT-I+INCLASS-I+2
IF(IAGES.EQ.1)WRITE(2,499)'TEST FOR TIME ',I
IF(IAGES.GT.1)WRITE(2,499)'TEST FOR TIME ',I,' AGE',NU-1
DO 407 KK=1,2
ISUM=0
DO 400 J=I+1,INCOHT
K=J-I
OBSERV(K,KK)=M(I,J,1,1,NU,KK)
400 ISUM=ISUM+OBSERV(K,KK)
DO 405 J=I,INCLASS
K=INCOHT-I+J-I+1
OBSERV(K,KK)=M(I,J,1,2,NU,KK)
405 ISUM=ISUM+OBSERV(K,KK)

```

```

407      OBSERV(IRO, KK)=N(I, NU, KK)-ISUM
        CALL CTABLE(OBSERV, IRO, ICOL, CHISQ, IDF)
        NDF=NDF+IDF
420      X2=X2+CHISQ

        WRITE(2, *) '(B) C(I, 2) COHORTS'
        WRITE(2, *) '      '
        ICOL=2
        DO 440 NU=1, IAGES
          DO 440 I=2, INCLASS-1
            IRO=INCOHT-I+INCLASS-I+1
            IF(IAGES.EQ.1)WRITE(2, 499)'TEST FOR TIME ', I
            IF(IAGES.GT.1)WRITE(2, 499)'TEST FOR TIME ', I, 'AGE ', NU-1
            DO 437 KK=1, 2
              ISUM=0
              DO 430 J=I+1, INCOHT
                K=J-I
                OBSERV(K, KK)=M(I, J, 2, 1, NU, KK)
430          ISUM=ISUM+OBSERV(K, KK)
              DO 435 J=I+1, INCLASS
                K=INCOHT-I+J-I
                OBSERV(K, KK)=M(I, J, 2, 2, NU, KK)
435          ISUM=ISUM+OBSERV(K, KK)
            DO 437 KK=1, 2
              OBSERV(IRO, KK)=NN(I, NU, KK)-ISUM
              CALL CTABLE(OBSERV, IRO, ICOL, CHISQ, IDF)
              NDF=NDF+IDF
440      X2=X2+CHISQ

        CALL CDTR(X2, NDF, SVALUE, IERR2)
        PVALUE=1-SVALUE
        WRITE(2, *) 'OMNIBUS TRAP-DEPENDENCE TEST'
        WRITE(UNIT=2, FMT='(A8, F8.4, 3X, A5, I3, 3X, A4, F6.4)')
        &'CHISQ = ', X2, 'DF = ', NDF, 'P = ', PVALUE
        WRITE(UNIT=2, FMT='(A5)') '      '

450 CONTINUE

```

END

Subroutine SUMMARY

SUBROUTINE SUMMARY(INCOHT,INCLASS,IAGES,IFTRAP,M,RI1,RI2,CI,OI,
&R1,R2,NSUM,NNSUM,R1SUM,R2SUM,CSUM,OSUM,Z,ZSUM,T,R,TSUM,RSUM)

C

C THIS SUBROUTINE RETURNS THE SUMMARY STATISTICS

C

INCLUDE 'MPAR'

C

INITIALISE TO ZERO

DO 100 NU=1,IAGES

DO 100 KK=1,IFTRAP+1

DO 100 I=1,INCLASS

RI1(I,NU,KK)=0

RI2(I,NU,KK)=0

CI(I+1,NU+1,KK)=0

100 OI(I,NU,KK)=0

C

C FIND ROW TOTALS RI1(I,NU,OMEGA) AND RI2(I,NU,OMEGA)

C

DO 700 NU=1,IAGES

DO 500 OMEGA=1,IFTRAP+1

DO 500 I=1,MAX(INCOHT,INCLASS-1)

DO 450 J=2,INCOHT

450 RI1(I,NU,OMEGA)=RI1(I,NU,OMEGA)+M(I,J,1,1,NU,OMEGA)

DO 460 J=1,INCLASS

460 RI1(I,NU,OMEGA)=RI1(I,NU,OMEGA)+M(I,J,1,2,NU,OMEGA)

DO 470 J=2,INCOHT

470 RI2(I,NU,OMEGA)=RI2(I,NU,OMEGA)+M(I,J,2,1,NU,OMEGA)

DO 480 J=2,INCLASS

480 RI2(I,NU,OMEGA)=RI2(I,NU,OMEGA)+M(I,J,2,2,NU,OMEGA)

500 CONTINUE

C

C FIND COLUMN TOTALS - NOTE THESE ARE PARTIAL

C

```
DO 550 J=2,INCOHT
  DO 550 I=1,J-1
    ICLASS=NU+J-I
    IF(ICLASS.GT.IAGES+1)ICLASS=IAGES+1
    IF(IFTRAP.EQ.1) THEN
      IF(I.EQ.J-1)THEN
        CI(J,ICLASS,1)=M(I,J,1,1,NU,1)+M(I,J,2,1,NU,1)
        CI(J,ICLASS,2)=CI(J,ICLASS,2)+M(I,J,1,1,NU,2)
&          +M(I,J,2,1,NU,2)
      ELSE
        CI(J,ICLASS,2)=CI(J,ICLASS,2)+M(I,J,1,1,NU,2)
&          +M(I,J,2,1,NU,2)+M(I,J,1,1,NU,1)+M(I,J,2,1,NU,1)
      ENDIF
      GOTO 550
    ENDIF
    CI(J,ICLASS,1)=CI(J,ICLASS,1)+M(I,J,1,1,NU,1)
&          +M(I,J,2,1,NU,1)
550 CONTINUE
```

```
DO 560 J=1,INCLASS
  DO 560 I=1,J
    ICLASS=NU+J-I
    IF(ICLASS.GT.IAGES)ICLASS=IAGES
    IF(IFTRAP.EQ.1)THEN
      IF(I.EQ.J) THEN
        OI(J,ICLASS,1)=M(I,J,1,2,NU,1)+M(I,J,2,2,NU,1)
        OI(J,ICLASS,2)=OI(J,ICLASS,2)+M(I,J,1,2,NU,2)
&          +M(I,J,2,2,NU,2)
      ELSE
        OI(J,ICLASS,2)=OI(J,ICLASS,2)+M(I,J,1,2,NU,2)
&          +M(I,J,2,2,NU,2)+M(I,J,1,2,NU,1)+M(I,J,2,2,NU,1)
      ENDIF
      GOTO 560
```

```

                ENDIF
                OI(J,ICLASS,1)=OI(J,ICLASS,1)+M(I,J,1,2,NU,1)+
&                M(I,J,2,2,NU,1)
560 CONTINUE
700 CONTINUE
C
C COMPUTE MARGINAL TOTALS
C
    DO 740 OMEGA=1,2
    DO 710 I=1,INCOHT
        DO 710 NU=1,IAGES
            R1(I,OMEGA)=R1(I,OMEGA)+RI1(I,NU,OMEGA)
710     NSUM(I,OMEGA)=NSUM(I,OMEGA)+N(I,NU,OMEGA)
        DO 720 I=1,INCLASS-1
            DO 720 NU=1,IAGES
                NNSUM(I,OMEGA)=NNSUM(I,OMEGA)+NN(I,NU,OMEGA)
720     R2(I,OMEGA)=R2(I,OMEGA)+RI2(I,NU,OMEGA)
        DO 730 I=2,INCOHT
            DO 730 NU=1,IAGES+1
730     CSUM(I,OMEGA)=CSUM(I,OMEGA)+CI(I,NU,OMEGA)
        DO 740 I=1,INCLASS
            DO 740 NU=1,IAGES
740     OSUM(I,OMEGA)=OSUM(I,OMEGA)+OI(I,NU,OMEGA)
C
C NOW COMPUTE Z(I)'S
C
    Z(1,1,1)=0
    Z(1,1,2)=0
    IF(IFTRAP.EQ.1)THEN
        DO 750 NU=2,IAGES
            Z(1,NU,2)=0
            DO 750 I=2,INCLASS
                Z(I,NU,1)=RI1(I-1,NU-1,1)+RI2(I-1,NU-1,1)-CI(I,NU,1)
&                -OI(I-1,NU-1,1)

```

```

C      PRINT*,RI1(I-1,NU-1,1),RI2(I-1,NU-1,1),CI(I,NU,1),
C      &      -OI(I-1,NU-1,1)

750    Z(I,NU,2)=Z(I-1,NU-1,1)+Z(I-1,NU-1,2)+RI1(I-1,NU-1,2)
      &      +RI2(I-1,NU-1,2)-CI(I,NU,2)-OI(I-1,NU-1,2)

      DO 760 I=2,INCLASS
          Z(I,IAGES+1,1)=RI1(I-1,IAGES,1)+RI2(I-1,IAGES,1)
      &      -CI(I,IAGES+1,1)-OI(I-1,IAGES,1)
760    Z(I,IAGES+1,2)=Z(I-1,IAGES,1)+Z(I-1,IAGES+1,1)+
      &      Z(I-1,IAGES,2)+Z(I-1,IAGES+1,2)+RI1(I-1,IAGES,2)+
      &      RI2(I-1,IAGES,2)-CI(I,IAGES+1,2)-OI(I-1,IAGES,2)
      ELSE
          DO 761 NU=2,IAGES
              Z(1,NU,1)=0
          DO 761 I=2,INCLASS
761    Z(I,NU,1)=Z(I-1,NU-1,1)+RI1(I-1,NU-1,1)
      &      +RI2(I-1,NU-1,1)-CI(I,NU,1)-OI(I-1,NU-1,1)
          DO 762 I=2,INCLASS
762    Z(I,IAGES+1,1)=Z(I-1,IAGES,1)+Z(I-1,IAGES+1,1)
      &      +RI1(I-1,IAGES,1)+
      &      RI2(I-1,IAGES,1)-CI(I,IAGES+1,1)-OI(I-1,IAGES,1)
      ENDIF
C
C COMPUTE R(I)'S
C
      IF(IFTRAP.EQ.1)THEN
          DO 764 I=1,INCLASS
              R(I,1,1)=RI1(I,1,1)
              R(I,1,2)=RI1(I,1,2)
              R(I,IAGES,1)=RI1(I,IAGES,1)
              R(I,IAGES,2)=Z(I,IAGES,1)+Z(I,IAGES+1,1)+Z(I,IAGES,2)+
      &      Z(I,IAGES+1,2)+RI1(I,IAGES,2)
764    IF(I.GT.INCOHT+1)R(I,IAGES,2)=Z(I,IAGES,1)+Z(I,IAGES+1,1)+

```

```

&          Z(I,IAGES,2)+Z(I,IAGES+1,2)

DO 765 NU=2,IAGES-1
DO 765 I=1,INCLASS
R(I,NU,1)=RI1(I,NU,1)
R(I,NU,2)=Z(I,NU,1)+Z(I,NU,2)+RI1(I,NU,2)
765      IF(I.GT.INCOHT+1)R(I,NU,2)=Z(I,NU,1)+Z(I,NU,2)
ELSE
DO 766 I=1,INCLASS
R(I,1,1)=RI1(I,1,1)
R(I,IAGES,1)=Z(I,IAGES,1)+Z(I,IAGES+1,1)+RI1(I,IAGES,1)
766      IF(I.GT.INCOHT+1)R(I,IAGES,1)=Z(I,IAGES,1)+Z(I,IAGES+1,1)
DO 767 NU=2,IAGES-1
DO 767 I=1,INCLASS
R(I,NU,1)=Z(I,NU,1)+RI1(I,NU,1)
767      IF(I.GT.INCOHT+1)R(I,NU,1)=Z(I,NU,1)
ENDIF

C
C COMPUTE T(I)'S
C
DO 768 OMEGA=1,IFTRAP+1
DO 768 NU=2,IAGES+1
DO 768 I=1,INCLASS
768      T(I,NU,OMEGA)=Z(I,NU,OMEGA)+CI(I,NU,OMEGA)
C
C COMPUTE MARGINALS FOR Z(I)'S, T(I)'S AND R(I)'S
C

DO 772 OMEGA=1,IFTRAP+1
DO 770 I=2,INCLASS
DO 770 NU=1,IAGES+1
770      ZSUM(I,OMEGA)=ZSUM(I,OMEGA)+Z(I,NU,OMEGA)
DO 771 I=1,INCLASS
DO 771 NU=1,IAGES
771      RSUM(I,OMEGA)=RSUM(I,OMEGA)+R(I,NU,OMEGA)
DO 772 I=2,INCOHT

```

```

          DO 772 NU=1,IAGES+1
772      TSUM(I,OMEGA)=TSUM(I,OMEGA)+T(I,NU,OMEGA)

      RETURN
      END

```

Subroutine GOF

```

      SUBROUTINE GOF(M,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,IFTRAP,
&X2,NDF,CPOOL)
      IMPLICIT DOUBLE PRECISION (A-H,O-Z)
C
C GOF COMPUTES GOODNESS OF FIT TESTS STATISTIC
C
C IFTRAP = 0 MODEL WITH NO TRAP RESPONSE
C           1 MODEL WITH TRAP RESPONSE
C
      INCLUDE 'MPAR'
C
C LOCAL VARIABLES
C
      1 FORMAT(20I4)
      INTEGER CPOOL

      IK=IFTRAP+1
C
C OBTAIN PARTIAL COLUMN TOTALS
C
      CALL MPARTIAL(M,MP,INCOHT,INCLASS,IAGES,IFTRAP)
C
C COMPONENT 1 T(I+1) // C(I+1)
C
      WRITE(UNIT=2,FMT='(A5)')
      WRITE(UNIT=2,FMT='(A23)') 'OVERALL GOODNESS-OF-FIT'
      WRITE(UNIT=2,FMT='(A20)') '(A) T(I+1) // C(I+1)'

      X2=0.

```

```

NDF=0
IRO=2
ICOL=2

IF(IFTRAP.EQ.1) THEN
  DO 10 NU=1,IAGES
    DO 10 K=1,2
C
C NB IF FIRST AGE CLASS AND SECOND TRAP CLASS, TABLE DOES NOT EXIST
C
C   IF(NU.EQ.1 .AND. K.EQ.2)GOTO 10
      DO 10 I=K,INCOHT-2
        IF(IAGES.GT.1 .AND. IFTRAP.EQ.1) THEN
          WRITE(UNIT=2,FMT='(A3,I3,1X,A10,I2,1X,A4,I3)')
&          'AGE',NU,'TRAP CLASS',K-1,'YEAR',I
        ELSEIF(IAGES.GT.1 .AND. IFTRAP.EQ.0)THEN
          WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
&          'AGE',NU,'YEAR',I
        ELSEIF(IAGES.EQ.1 .AND. IFTRAP.EQ.1)THEN
          WRITE(UNIT=2,FMT='(A10,I2,1X,A4,I3)')
&          'TRAP CLASS',K-1,'YEAR',I
        ELSE
          WRITE(UNIT=2,FMT='(A4,I3)')'YEAR',I
        ENDIF
        OBSERV(1,1)=MP(I,I+1,1,NU,K)
        OBSERV(1,2)=M(I,I+1,2,1,NU,K)
        OBSERV(2,1)=R(I,NU,K)-OI(I,NU,K)-OBSERV(1,1)
        OBSERV(2,2)=RI2(I,NU,K)-OBSERV(1,2)
        CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
        X2=X2+CHISQ
        NDF=NDF+IDF
        IRO=2
        ICOL=2
10    CONTINUE
      ELSE
        DO 20 NU=1,IAGES

```

```

DO 20 I=1,INCOHT-1
  IF(IAGES.EQ.1) THEN
    WRITE(UNIT=2,FMT='(A4,I3)')'YEAR',I
  ELSE
    WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
&      'AGE',NU,'YEAR',I
  ENDIF

  OBSERV(1,1)=M(I,I+1,2,1,NU,1)+M(I,I+1,2,1,NU,2)
  OBSERV(1,2)=CI(I+1,NU+1,1)-M(I,I+1,2,1,NU,1)+
&      CI(I+1,NU+1,2)-M(I,I+1,2,1,NU,2)
  OBSERV(2,1)=RI2(I,NU,1)+RI2(I,NU,2)-OBSERV(1,1)
  OBSERV(2,2)=R(I,NU,1)-OI(I,NU,1)+R(I,NU,2)-OI(I,NU,2)
&      -OBSERV(1,2)
  CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
  X2=X2+CHISQ
  NDF=NDF+IDF
  IRO=2
20  ICOL=2
  ENDIF

C
C NOW COMPUTE R(I) // [M(I,J,K,L,NU,OMEGA)] COMPONENTS
C
  WRITE(UNIT=2,FMT='(A32)')'(B) R(I+1) // MP(I,J,K,NU,OMEGA)'

  IRO=(INCOHT-1)+INCLASS
  ICOL=3
  DO 360 NU=1,IAGES-1
    IF(IAGES.GT.1) THEN
      WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
&      'AGE',NU,'YEAR',1
    ELSE
      WRITE(UNIT=2,FMT='(A4,I3)')'YEAR',1
    ENDIF
  DO 300 J=3,INCOHT
    K=J-2

```

```

OBSERV(K,1)=MP(1,J,1,NU,1)
OBSERV(K,2)=M(1,J,2,1,NU,1)
OBSERV(K,3)=M(2,J,1,1,NU+1,1)
300 IF(IFTRAP.EQ.1)OBSERV(K,3)=M(2,J,1,1,NU+1,2)
DO 310 J=2,INCLASS
K=INCOHT-2+J-1
OBSERV(K,1)=MP(1,J,2,NU,1)
OBSERV(K,2)=M(1,J,2,2,NU,1)
OBSERV(K,3)=M(2,J,1,2,NU+1,1)
310 IF(IFTRAP.EQ.1)OBSERV(K,3)=M(2,J,1,2,NU+1,2)

C
C IF CAPTURE/OBSERVATIONS FROM ANIMALS LAST RELEASED FOLLOWING OBSERVATION
C ARE SPARSE, CPOOL CAN BE SET TO 1 TO POOL DATA FROM THESE ANIMALS
C WITH DATA FROM ANIMALS LAST RELEASED FOLLOWING CAPTURE
C
IF(CPOOL.EQ.1) THEN
DO 315 II=1,IRO
OBSERV(II,1)=OBSERV(II,1)+OBSERV(II,2)
315 OBSERV(II,2)=OBSERV(II,3)
ICOL=2
ENDIF
CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
X2=X2+CHISQ
NDF=NDF+IDF

C
C NOW DO FOR THE REMAINING YEARS
C
IRO=(INCOHT-I-1)+INCLASS-J-1
ICOL=2*(IFTRAP+1)+1
IMAX=INCOHT-2
IF(INCLASS.GT.INCOHT)IMAX=INCOHT-1
DO 360 I=2,INCOHT-2
IF(IAGES.GT.1)THEN
WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
& 'AGE',NU,'YEAR',I

```

```

ELSE
    WRITE(UNIT=2,FMT='(A4,I3)') 'YEAR', I
ENDIF
DO 330 J=I+2, INCOHT
    K=J-I-1
    INDEX=1
    DO 320 KK=1, IFTRAP+1
C
C SKIP IF FIRST AGE CLASS AND SECOND TRAP CLASS
C
        IF(NU.EQ.1 .AND. KK.EQ.2) GOTO320
        OBSERV(K,INDEX)=MP(I,J,1,NU,KK)
        INDEX=INDEX+1
        OBSERV(K,INDEX)=M(I,J,2,1,NU,KK)
        INDEX=INDEX+1
320    CONTINUE
330    OBSERV(K,INDEX)=M(I+1,J,1,1,NU+1,1)
DO 350 J=I+1, INCOHT
    K=INCOHT-I-1+J-1
    INDEX=1
    DO 340 KK=1, IFTRAP+1
        IF(NU.EQ.1 .AND. KK.EQ.2) GOTO340
        OBSERV(K,INDEX)=MP(I,J,2,NU,KK)
        INDEX=INDEX+1
        OBSERV(K,INDEX)=M(I,J,2,2,NU,KK)
        INDEX=INDEX+1
340    CONTINUE
350    OBSERV(K,2*(INDEX)+1)=M(I+1,J,1,2,NU+1,IK)
C
C NOW POOL COLUMNS IF REQUIRED
C
    IF(CPOOL.EQ.1) THEN
        IF(ITRAP.EQ.0) THEN
            DO 355 II=1, IRO
                OBSERV(II,1)=OBSERV(II,1)+OBSERV(II,2)
355    OBSERV(II,2)=OBSERV(II,3)

```

```

        ICOL=2
    ELSE
        DO 356 II=1,IRO
            OBSERV(II,1)=OBSERV(II,1)+OBSERV(II,2)
            OBSERV(II,2)=OBSERV(II,3)+OBSERV(II,4)
356     OBSERV(II,3)=OBSERV(II,5)
        ICOL=2
    ENDIF
ENDIF
CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
X2=X2+CHISQ
NDF=NDF+IDF
IRO=(INCOHT-2)+INCLASS-1
360 ICOL=2*(IFTRAP+1)+1

C
C NOW FOR THE LAST AGE GROUP
C
        WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
&         'AGE',IAGES,'YEAR',1
        ICOL=5
        IRO=INCOHT-2+INCLASS-1
        DO 370 J=3,INCOHT
            K=J-2
            IF(IAGES.EQ.1) THEN
                ICOL=3
                OBSERV(K,1)=MP(1,J,1,IAGES,1)
                OBSERV(K,2)=M(1,J,2,1,IAGES,1)
                OBSERV(K,3)=M(2,J,1,1,IAGES,1)
                IF(IFTRAP.EQ.1)OBSERV(K,3)=M(2,J,1,1,IAGES,2)
            ELSE
                OBSERV(K,1)=MP(1,J,1,IAGES-1,1)
                OBSERV(K,2)=MP(1,J,1,IAGES,1)
                OBSERV(K,3)=M(1,J,2,1,IAGES-1,1)
                OBSERV(K,4)=M(1,J,2,1,IAGES,1)
                OBSERV(K,5)=M(2,J,1,1,IAGES,1)
            
```

```

        IF(IFTRAP.EQ.1)OBSERV(K,5)=M(2,J,1,1,IAGES,2)
370    ENDIF
    DO 380 J=2,INCLASS
        K=INCOHT-2+J-1
        IF(IAGES.EQ.1)THEN
            OBSERV(K,1)=MP(1,J,2,IAGES,1)
            OBSERV(K,2)=M(1,J,2,2,IAGES,1)
            OBSERV(K,3)=M(2,J,1,2,IAGES,1)
            IF(IFTRAP.EQ.1)OBSERV(K,3)=M(2,J,1,2,IAGES,2)
        ELSE
            OBSERV(K,1)=MP(1,J,2,IAGES-1,1)
            OBSERV(K,2)=MP(1,J,2,IAGES,1)
            OBSERV(K,3)=M(1,J,2,2,IAGES-1,1)
            OBSERV(K,4)=M(1,J,2,2,IAGES,1)
            OBSERV(K,5)=M(2,J,1,2,IAGES,1)
            IF(IFTRAP.EQ.1)OBSERV(K,5)=M(2,J,1,2,IAGES,2)
380    ENDIF
C
C NOW POOL COLUMNS IF REQUIRED
C
        IF(CPOOL.EQ.1) THEN
            DO 385 II=1,IRO
                IF(IAGES.EQ.1)THEN
                    OBSERV(II,1)=OBSERV(II,1)+OBSERV(II,2)
                    OBSERV(II,2)=OBSERV(II,3)
                    ICOL=2
                ELSE
                    OBSERV(II,1)=OBSERV(II,1)+OBSERV(II,3)
                    OBSERV(II,2)=OBSERV(II,2)+OBSERV(II,4)
                    OBSERV(II,3)=OBSERV(II,5)
                    ICOL=3
385            ENDIF
        ENDIF
    CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
    X2=X2+CHISQ
    NDF=NDF+IDF

```

C

C NOW DO FOR THE REMAINING YEARS

C

```
      IMAX=INCOHT-2
      IF(INCLASS.GT.INCOHT)IMAX=INCOHT-1
      DO 430 I=2,IMAX
          IRO=(INCOHT-I-1)+INCLASS-I
          WRITE(UNIT=2,FMT='(A3,I3,1X,A4,I3)')
&              'AGE',IAGES,'YEAR',I

      DO 400 J=I+2,INCOHT
          K=J-I-1
          INDEX=1
          DO 390 KK=1,IFTRAP+1
              ISTART=IAGES-1
              IF(IAGES.EQ.1)ISTART=1
              DO 390 NU=ISTART,IAGES
                  IF(NU.EQ.1 .AND.KK.EQ.2) GOTO 390
                  OBSERV(K,INDEX)=MP(I,J,1,NU,KK)
                  INDEX=INDEX+1
                  OBSERV(K,INDEX)=M(I,J,2,1,NU,KK)
                  INDEX=INDEX+1
390          CONTINUE
400          OBSERV(K,INDEX)=M(I+1,J,1,1,IAGES,IK)
      DO 420 J=I+1,INCLASS
          K=INCOHT-I-1+J-I
          INDEX=1
          DO 410 KK=1,IFTRAP+1
              DO 410 NU=ISTART,IAGES
                  IF(NU.EQ.1 .AND.KK.EQ.2) GOTO 410
                  OBSERV(K,INDEX)=MP(I,J,2,NU,KK)
                  INDEX=INDEX+1
                  OBSERV(K,INDEX)=M(I,J,2,2,NU,KK)
                  INDEX=INDEX+1
410          CONTINUE
```

```

420      OBSERV(K,INDEX)=M(I+1,J,1,2,IAGES,IK)

C
C NOW POOL COLUMNS IF REQUIRED
C
      IF(CPOOL.EQ.1)THEN
        DO 428 II=1,IRO
          INDEX=1
          INDX=1
          DO 425 KK=1,IFTRAP+1
            ISTART=IAGES-1
            IF(IAGES.EQ.1)ISTART=1
            DO 425 NU=ISTART,IAGES
              OBSERV(II,INDEX)=OBSERV(II,INDX)+OBSERV(II,INDX+1)
              INDEX=INDEX+1
425          INDX=INDX+2
428      OBSERV(II,INDEX)=OBSERV(II,INDX)
        ENDIF
        ICOL=INDEX

        CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
        X2=X2+CHISQ
        NDF=NDF+IDF
430      IRO=(INCOHT-I-1)+INCLASS-I
C
C IF THERE ARE OBSERVATIONS BEYOND THE LAST CAPTURE PERIOD COMPUTE
C ADDITIONAL TERM
C
      IF(INCLASS.LE.INCOHT+1)GOTO 600
      IRO=INCLASS-INCOHT
      I=INCOHT
      DO 550 NU=1,IAGES
        IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 550
      DO 540 J=I+1,INCLASS
        K=J-I

```

```

        INDEX=1
        DO 540 KK=1,IFTRAP+1
            IF(NU.EQ.1.AND.KK.EQ.2)GOTO 540
            OBSERV(K,INDEX)=MP(I,J,2,NU,KK)
            INDEX=INDEX+1
            OBSERV(K,INDEX)=M(I,J,2,2,NU,KK)
            INDEX=INDEX+1
540      CONTINUE
        ICOL=INDEX
550      CONTINUE
C
C NOW POOL COLUMNS IF REQUIRED
C
        IF(CPOOL.EQ.1)THEN
            DO 560 II=1,IRO
                INDEX=1
                INDX=1
                DO 555 KK=1,IFTRAP+1
                    ISTART=IAGES-1
                    IF(IAGES.EQ.1)ISTART=1
                    DO 555 NU=ISTART,IAGES
                        OBSERV(II,INDEX)=OBSERV(II,INDX)+OBSERV(II,INDX+1)
                        INDEX=INDEX+1
555          INDX=INDX+2
560      OBSERV(II,INDEX)=OBSERV(II,INDX)
                ENDIF
                ICOL=INDEX
                CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
                X2=X2+CHISQ
                NDF=NDF+IDF
                IRO=(INCOHT-I-1)+INCLASS-I
600      CONTINUE

        WRITE(UNIT=2,FMT='(A42)')'TEST STATISTIC FOR OVERALL GOODNESS-OF-F
&IT'
```

```

      IF(NDF.EQ.0)WRITE(UNIT=2,FMT='(A47)')'ZERO DEGREES OF FREEDOM AFTE
&R POOLING'
      CALL CDTR(X2,NDF,SVALUE,IERR2)
      PVALUE=1-SVALUE
      WRITE(UNIT=2,FMT='(A8,F8.4,3X,A5,I3,3X,A4,F6.4)')
&'CHISQ = ',X2,'DF = ',NDF,'P = ',PVALUE
      RETURN
      END

```

Subroutine CTABLE

```

C   COMPUTES CONTINGENCY TABLE TEST STATISTIC
      SUBROUTINE CHI(OBSERV,EXPECT,IROWS,ICOLS,CHISQ,IERR)

      INCLUDE 'MPAR'

      IMPLICIT DOUBLE PRECISION (A-H,O-Z)
      INTEGER ISKIP(MXCLAS*2),OBSERV2(MXCLAS*2,MXCOL),MM1(MXCLAS*2),
&MM2(MXCOL)
      DOUBLE PRECISION CHISQ
      INTEGER NDF

C -
C   OBSERV  - ARRAY OF OBSERVED CELL FREQUENCIES
C   EXPECT  - ARRAY OF EXPECTED CELL FREQUENCIES
C   IRO     - THE NUMBER OF ROWS IN THE TABLE
C   ICOL    - THE NUMBER OF COLUMNS IN THE TABLE
C   NDF     - NUMBER OF DEGREES OF FREEDOM IN TABLE
C   CHISQ   - CALCULATED CHI-SQUARE STATISTIC AFTER POOLING
C   IERR    - AN ERROR INDICATOR VARIABLE
C           - IERR = 0 ... NO ERROR
C           - IERR = 1 ... TOO FEW ROWS REMAINING AFTER POOLING
C                   TO COMPUTE CHI-SQUARE STATISTIC
C
      IERR=0

C
C   FIRST ELIMINATE ROWS OR COLUMNS WITH ZERO MARGINALS

```

C

```
DO 5 I=1,IROWS
  DO 5 J=1,ICOLS
    MM1(I)=MM1(I)+OBSERV(I,J)
5    MM2(J)=MM2(J)+OBSERV(I,J)

INDEX=1
DO 10 I=1,IROWS
  IF(MM1(I).NE.0)THEN
    DO 7 J=1,IROWS
7      OBSERV(INDEX,J)=OBSERV(I,J)
      INDEX=INDEX+1
10    ENDIF
    IROWS=INDEX-1
    INDEX=1
    DO 15 J=1,ICOLS
      IF(MM2(J).NE.0)THEN
        DO 12 I=1,IRO
12      OBSERV(I,INDEX)=OBSERV(I,J)
        INDEX=INDEX+1
15    ENDIF
    ICOLS=INDEX-1
```

C

C CALL EXPECT TO FIND EXPECTED VALUES

C

```
CALL EVALUES(OBSERV,EXPECT,IROWS,ICOLS)
```

C

C POOL ROWS BASED ON EXPECTED VALUES

C

C

```

C     CYCLE UNTIL NO MORE ROWS ARE POOLED (IFLAG REMAINS AT 0)
C
      DMIN=2.

30  CONTINUE
      IFLAG=0
C
C  ASSIGN OBSERV TO OBSERV2
C
      DO 31 I=1,IROWS
          DO 31 J=1,ICOLS
31      OBSERV2(I,J)=OBSERV(I,J)
C
C  ISKIP MUST BE RESET TO ZERO ON EACH PASS
C
      DO 35 I=1,IROWS
35      ISKIP(I)=0
      DO 60 I=1,IROWS
          DO 50 J=1,ICOLS
              IF(EXPECT(I,J).LT.DMIN) THEN
                  IFLAG=1
                  ISKIP(I)=1
                  IF(I.EQ.1) THEN
                      DO 40 K=1,ICOLS
40                          OBSERV2(I+1,K)=OBSERV(I,K)+OBSERV(I+1,K)
                      ELSE
                          DO 45 K=1,ICOLS
45                          OBSERV2(I-1,K)=OBSERV(I,K)+OBSERV(I-1,K)
                      ENDIF
                  GOTO 62
              ENDIF
          ENDIF
50      CONTINUE
60      CONTINUE

```

```

C
C IF POOLING HAS OCCURRED ASSIGN THE RELEVANT ROWS OF OBSERV2
C TO OBSERV
C
62 IF(IFLAG.EQ.0) GOTO 80
    IT=0
    DO 70 I=1,IROWS
        IF(ISKIP(I).EQ.0)THEN
            DO 65 J=1,ICOLS
65         OBSERV(I-IT,J)=OBSERV2(I,J)
            ELSE
                IT=IT+1
70        ENDIF

        IROWS=IROWS-IT
C
C COMPUTE NEW EXPECTED VALUES AND REPEAT THE CYCLE
C
        CALL EVALUES(OBSERV, EXPECT, IROWS, ICOLS)

        GOTO 30
C
C NOW COMPUTE CHI-SQUARE STATISTIC
C
80 CHISQ=0.
    IF(IROWS .LE. 1) THEN
        IERR=1
        GOTO 110
    ENDIF

    DO 100 I=1,IROWS
        DO 100 J=1,ICOLS
100    CHISQ=CHISQ+((OBSERV(I,J)-EXPECT(I,J))**2)/EXPECT(I,J)

```

110 RETURN

END

Subroutine EVALUES

C COMPUTES CONTINGENCY TABLE EXPECTED VALUES
SUBROUTINE EVALUES(OBSERV, EXPECT, IRO, ICOL)

INCLUDE 'MPAR'

IMPLICIT DOUBLE PRECISION (A-H, O-Z)

INTEGER MARG1(MXCLAS+1), MARG2(MXCOL)

C

C FIND MARGINALS AND GRAND TOTAL

C

ITOTAL=0

C

C INITIALISE MARGINALS TO ZERO

C

DO 5 I=1, IRO

5 MARG1(I)=0

DO 6 J=1, ICOL

6 MARG2(J)=0

DO 10 I=1, IRO

DO 10 J=1, ICOL

MARG1(I)=MARG1(I)+OBSERV(I, J)

MARG2(J)=MARG2(J)+OBSERV(I, J)

10 ITOTAL=ITOTAL+OBSERV(I, J)

C

C COMPUTE EXPECTED VALUES

C

C

C IF THERE ARE NO OBSERVATIONS SET EXPECTED VALUES TO ZERO TO AVOID

C DIVISION ERROR

C

```

IF(ITOTAL.EQ.0)THEN
  DO 15 I=1,IRO
    DO 15 J=1,ICOL
15   EXPECT(I,J)=0
    GOTO 30
ENDIF

DO 20 I=1,IRO
  DO 20 J=1,ICOL
20  EXPECT(I,J)=FLOAT(MARG1(I))*FLOAT(MARG2(J))/FLOAT(ITOTAL)
30 RETURN
END

```

subsubsection Subroutine CDFCHI

```

C *DECK CDTR
C
C .....
C
C SUBROUTINE CDTR
C
C PURPOSE
C COMPUTES P(CHISQ) = PROBABILITY THAT THE RANDOM VARIABLE U,
C DISTRIBUTED ACCORDING TO THE CHI-SQUARE DISTRIBUTION WITH G
C DEGREES OF FREEDOM, IS LESS THAN OR EQUAL TO CHISQ. F(G,CHI
C ORDINATE OF THE CHI-SQUARE DENSITY AT CHISQ, IS ALSO COMPUTE
C
C USAGE
C CALL CDTR(CHISQ, IDF, SIGCHI, IER)
C
C DESCRIPTION OF PARAMETERS
C CHISQ - INPUT SCALAR FOR WHICH P(CHISQ) IS COMPUTED.
C IDF - NUMBER OF DEGREES OF FREEDOM OF THE CHI-SQUARE
C DISTRIBUTION. IDF IS AN INTEGER.
C SIGCHI - OUTPUT PROBABILITY.
C IER - RESULTANT ERROR CODE WHERE
C IER= 0 --- NO ERROR

```

C IER=-1 --- AN INPUT PARAMETER IS INVALID. X IS LESS
 C THAN 0.0, OR IDF IS LESS THAN 0.0 OR GREATER
 C THAN 2*10**(+5). P AND D ARE SET TO -1.E25.
 C IER=-2 --- IDF = 0, P SET TO 0.
 C IER=+1 --- INVALID OUTPUT. P IS LESS THAN ZERO OR
 C GREATER THAN ONE, OR SERIES FOR T1 (SEE
 C MATHEMATICAL DESCRIPTION) HAS FAILED TO
 C CONVERGE. P IS SET TO 1.E25.

C SUBROUTINES AND FUNCTION SUBPROGRAMS REQUIRED

C NDTR

C METHOD

C THIS FUNCTION WAS LIFTED FROM "NWAY" WRITTEN BY THE STANFORD
 C COMPUTATION CENTER. THE SCC BORROWED IT FROM JOHN MORRIS OF THE
 C COMPUTER INSTITUTE FOR SOCIAL SCIENCE RESEARCH AT MICHIGAN STATE
 C UNIVERSITY.

C SUBROUTINE CDTR (CHISQ, IDF, SIGCHI, IER)

C INTEGER IDF, IER

C DOUBLE PRECISION CHISQ, SIGCHI

C DOUBLE PRECISION FACT(0:30), ANSCHI, FF, P, XI, PP, TERM, ARGNRM,

C 1 GAM, TXX

C INTEGER I

C

C FACTORIALS OF 0 THROUGH 30. .

C DATA FACT /1.00000000000000D00,1.00000000000000D00,2.000000

C 1 00000000D00,6.00000000000000D00,2.40000000000000D01,1.200000000000

C 2 000D02,7.20000000000000D02,5.04000000000000D03,4.03200000000000D0

C 3 4,3.62880000000000D05,3.62880000000000D06,3.99168000000000D07,4.7

C 4 90016000000000D08,6.22702080000000D09,8.71782912000000D10,1.307674

C 5 36800000D12,2.09227898880000D13,3.55687428096000D14,6.40237370572

C 6 800D15,1.21645100408832D17,2.43290200817664D18,5.10909421717094D1

C 7 9,1.12400072777761D21,2.58520167388850D22,6.20448401733239D23,1.5

C 8 5112100433310D25,4.03291461126606D26,1.08888694504184D28,3.048883

9 44611714D29,8.84176199373970D30,2.65252859812191D32/

C

```
IER=0
ANSCHI=1.
IF (CHISQ.LT.0..OR.IDF.LT.0) THEN
    IER=-1
    SIGCHI=-1.D25
ELSE IF (IDF.EQ.0) THEN
    IER=-2
    SIGCHI=0.
ELSE IF (CHISQ+100..EQ.100.) THEN
    IER=0
    SIGCHI=0.
ELSE
```

C

C

```
GT 60 D.F. OR CHI GT 100 - USE A NORMAL APPROXIMATION
IF (IDF.GT.60 .OR. CHISQ.GT.100.) THEN
    ARGNRM=SQRT(2.DO*CHISQ)-SQRT(2.DO*DBLE(IDF)-1.DO)
    CALL NDTR (ARGNRM,SIGCHI)
ELSE
    FF=IDF-2
    P=0.5*FF
    XI=0.5*CHISQ
    PP=P+2.0
    TERM=XI/PP
    DO 10 I=1,100
    ANSCHI=ANSCHI+TERM
    IF (ABS(TERM).LT.1.0D-6) GO TO 20
    PP=PP+1.0
10    TERM=TERM*XI/PP
20    GAM=1.0
    IF (MOD(IDF,2).EQ.0) THEN
        GAM=FACT(IDF/2)
    ELSE
30        DO 40 I=1, IDF, 2
40        GAM=GAM*DBLE(I)*0.5DO
```

```

      GAM=GAM*1.7724588509
      ENDIF
      TXX=(P+1.0)*LOG(XI)- XI + LOG(ANSCHI/GAM)
      IF (TXX.LE.88.0) THEN
        IF (TXX.GT.-88.0) THEN
          ANSCHI=EXP(TXX)
        ELSE
          ANSCHI=0.
        ENDIF
      ELSE
        ANSCHI=1.
      ENDIF
C      IF (ANSCHI.LT.0.) THEN
C        ANSCHI=0.
C      ELSEIF (ANSCHI.GT.1.) THEN
C        ANSCHI=1.
C      ENDIF
      SIGCHI=ANSCHI
      ENDIF
      IF (SIGCHI.LT.0..OR.SIGCHI.GT.1.) THEN
        IER=1
        SIGCHI=1.D25
      ENDIF
    ENDIF
  RETURN
END
C *DECK NDTR
C   SUBROUTINE NDTR
C
C   PURPOSE
C     COMPUTES  $Y = P(X) =$  PROBABILITY THAT THE RANDOM VARIABLE  $U$ ,
C     DISTRIBUTED NORMALLY(0,1), IS LESS THAN OR EQUAL TO  $X$ .
C      $F(X)$ , THE ORDINATE OF THE NORMAL DENSITY AT  $X$ , IS ALSO
C     COMPUTED.
C
C   USAGE

```

```

C          CALL NDTR(X,P)
C
C          DESCRIPTION OF PARAMETERS
C          X--INPUT SCALAR FOR WHICH P(X) IS COMPUTED.
C          P--OUTPUT PROBABILITY.
C
C          REMARKS
C          MAXIMUM ERROR IS 0.0000007.
C
C          SUBROUTINES AND SUBPROGRAMS REQUIRED
C          NONE
C
C          METHOD
C          BASED ON APPROXIMATIONS IN C. HASTINGS, APPROXIMATIONS FOR
C          DIGITAL COMPUTERS, PRINCETON UNIV. PRESS, PRINCETON, N.J.,
C          1955. SEE EQUATION 26.2.17, HANDBOOK OF MATHEMATICAL
C          FUNCTIONS, ABRAMOWITZ AND STEGUN, DOVER PUBLICATIONS, INC.,
C          NEW YORK.
C
C          *****
C
C          SUBROUTINE NDTR (X,P)
C          DOUBLE PRECISION X,P,T,D
C
C          T=1.DO/(1.DO+.2316419D0*ABS(X))
C          IF (-X*X*0.5D0.LT.-700.D0) THEN
C              D=0.3989423D0*EXP(-700.D0)
C          ELSE
C              D=0.3989423D0*EXP(-X*X*0.5D0)
C          ENDIF
C          P=1.0D0-D*T*(((1.330274D0*T-1.821256D0)*T+1.781478D0)*T
1 -0.3565638D0)*T+0.3193815D0)
C          IF (X .LT. 0.D0) THEN
C              P=1.DO-P
C          ENDIF
20 RETURN

```

END

Subroutine MPARTIAL

SUBROUTINE MPARTIAL(M,MP,INCOHT,INCLASS,IAGES,IFTRAP)

IMPLICIT DOUBLE PRECISION (A-H,O-Z)

C

C RETURNS PARTIAL COLUMN TOTALS

C

C ICLASS = 1 ONE-AGE MODEL

C L L-AGE MODEL

C IFTRAP = 0 MODEL WITH NO TRAP RESPONSE

C 1 MODEL WITH TRAP RESPONSE

C

INCLUDE 'MPAR'

C

C INITIALIZE TO ZERO

C

DO 100 K=1,IFTRAP+1

DO 100 NU=1,IAGES

DO 100 I=1,INCOHT

DO 90 J=I+1,INCOHT

90 MP(I,J,1,NU,K)=0

DO 100 J=I,INCOHT

100 MP(I,J,2,NU,K)=0

DO 106 I=1,INCOHT

DO 105 J=I+1,INCOHT

MP(I,J,1,1,1)=M(I,J,1,1,1,1)

105 MP(I,J,1,1,2)=0

DO 106 J=I,INCLASS

MP(I,J,2,1,1)=M(I,J,1,2,1,1)

106 MP(I,J,2,1,2)=0

DO 130 NU=2,IAGES-1

DO 110 J=2,INCOHT

```

MP(1,J,1,NU,1)=M(1,J,1,1,NU,1)
MP(1,J,1,NU,2)=M(1,J,1,1,NU,2)
IF(J.NE.2)MP(2,J,1,NU,1)=M(2,J,1,1,NU,1)
110 IF(J.NE.2)MP(2,J,1,NU,2)=M(2,J,1,1,NU,2)+
& M(1,J,1,1,NU-1,1)+M(1,J,2,1,NU-1,1)
DO 112 J=1,INCLASS
MP(1,J,2,NU,1)=M(1,J,1,2,NU,1)
MP(1,J,2,NU,2)=M(1,J,1,2,NU,2)
IF(J.NE.1)MP(2,J,2,NU,1)=M(2,J,1,2,NU,1)
112 IF(J.NE.1)MP(2,J,2,NU,2)=M(2,J,1,2,NU,2)+M(1,J,1,2,NU-1,1)
& +M(1,J,2,2,NU-1,1)

DO 130 I=2,INCOHT-1
DO 122 J=I+2,INCOHT
MP(I+1,J,1,NU,1)=M(I+1,J,1,1,NU,1)
122 MP(I+1,J,1,NU,2)=M(I+1,J,1,1,NU,2)+MP(I,J,1,NU-1,1)+
& MP(I,J,1,NU-1,2)+M(I,J,2,1,NU-1,1)+M(I,J,2,1,NU-1,2)
C 122 MP(I+1,J,1,NU,2)=M(I+1,J,1,1,NU,2)+M(I,J,1,1,NU-1,1)+
C & M(I,J,1,1,NU-1,2)+M(I,J,2,1,NU-1,1)+M(I,J,2,1,NU-1,2)
DO 124 J=I+1,INCLASS
MP(I+1,J,2,NU,1)=M(I+1,J,1,2,NU,1)
124 MP(I+1,J,2,NU,2)=M(I+1,J,1,2,NU,2)+MP(I,J,2,NU-1,1)+
& MP(I,J,2,NU-1,2)+M(I,J,2,2,NU-1,1)+M(I,J,2,2,NU-1,2)
C 124 MP(I+1,J,2,NU,2)=M(I+1,J,1,2,NU,2)+M(I,J,1,2,NU-1,1)+
C & M(I,J,1,2,NU-1,2)+M(I,J,2,2,NU-1,1)+M(I,J,2,2,NU-1,2)

130 CONTINUE
C
C THEN DO FOR LAST AGE GROUP
C
DO 140 J=2,INCOHT
MP(1,J,1,IAGES,1)=M(1,J,1,1,IAGES,1)
MP(1,J,1,IAGES,2)=M(1,J,1,1,IAGES,2)
IF(J.NE.2)MP(2,J,1,IAGES,1)=M(2,J,1,1,IAGES,1)
IF (IAGES.EQ.1)THEN
IF(J.NE.2)MP(2,J,1,IAGES,2)=M(2,J,1,1,IAGES,2)+

```

```

&      M(1,J,1,1,IAGES,1)+M(1,J,2,1,IAGES,1)
      ELSE
        IF(J.NE.2)MP(2,J,1,IAGES,2)=M(2,J,1,1,IAGES,2)
&      +M(1,J,1,1,IAGES-1,1)+
&      M(1,J,1,1,IAGES,1)+M(1,J,2,1,IAGES-1,1)+M(1,J,2,1,IAGES,1)
140    ENDIF
      DO 150 J=1,INCLASS
        MP(1,J,2,IAGES,1)=M(1,J,1,2,IAGES,1)
        MP(1,J,2,IAGES,2)=M(1,J,1,2,IAGES,2)
        IF(J.NE.1)MP(2,J,2,IAGES,1)=M(2,J,1,2,IAGES,1)
        IF(IAGES.EQ.1)THEN
          IF(J.NE.1)MP(2,J,2,IAGES,2)=M(2,J,1,2,IAGES,2)+
&      M(1,J,1,2,IAGES,1)+M(1,J,2,2,IAGES,1)
        ELSE
          IF(J.NE.1)MP(2,J,2,IAGES,2)=M(2,J,1,2,IAGES,2)+
&      M(1,J,1,2,IAGES-1,1)+
&      M(1,J,1,2,IAGES,1)+M(1,J,2,2,IAGES-1,1)+M(1,J,2,2,IAGES,1)
150    ENDIF
      DO 170 I=2,INCOHT-1
        DO 160 J=I+2,INCOHT
          MP(I+1,J,1,IAGES,1)=M(I+1,J,1,1,IAGES,1)
          IF(IAGES.EQ.1) THEN
            MP(I+1,J,1,IAGES,2)=M(I+1,J,1,1,IAGES,2)+
&      MP(I,J,1,IAGES,2)+MP(I,J,1,IAGES,1)+
&      M(I,J,2,1,IAGES,2)+M(I,J,2,1,IAGES,1)
          ELSE
            MP(I+1,J,1,IAGES,2)=M(I+1,J,1,1,IAGES,2)+
&      MP(I,J,1,IAGES-1,2)+MP(I,J,1,IAGES,2)
&      +MP(I,J,1,IAGES-1,1)+MP(I,J,1,IAGES,1)
&      +M(I,J,2,1,IAGES-1,2)+M(I,J,2,1,IAGES,2)
&      +M(I,J,2,1,IAGES-1,1)+M(I,J,2,1,IAGES,1)
160    ENDIF
      DO 170 J=I+1,INCLASS
        MP(I+1,J,2,IAGES,1)=M(I+1,J,1,2,IAGES,1)
        IF(IAGES.EQ.1)THEN
          MP(I+1,J,2,IAGES,2)=M(I+1,J,1,2,IAGES,2)+

```

```

&          MP(I,J,2,IAGES,2)+MP(I,J,2,IAGES,1)
&          +M(I,J,2,2,IAGES,2)+M(I,J,2,2,IAGES,1)
          ELSE
              MP(I+1,J,2,IAGES,2)=M(I+1,J,1,2,IAGES,2)+
&          MP(I,J,2,IAGES-1,2)+MP(I,J,2,IAGES,2)
&          +MP(I,J,2,IAGES-1,1)+MP(I,J,2,IAGES,1)
&          +M(I,J,2,2,IAGES-1,2)+M(I,J,2,2,IAGES,2)
&          +M(I,J,2,2,IAGES-1,1)+M(I,J,2,2,IAGES,1)
170          ENDIF

```

```

          IF(IFTRAP.EQ.1)GOTO 250
          DO 210 NU=1,IAGES
              DO 200 I=1,INCOHT
                  DO 200 J=I+1,INCOHT
200          MP(I,J,1,NU,1)=MP(I,J,1,NU,1)+MP(I,J,1,NU,2)
                  DO 210 I=1,INCOHT
                      DO 210 J=I,INCLASS
210          MP(I,J,2,NU,1)=MP(I,J,2,NU,1)+MP(I,J,2,NU,2)

250 CONTINUE

```

```

          RETURN
          END

```

Subroutine PAREST

```

          SUBROUTINE PAREST(M,N,NN,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,
&IAGES,IFTRAP,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)
          IMPLICIT DOUBLE PRECISION (A-H,O-Z)

C
C RETURNS PARAMETER ESTIMATES FOR RANDOM EMIGRATION MODEL
C
C IFTRAP = 0 MODEL WITH NO TRAP RESPONSE
C          1 MODEL WITH TRAP RESPONSE
C
          INCLUDE 'MPAR'
C

```

```

C INITIALISE TO ZERO
C
      DO 5 NU=1,IAGES
        DO 5 KK=1,IFTRAP+1
          DO 5 I=1,INCLASS
            PHAT(I,NU,KK)=0.
            FHAT(I,NU,KK)=0.
            THETAHAT(I,NU,KK)=0.
            SHAT(I,NU,KK)=0.
            XI(I,NU,KK)=0
          DO 5 J=1,INCLASS
5           ZETA(I,J,NU,KK)=0.

      DO 50 NU=1,IAGES
        OMEGA=NU+1
        IF(OMEGA.GT.IAGES)OMEGA=IAGES
        INDEX=IFTRAP+1
        DO 50 K=1,IFTRAP+1

C
C NB PARAMETERS ARE STRUCTURALLY ZERO FOR FIRST AGE CLASS AND SECOND
C TRAP CLASS
C
      IF(IAGES.NE.1 .AND. NU.EQ.1 .AND. K .EQ. 2)GOTO 50
      DO 10 I=1,INCOHT

C
C IF I==1 AND K==2 NO PARAMETERS ARE ESTIMIBLE
C
      IF(I.EQ.1 .AND.K.EQ.2)GOTO 10
      FHAT(I,NU,K)=RI1(I,NU,K)*OI(I,NU,K)/FLOAT(N(I,NU,K))
&      /FLOAT(R(I,NU,K))
10     CONTINUE
      DO 20 I=2,INCOHT
        IF(I.EQ.2 .AND.K.EQ.2)GOTO 20
        MHAT(I,NU+1,K)=N(I,OMEGA,INDEX)*Z(I,NU+1,K)/
&DBLE(RI1(I,OMEGA,INDEX))+DBLE(CI(I,NU+1,K))

```

```

        PHAT(I,NU,K)=CI(I,NU+1,K)/MHAT(I,NU+1,K)
20    CONTINUE
        DO 30 I=1,INCOHT-1
            IF(I.EQ.1 .AND.K.EQ.2)GOTO 30
            THETAHAT(I,NU,K)=NN(I,NU,K)*(R(I,NU,K)-OI(I,NU,K))
&            /FLOAT(R(I,NU,K)*NN(I,NU,K)+OI(I,NU,K)*(RI2(I,NU,K)
&            -NN(I,NU,K)))
            IF(NN(I,NU,K).EQ.0)THETAHAT(I,NU,K)=1
30    CONTINUE
        DO 40 I=1,INCOHT
            IF(I.EQ.1 .AND.K.EQ.2)GOTO 40
C
C AUTOMATICALLY COMPUTE LI(2) AS THE DIFFERENCE BETWEEN OBSERVED AND RELEASED
C
        L2(I,NU,K)=OI(I,NU,K)-NN(I,NU,K)
        PART1=RI1(I,NU,K)/DBLE(N(I,NU,K))/DBLE(R(I,NU,K))
        PART2=RI1(I,NU,K)*RI2(I,NU,K)*DBLE(L2(I,NU,K))/
&DBLE(NN(I,NU,K))/DBLE(N(I,NU,K))/DBLE(T(I+1,NU+1,K))
&/DBLE(R(I,NU,K))
        IF(NN(I,NU,K).EQ.0)PART2=0.
        SHAT(I,NU,K)=(PART1+PART2)*MHAT(I+1,NU+1,K)
40    CONTINUE
50    CONTINUE
C
C IF THERE ARE EXTRA OBSERVATIONS BEYOND THE FINAL CAPTURE PERIOD
C COMPUTE THETAHAT(T), XI(I) AND ZETA(I,J)
C
        CALL MPARTIAL(M,MP,INCOHT,INCLASS,IAGES,IFTRAP)
        IF(INCLASS.EQ.INCOHT)GOTO 200
        IT=INCOHT
        DO 70 NU=1,IAGES
            DO 70 K=1,IFTRAP+1
                THETAHAT(IT,NU,K)=NN(IT,NU,K)*(R(IT,NU,K)-
&                OI(IT,NU,K))/FLOAT(R(IT,NU,K)*NN(IT,NU,K)+OI(IT,NU,K)*

```

```

&      (RI2(IT,NU,K)-NN(IT,NU,K))
70     IF(NN(IT,NU,K).EQ.0)THETAHAT(IT,NU,K)=1
      DO 100 NU=1,IAGES
        DO 100 K=1,IFTRAP+1
          DO 80 J=INCOHT+1,INCLASS
            MDOT=MP(INCOHT,J,2,NU,K)+M(INCOHT,J,2,2,NU,K)
            XI(J,NU,K)=0.
80     IF(Z(INCOHT+1,NU+1,K).GT.0) XI(J,NU,K)=MDOT/
&DBLE(Z(INCOHT+1,NU+1,K))*RI1(INCOHT,NU,K)/
&DBLE(N(INCOHT,NU,K))*(R(INCOHT,NU,K)-OI(INCOHT,NU,K))/
&DBLE(R(INCOHT,NU,K))

      INDEX=INCLASS-1
      IF(NU.LT.IAGES)INDEX=MIN(INCOHT+NU-1,INCLASS-1)
      DO 90 I=INCOHT+1,INDEX
        DO 90 J=I+1,INCLASS
          IF(MN(I,NU,K).EQ.0)ZETA(I,J,NU,K)=0.
90     IF(MN(I,NU,K).GT.0)ZETA(I,J,NU,K)=M(I,J,2,2,NU,K)
&/DBLE(NN(I,NU,K))
100 CONTINUE

200 RETURN
      END

```

Subroutine PRMSS

```

SUBROUTINE PRMSS(M,N,NN,RI1,RI2,CI,OI,T,R,Z,IAGES,INCOHT,INCLASS,
&IFTRAP,XLL1)

```

```

IMPLICIT DOUBLE PRECISION (A-H,O-Z)

```

```

C
C COMPUTES THE PR(MSS) COMPONENT OF THE LOG-LIKELIHOOD
C
C IFTRAP = 0 MODEL WITH NO TRAP RESPONSE
C       1 MODEL WITH TRAP RESPONSE
C

```

```

INCLUDE 'MPAR'

DOUBLE PRECISION LAM1(MXCOHT,MXAGE,2),LAM2(MXCLAS,MXAGE,2),
&TAU1(MXCOHT,MXAGE,2),TAU2(MXCLAS,MXAGE,2)

SUM=0.

C
C COMPUTE VALUES FOR CANONICAL PARAMETERS
C

SMALL=1E-4
INDEX=IFTRAP+1
DO 51 NU=1,IAGES
    OMEGA=NU+1
    IF(OMEGA.GT.IAGES)OMEGA=IAGES

    DO 51 K=1,IFTRAP+1

C
C SKIP FOR FIRST AGE-CLASS AND SECOND TRAP-CLASS (STRUCTURALLY ZERO)
C - ONLY IF THERE IS MORE THAN ONE AGE-CLASS
C

    IF(IAGES.NE.1 .AND. NU.EQ.1 .AND.K.EQ.2)GOTO 51
    DO 10 I=1,INCOHT
        LAM1(I,NU,K)=SMALL
        IF(N(I,NU,K).NE.0 .AND.RI1(I,NU,K).NE.0)LAM1(I,NU,K)=
&RI1(I,NU,K)/DBLE(N(I,NU,K))
10    IF(LAM1(I,NU,K).EQ.1)LAM1(I,NU,K)=1-SMALL

        DO 20 I=1,INCLASS-1
            LAM2(I,NU,K)=SMALL
            IF(NN(I,NU,K).NE.0 .AND.RI2(I,NU,K).NE.0)LAM2(I,NU,K)=
&RI2(I,NU,K)/DBLE(NN(I,NU,K))
20    IF(LAM2(I,NU,K).EQ.1)LAM2(I,NU,K)=1-SMALL

        DO 30 I=2,INCOHT
            TAU1(I,NU+1,K)=SMALL
            IF(T(I,NU+1,K).NE.0.AND.CI(I,NU+1,K).NE.0)TAU1(I,NU+1,K)=
&CI(I,NU+1,K)/DBLE(T(I,NU+1,K))

```

```

30     IF(TAU1(I,NU+1,K).EQ.1)TAU1(I,NU+1,K)=1-SMALL
      DO 40 I=1,INCOHT
        TAU2(I,NU,K)=SMALL
        IF(R(I,NU,K).NE.0.AND.OI(I,NU,K).NE.0)TAU2(I,NU,K)=
&OI(I,NU,K)/DBLE(R(I,NU,K))
40     IF(TAU2(I,NU,K).EQ.1)TAU2(I,NU,K)=1-SMALL
51     CONTINUE

```

C

C NOW COMPUTE PR(MSS)

C

```

      DO 140 NU=1,IAGES
        DO 140 K=1,IFTRAP+1

```

C

C SKIP IF FIRST AGE-CLASS AND SECOND TRAP-CLASS

C

```

          IF(IAGES.NE.1 .AND. NU.EQ.1 .AND.K.EQ.2)GOTO 140
          DO 100 I=K,INCOHT
            CONSTANT=DLGAMA(DBLE(N(I,NU,K)+1))
            &-DLGAMA(DBLE(N(I,NU,K)-RI1(I,NU,K)+1))-DLGAMA(DBLE(RI1(I,NU,K)+1))
100         SUM=SUM+CONSTANT+RI1(I,NU,K)*DLOG(LAM1(I,NU,K))+
            &(N(I,NU,K)-RI1(I,NU,K))*DLOG(1-LAM1(I,NU,K))
            DO 110 I=K,INCOHT-1
              CONSTANT=DLGAMA(DBLE(NN(I,NU,K)+1))-
              &DLGAMA(DBLE(NN(I,NU,K)-RI2(I,NU,K)+1))-DLGAMA(DBLE(RI2(I,NU,K)+1))
110         SUM=SUM+CONSTANT+RI2(I,NU,K)*DLOG(LAM2(I,NU,K))+
            &(NN(I,NU,K)-RI2(I,NU,K))*DLOG(1-LAM2(I,NU,K))
            DO 120 I=K+1,INCOHT
              CONSTANT=DLGAMA(DBLE(T(I,NU+1,K)+1))-
              &DLGAMA(DBLE(T(I,NU+1,K)-CI(I,NU+1,K)+1))
              &-DLGAMA(DBLE(CI(I,NU+1,K)+1))
120         SUM=SUM+CONSTANT+CI(I,NU+1,K)*DLOG(TAU1(I,NU+1,K))+
            &(T(I,NU+1,K)-CI(I,NU+1,K))*DLOG(1-TAU1(I,NU+1,K))
            DO 130 I=K,INCOHT-1
              CONSTANT=DLGAMA(DBLE(R(I,NU,K)+1))-

```

```

      &DLGAMA(DBLE(R(I,NU,K)-OI(I,NU,K)+1))-DLGAMA(DBLE(OI(I,NU,K)+1))
130      SUM=SUM+CONSTANT+OI(I,NU,K)*DLOG(TAU2(I,NU,K))+
      &(R(I,NU,K)-OI(I,NU,K))*DLOG(1-TAU2(I,NU,K))
140 CONTINUE

      SUM1=SUM
      SUM=0.
      SUM2=0.

C
C COMPUTE ADDITIONAL TERMS IF THERE ARE OBSERVATIONS BEYOND THE LAST CAPTURE
C PERIOD
C
      IF(INCLASS.EQ.INCOHT)GOTO 300
      DO 200 NU=1,IAGES
      DO 200 K=1,IFTRAP+1
      IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 200
      DO 150 I=INCOHT,INCLASS-1
      CONSTANT=DLGAMA(DBLE(NN(I,NU,K)+1))-
      &DLGAMA(DBLE(NN(I,NU,K)-RI2(I,NU,K)+1))-DLGAMA(DBLE(RI2(I,NU,K)+1))
150      SUM=SUM+CONSTANT+RI2(I,NU,K)*DLOG(LAM2(I,NU,K))+
      &(NN(I,NU,K)-RI2(I,NU,K))*DLOG(1-LAM2(I,NU,K))
200 CONTINUE

C
C TERM FOR PR(O(T)|R(T))
C
      I=INCOHT
      DO 220 NU=1,IAGES
      DO 220 K=1,IFTRAP+1
      IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 220
      CONSTANT=DLGAMA(DBLE(R(I,NU,K)+1))-
      &DLGAMA(DBLE(R(I,NU,K)-OI(I,NU,K)+1))-DLGAMA(DBLE(OI(I,NU,K)+1))
      SUM=SUM+CONSTANT+OI(I,NU,K)*DLOG(TAU2(I,NU,K))+
      &(R(I,NU,K)-OI(I,NU,K))*DLOG(1-TAU2(I,NU,K))
220 CONTINUE

C
C TERM FOR MARGINAL DISTRIBUTION OF {R(T)-O(T)+R(T,2)}|Z(T+1)

```

C

```
CALL MPARTIAL(M,MP,INCOHT,INCLASS,IAGES,IFTRAP)
```

```
I=INCOHT
```

```
DO 240 NU=1,IAGES
```

```
DO 240 K=1,IFTRAP+1
```

```
IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 240
```

```
TERM1=DLGAMA(DBLE(Z(I+1,NU+1,K)+1))
```

```
TMPSUM=0.
```

```
DO 230 J=I+1,INCLASS
```

```
MDOT=MP(I,J,2,NU,K)+M(I,J,2,2,NU,K)
```

```
TERM1=TERM1-DLGAMA(DBLE(MDOT)+1)
```

```
PIE=SMALL
```

```
IF(Z(I+1,NU+1,K).NE.0.AND.MDOT.NE.0)PIE=
```

```
&MDOT/DBLE(Z(I+1,NU+1,K))
```

```
IF(PIE.EQ.1)PIE=1-SMALL
```

```
230 TMPSUM=TMPSUM+MDOT*DLOG(PIE)
```

```
SUM=SUM+TERM1+TMPSUM
```

```
240 CONTINUE
```

C

```
C TERM FOR PR({M(I,J,2,2)}|R(I,2))
```

C

```
DO 260 I=INCOHT+1,INCLASS-2
```

```
DO 260 NU=1,IAGES
```

```
DO 260 K=1,IFTRAP+1
```

```
IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2) GOTO 260
```

```
TERM1=DLGAMA(DBLE(RI2(I,NU,K)+1))
```

```
TMPSUM=0.
```

```
DO 250 J=I+1,INCLASS
```

```
TERM1=TERM1-DLGAMA(DBLE(M(I,J,2,2,NU,K))+1)
```

```
PIE=SMALL
```

```
IF(RI2(I,NU,K).NE.0.AND.M(I,J,2,2,NU,K).NE.0)PIE=
```

```
&M(I,J,2,2,NU,K)/DBLE(RI2(I,NU,K))
```

```
IF(PIE.EQ.1)PIE=1-SMALL
```

```
250 TMPSUM=TMPSUM+M(I,J,2,2,NU,K)*DLOG(PIE)
```

```
SUM=SUM+TERM1+TMPSUM
```

```

260 CONTINUE
      SUM2=SUM
300 XLL1=SUM1+SUM2

      RETURN
      END

```

Subroutine PRDATA

```

      SUBROUTINE PRDATA(M,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,IFTRAP,
&XLL2)
      IMPLICIT DOUBLE PRECISION (A-H,O-Z)

C
C COMPUTES PR(DATA | MSS) COMPONENT OF THE LOG-LIKELIHOOD
C
C IFTRAP = 0  MODEL WITH NO TRAP RESPONSE
C           1  MODEL WITH TRAP RESPONSE
C
      INCLUDE 'MPAR'

C
C FIRST OBTAIN PARTIAL COLUMN TOTALS
C
      CALL MPARTIAL(M,MP,INCOHT,INCLASS,IAGES,IFTRAP)
C
C FIRST TERM
C
      SUM1=0.
      DO 210 NU=1,IAGES
        DO 210 K=1,IFTRAP+1
          IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 210
          DO 200 I=K,INCOHT-1
            X=DBLE(R(I,NU,K)-OI(I,NU,K))
            Y=DBLE(MP(I,I+1,1,NU,K))
            TERM1=DLGAMA(X+1)-DLGAMA(Y+1)-DLGAMA(X-Y+1)
            X=DBLE(RI2(I,NU,K))
            Y=DBLE(M(I,I+1,2,1,NU,K))

```

```

TERM2=DLGAMA(X+1)-DLGAMA(Y+1)-DLGAMA(X-Y+1)
X=DBLE(T(I+1,NU+1,K))
Y=DBLE(CI(I+1,NU+1,K))
TERM3=DLGAMA(X+1)-DLGAMA(Y+1)-DLGAMA(X-Y+1)
200      SUM1=SUM1+TERM1+TERM2-TERM3
210 CONTINUE
C
C COMPUTE SECOND COMPONENT
C
      SUM2=0.
      INDEX=IFTRAP+1
      DO 315 NU=1,IAGES-2
          TERM1=DLGAMA(DBLE(R(1,NU,1)-OI(1,NU,1)-MP(1,2,1,NU,1)+1))
          DO 305 J=3,INCOHT
305              TERM1=TERM1-DLGAMA(DBLE(MP(1,J,1,NU,1)+1))
          DO 306 J=2,INCLASS
306              TERM1=TERM1-DLGAMA(DBLE(MP(1,J,2,NU,1)+1))
          TERM2=DLGAMA(DBLE(RI2(1,NU,1)-M(1,2,2,1,NU,1)+1))
          DO 307 J=3,INCOHT
307              TERM2=TERM2-DLGAMA(DBLE(M(1,J,2,1,NU,1)+1))
          DO 308 J=2,INCLASS
308              TERM2=TERM2-DLGAMA(DBLE(M(1,J,2,2,NU,1)+1))

          TERM3=DLGAMA(DBLE(RI1(2,NU+1,INDEX)+1))
          DO 309 J=3,INCOHT
309              TERM3=TERM3-DLGAMA(DBLE(M(2,J,1,1,NU+1,INDEX)+1))
          DO 310 J=2,INCLASS
310              TERM3=TERM3-DLGAMA(DBLE(M(2,J,1,2,NU+1,INDEX)+1))

          TERM4=DLGAMA(DBLE(R(2,NU+1,INDEX)+1))
          DO 311 J=3,INCOHT
311              TERM4=TERM4-DLGAMA(DBLE(MP(2,J,1,NU+1,INDEX)+1))
          DO 312 J=2,INCLASS
312              TERM4=TERM4-DLGAMA(DBLE(MP(2,J,2,NU+1,INDEX)+1))
C      PRINT*,IAGES,TERM1,TERM2,TERM3,TERM4
315      SUM2=SUM2+TERM1+TERM2+TERM3-TERM4

```

C

C REPEAT FOR LAST AGE CLASS

C

```
      ISTART=IAGES-1
      IF(IAGES.EQ.1)ISTART=1
      TMPSUM=0.
      DO 327 NU=ISTART,IAGES
          TERM1=DLGAMA(DBLE(R(1,NU,1)-OI(1,NU,1)-MP(1,2,1,NU,1)+1))
          DO 320 J=3,INCOHT
320             TERM1=TERM1-DLGAMA(DBLE(MP(1,J,1,NU,1)+1))
          DO 321 J=2,INCLASS
321             TERM1=TERM1-DLGAMA(DBLE(MP(1,J,2,NU,1)+1))
          TERM2=DLGAMA(DBLE(RI2(1,NU,1)-M(1,2,2,1,NU,1)+1))
          DO 325 J=3,INCOHT
325             TERM2=TERM2-DLGAMA(DBLE(M(1,J,2,1,NU,1)+1))
          DO 326 J=2,INCLASS
326             TERM2=TERM2-DLGAMA(DBLE(M(1,J,2,2,NU,1)+1))
327             TMPSUM=TMPSUM+TERM1+TERM2

          TERM3=DLGAMA(DBLE(RI1(2,IAGES,INDEX)+1))
          DO 330 J=3,INCOHT
330             TERM3=TERM3-DLGAMA(DBLE(M(2,J,1,1,IAGES,INDEX)+1))
          DO 331 J=2,INCLASS
331             TERM3=TERM3-DLGAMA(DBLE(M(2,J,1,2,IAGES,INDEX)+1))
          TERM4=DLGAMA(DBLE(R(2,IAGES,INDEX)+1))
          DO 332 J=3,INCOHT
332             TERM4=TERM4-DLGAMA(DBLE(MP(2,J,1,IAGES,INDEX)+1))
          DO 333 J=2,INCLASS
333             TERM4=TERM4-DLGAMA(DBLE(MP(2,J,2,IAGES,INDEX)+1))
          SUM2=SUM2+TMPSUM+TERM3-TERM4
```

C

C NOW REPEAT FOR REMAINING YEARS

C

```
      DO 400 NU=1,IAGES-2
          IMAX=INCOHT-2
```

```

IF(INCLASS.GT.INCOHT)IMAX=INCOHT-1
DO 400 I=2,IMAX
  TMPSUM=0.
  DO 350 K=1,IFTRAP+1
    TERM1=DLGAMA(DBLE(R(I,NU,K)-OI(I,NU,K)
&-MP(I,I+1,1,NU,K)+1))
    DO 340 J=I+2,INCOHT
340      TERM1=TERM1-DLGAMA(DBLE(MP(I,J,1,NU,K)+1))
    DO 341 J=I+1,INCLASS
341      TERM1=TERM1-DLGAMA(DBLE(MP(I,J,2,NU,K)+1))

    TERM2=DLGAMA(DBLE(RI2(I,NU,K)-M(I,I+1,2,1,NU,K)+1))
    DO 342 J=I+2,INCOHT
342      TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,1,NU,K)+1))
    DO 343 J=I+1,INCLASS
343      TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,2,NU,K)+1))
350    TMPSUM=TMPSUM+TERM1+TERM2
    TERM3=DLGAMA(DBLE(RI1(I+1,NU+1,INDEX)+1))
    DO 351 J=I+2,INCOHT
351      TERM3=TERM3-DLGAMA(DBLE(M(I+1,J,1,1,NU+1,INDEX)+1))
    DO 352 J=I+1,INCLASS
352      TERM3=TERM3-DLGAMA(DBLE(M(I+1,J,1,2,NU+1,INDEX)+1))
    TERM4=DLGAMA(DBLE(R(I+1,NU+1,INDEX)+1))
    DO 353 J=I+2,INCOHT
353      TERM4=TERM4-DLGAMA(DBLE(MP(I+1,J,1,NU+1,INDEX)+1))
    DO 354 J=I+1,INCLASS
354      TERM4=TERM4-DLGAMA(DBLE(MP(I+1,J,2,NU+1,INDEX)+1))
C      PRINT*,TMPSUM,TERM3,TERM4
400    SUM2=SUM2+TMPSUM+TERM3-TERM4
C
C REPEAT FOR LAST AGE CLASS
C
    IMAX=INCOHT-2
    IF(INCLASS.GT.INCOHT)IMAX=INCOHT-1
    DO 450 I=2,IMAX
    TMPSUM=0.

```

```

DO 425 NU=ISTART,IAGES
  DO 425 K=1,IFTRAP+1
    TERM1=DLGAMA(DBLE(R(I,NU,K)-OI(I,NU,K)
&
    -MP(I,I+1,1,NU,K)+1))
    DO 410 J=I+2,INCOHT
410    TERM1=TERM1-DLGAMA(DBLE(MP(I,J,1,NU,K)+1))
    DO 411 J=I+1,INCLASS
411    TERM1=TERM1-DLGAMA(DBLE(MP(I,J,2,NU,K)+1))
    TERM2=DLGAMA(DBLE(RI2(I,NU,K)-M(I,I+1,2,1,NU,K)+1))
    DO 412 J=I+2,INCOHT
412    TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,1,NU,K)+1))
    DO 413 J=I+1,INCLASS
413    TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,2,NU,K)+1))
415    TMPSUM=TMPSUM+TERM1+TERM2

    TERM3=DLGAMA(DBLE(RI1(I+1,IAGES,INDEX)+1))
    DO 420 J=I+2,INCOHT
420    TERM3=TERM3-DLGAMA(DBLE(M(I+1,J,1,1,IAGES,INDEX)+1))
    DO 421 J=I+1,INCLASS
421    TERM3=TERM3-DLGAMA(DBLE(M(I+1,J,1,2,IAGES,INDEX)+1))

    TERM4=DLGAMA(DBLE(R(I+1,IAGES,INDEX)+1))
    DO 422 J=I+2,INCOHT
422    TERM4=TERM4-DLGAMA(DBLE(MP(I+1,J,1,IAGES,INDEX)+1))
    DO 423 J=I+1,INCLASS
423    TERM4=TERM4-DLGAMA(DBLE(MP(I+1,J,2,IAGES,INDEX)+1))
425    CONTINUE
    SUM2=SUM2+TMPSUM+TERM3-TERM4
450 CONTINUE
C
C IF THERE ARE OBSERVATIONS BEYOND THE LAST CAPTURE PERIOD THEN COMPUTE
C ADDITIONAL TERMS
C
SUM3=0.
IF(INCLASS.EQ._INCOHT)GOTO 600

```

```

I=INCOHT
DO 550 NU=1,IAGES
    DO 550 K=1,IFTRAP+1
        IF(IAGES.NE.1 .AND. NU.EQ.1.AND.K.EQ.2)GOTO 550
        TERM1=DLGAMA(DBLE(R(I,NU,K)-OI(I,NU,K))+1)
        DO 540 J=I+1,INCLASS
540          TERM1=TERM1-DLGAMA(DBLE(MP(I,J,2,NU,K))+1)
        TERM2=DLGAMA(DBLE(RI2(I,NU,K))+1)
        DO 542 J=I+1,INCLASS
542          TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,2,NU,K))+1)
        TERM3=DLGAMA(DBLE(T(I+1,NU+1,K))+1)
        DO 544 J=I+1,INCLASS
544          TERM3=TERM3-DLGAMA(DBLE(MP(I,J,2,NU,K)+M(I,J,2,2,NU,K))+1)
        SUM3=SUM3+TERM1+TERM2-TERM3
550 CONTINUE
600 CONTINUE
    XLL2=SUM1+SUM2+SUM3
700 RETURN
    END

```

Subroutine DLGAMA

```

C *DECK DLGAMA
    DOUBLE PRECISION FUNCTION DLGAMA (ARG)
C
C THIS ROUTINE FOR COMPUTING DLGAMA IS BASED ON THE ALGOL ROUTINE
C IN ACM ALGORITHM NUMBER 291. THE SIGNIFICANT CHANGES ARE THE
C TRUNCATION OF THE ARGUMENT TO THE RANGE 1.E-35 THRU 1.E+30,
C TAKING THE LOG OF LOCAL VARIABLE *F* EVEN WHEN THE ARGUMENT
C IS GREATER THAN OR EQUAL TO 7, AND HANDLING ARGUMENT VALUES
C LARGER THAN 1.E10 AS IN THE SSP ROUTINE TO AVOID EXPONENT
C OVERFLOW.
C
    IMPLICIT DOUBLE PRECISION (A-H,O-Z)
    DOUBLE PRECISION ARG
    DOUBLE PRECISION ALNG, F, Z, X
C

```

```

      X=ARG
C
C      **CHECK MAGNITUDE OF ARGUMENT
C
      IF (X.LT.1.E10) GO TO 10
C
C      **AVOID LARGISH ARGUMENT
C
      X=MIN(X,1.D30)
      ALNG=X*(LOG(X)-1.)
      GO TO 40
C      ELSE
10  CONTINUE
C
C      **AVOID SMALLISH ARGUMENT
C
      X=MAX(X,1.D-35)
C
C      **ALGORITHM 291 STARTS HERE
C
      F=1.
C      DO WHILE
20  IF (X.GE.7.) GO TO 30
      F=F*X
      X=X+1.
      GO TO 20
C      ENDDO
30  CONTINUE
      F=-LOG(F)
      Z=1./(X*X)
      ALNG=F+(X-0.5)*LOG(X)-X+.918938533204673+(((-.000595238095238*Z+.
1  000793650793651)*Z-.0027777777777778)*Z+.0833333333333333)/X
C      ENDIF
40  CONTINUE
      DLGAMA=ALNG
C

```

```
RETURN
END
```

Subroutine AGETEST

```
      SUBROUTINE AGETEST(M,N,NN,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,
&IFTRAP)
C
C CARRIES OUT TEST FOR AGE-DEPENDENCE ASSUMING RANDOM EMIGRATION
C
      IMPLICIT DOUBLE PRECISION(A-H,O-Z)
      INCLUDE 'MPAR'
C
C RETURNS AGE-DEPENDENCE TEST
C
      IRO=IAGES
      ICOL=2
      X2=0.
      NDF=0

      WRITE(UNIT=2,FMT='(A5)') ' '
      WRITE(UNIT=2,FMT='(A19)') 'AGE-DEPENDENCE TEST '
      WRITE(UNIT=2,FMT='(A19)') '-----'

      DO 90 KK=1,IFTRAP+1
        IF(IFTRAP.EQ.1)WRITE(UNIT=2,FMT='(A10,I2)') 'TRAP-CLASS',KK
        WRITE(UNIT=2,FMT='(A10)') '(A) R(I,1)'
        DO 20 I=1,INCOHT
          DO 10 NU=1,IAGES
            OBSERV(NU,1)=RI1(I,NU,KK)
10          OBSERV(NU,2)=N(I,NU,KK)-OBSERV(NU,1)
            CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
            X2=X2+CHISQ
            NDF=NDF+IDF
            IRO=IAGES
20          ICOL=2
            WRITE(UNIT=2,FMT='(A10)') '(B) R(I,2)'
```

```

DO 40 I=1,INCLASS-1
    DO 30 NU=1,IAGES
        OBSERV(NU,1)=RI2(I,NU,KK)
30     OBSERV(NU,2)=NN(I,NU,KK)-OBSERV(NU,1)
        CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
        X2=X2+CHISQ
        NDF=NDF+IDF
        IRO=IAGES
40     ICOL=2
        WRITE(UNIT=2,FMT='(A10)')'(C) C(I)'
        DO 60 I=2,INCOHT
            DO 50 NU=2,IAGES+1
                K=NU-1
                OBSERV(K,1)=CI(I,NU,KK)
50         OBSERV(K,2)=T(I,NU,KK)-OBSERV(K,1)
                CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
                X2=X2+CHISQ
                NDF=NDF+IDF
                IRO=IAGES
60         ICOL=2
                WRITE(UNIT=2,FMT='(A10)')'(D) R(I)'
                DO 80 I=1,INCOHT
                    DO 70 NU=1,IAGES
                        OBSERV(NU,1)=OI(I,NU,KK)
70         OBSERV(NU,2)=R(I,NU,KK)-OBSERV(NU,1)
                        CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
                        X2=X2+CHISQ
                        NDF=NDF+IDF
                        IRO=IAGES
80         ICOL=2

90     CONTINUE
        CALL CDTR(X2,NDF,SVALUE,IERR2)
        PVALUE=1-SVALUE
        WRITE(UNIT=2,FMT='(A27)')'OVERALL AGE-DEPENDENCE TEST'
        WRITE(UNIT=2,FMT='(A8,F8.4,3X,A5,I3,3X,A4,F6.4)')

```

```
&'CHISQ = ',X2,'DF = ',NDF,'P = ',PVALUE
```

```
RETURN
```

```
END
```

Subroutine TRAPTEST

```
      SUBROUTINE TRAPTEST(M,N,NN,RI1,RI2,CI,OI,T,R,IAGES,INCOHT,INCLASS,  
&IFTRAP)
```

```
C
```

```
C CARRIES OUT THE TEST FOR TRAP-DEPENDENCE ASSUMING RANDOM EMIGRATION
```

```
C
```

```
      IMPLICIT DOUBLE PRECISION(A-H,O-Z)
```

```
      INCLUDE 'MPAR'
```

```
C
```

```
C TRAP-DEPENDENCE TEST
```

```
C POOL ACROSS AGE CLASSES
```

```
C
```

```
      WRITE(UNIT=2,FMT='(A5)') '      '
```

```
      WRITE(UNIT=2,FMT='(A20)') 'TRAP-DEPENDENCE TEST '
```

```
      WRITE(UNIT=2,FMT='(A20)') '-----'
```

```
      IRO=2
```

```
      ICOL=2
```

```
      NDF=0
```

```
      X2=0.
```

```
      WRITE(UNIT=2,FMT='(A10)') '(A) R(I,1)'
```

```
      DO 30 NU=1,IAGES
```

```
        DO 30 I=1,INCOHT
```

```
          DO 20 KK=1,2
```

```
            OBSERV(KK,1)=RI1(I,NU,KK)
```

```
20          OBSERV(KK,2)=N(I,NU,KK)-OBSERV(KK,1)
```

```
          CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
```

```
          X2=X2+CHISQ
```

```
          NDF=NDF+IDF
```

```
          IRO=2
```

```
30        ICOL=2
```

```

WRITE(UNIT=2,FMT='(A10)')'(B) R(I,2)'
DO 60 I=1,INCOHT
  DO 60 NU=1,IAGES
    DO 50 KK=1,2
40      OBSERV(KK,1)=RI2(I,NU,KK)
50      OBSERV(KK,2)=NN(I,NU,KK)-OBSERV(KK,1)
    CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
    X2=X2+CHISQ
    NDF=NDF+IDF
    IRO=2
60 ICOL=2
    WRITE(UNIT=2,FMT='(A10)')'(C) C(I)'
    DO 90 I=1,INCOHT
      DO 90 NU=1,IAGES
        DO 80 KK=1,2
          K=NU+1
70      OBSERV(KK,1)=CI(I,K,KK)
80      OBSERV(KK,2)=T(I,K,KK)-OBSERV(KK,1)
    CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
    X2=X2+CHISQ
    NDF=NDF+IDF
    IRO=2
90 ICOL=2
    WRITE(UNIT=2,FMT='(A10)')'(D) O(I)'
    DO 120 I=1,INCOHT
      DO 120 NU=1,IAGES
        DO 110 KK=1,2
100     OBSERV(KK,1)=OI(I,NU,KK)
110     OBSERV(KK,2)=R(I,NU,KK)-OBSERV(KK,1)
    CALL CTABLE(OBSERV,IRO,ICOL,CHISQ,IDF)
    X2=X2+CHISQ
    NDF=NDF+IDF
    IRO=2
120 ICOL=2

CALL CDTR(X2,NDF,SVALUE,IERR2)

```

```

PVALUE=1-SVALUE
WRITE(UNIT=2,FMT='(A28)') 'OVERALL TRAP-DEPENDENCE TEST'
WRITE(UNIT=2,FMT='(A8,F8.4,3X,A5,I3,3X,A4,F6.4)')
&'CHISQ = ',X2,'DF = ',NDF,'P = ',PVALUE

RETURN
END

```

Subroutine NPARM

```

SUBROUTINE NPARM(INCOHT,INCLASS,IAGES,IFTRAP,NPAR)
C
C COMPUTES THE NUMBER OF PARAMETERS IN THE MODEL
C
IMPLICIT DOUBLE PRECISION (A-H,O-Z)
INCLUDE 'MPAR'

NPAR1=4*(INCOHT-1)+1
NPAR2=NPAR1
IF(INCLASS.GT.INCOHT) NPAR2=NPAR1+1+(INCLASS-INCOHT)*(1+(INCLASS
&-INCOHT-1)/2)

NPAR3=IAGES*NPAR2

IF(IFTRAP.EQ.1 .AND. IAGES.GT.1)THEN
NPAR=NPAR3*2-(IAGES-1)*4-NPAR2
ELSEIF(IFTRAP.EQ.1 .AND. IAGES.EQ.1)THEN
NPAR=NPAR3*2-4
ELSE
NPAR=NPAR3
ENDIF
RETURN
END

```

Subroutine Var

```

        SUBROUTINE VAR(M,N,NN,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,
C
C THIS SUBROUTINE COMPUTES ASYMPTOTIC VARIANCES
C
        &IAGES,IFTRAP,VFHAT,VPHAT,VTHAT,VSHAT)
        IMPLICIT DOUBLE PRECISION (A-H,O-Z)
C
C RETURNS PARAMETER ESTIMATES FOR RANDOM EMIGRATION MODEL
C
C IFTRAP = 0  MODEL WITH NO TRAP RESPONSE
C           1  MODEL WITH TRAP RESPONSE
C
        INCLUDE 'MPAR'

        CALL PAREST(M,N,NN,RI1,RI2,CI,OI,R,T,Z,INCOHT,INCLASS,
        &IAGES,IFTRAP,FHAT,PHAT,THETAHAT,SHAT,XI,ZETA)

C
C INITIALISE TO ZERO
C
        DO 5 NU=1,IAGES
            DO 5 KK=1,IFTRAP+1
                DO 5 I=1,INCLASS
                    VPHAT(I,NU,KK)=0.
                    VFHAT(I,NU,KK)=0.
                    VTHAT(I,NU,KK)=0.
5                VSHAT(I,NU,KK)=0.

        DO 50 NU=1,IAGES
            OMEGA=NU+1
            IF(OMEGA.GT.IAGES)OMEGA=IAGES
            INDEX=IFTRAP+1
            DO 50 K=1,IFTRAP+1
                IF(IAGES.NE.1 .AND. NU.EQ.1 .AND. K .EQ. 2)GOTO 50
                DO 10 I=1,INCOHT
C

```

C IF I==1 AND K==2 NO PARAMETERS ARE ESTIMIBLE

C

IF(I.EQ.1 .AND.K.EQ.2)GOTO 10

IF(IAGES.NE.1 .AND. NU .EQ.1)THEN

VFHAT(I,1,1)=FHAT(I,1,1)*(1-FHAT(I,1,1))/DBLE(N(I,NU,K))

ELSE

VFHAT(I,NU,K)=FHAT(I,NU,K)**2*(1/DBLE(RI1(I,NU,K))

&-1/DBLE(N(I,NU,K))+1/DBLE(OI(I,NU,K))-1/DBLE(R(I,NU,K)))

ENDIF

10 CONTINUE

DO 20 I=2,INCOHT

IF(I.EQ.2 .AND.K.EQ.2)GOTO 20

VPHAT(I,NU,K)=(PHAT(I,NU,K)*(1-PHAT(I,NU,K)))**2*

&(1/DBLE(RI1(I,OMEGA,INDEX))-1/DBLE(N(I,OMEGA,INDEX)))+

&1/DBLE(CI(I,NU+1,K))+1/DBLE(Z(I,NU+1,K)))

20 CONTINUE

IMAX=INCOHT-1

IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1

DO 30 I=1,IMAX

IF(I.EQ.1 .AND.K.EQ.2)GOTO 30

VTHAT(I,NU,K)=(THETAHAT(I,NU,K)*(1-THETAHAT(I,NU,K)))**2*

&(1/DBLE(OI(I,NU,K))+1/DBLE(R(I,NU,K)-OI(I,NU,K))+1/DBLE(RI2(I,NU,K)

&))-1/DBLE(NN(I,NU,K)))

IF(THETAHAT(I,NU,K).EQ.1)VTHAT(I,NU,K)=0

30 CONTINUE

DO 40 I=1,INCOHT-1

IF(I.EQ.1 .AND.K.EQ.2)GOTO 40

PART1=1/DBLE(RI1(I,NU,K))-1/DBLE(N(I,NU,K))

PART2=(1-PHAT(I+1,NU,K))**2*(1/DBLE(RI1(I+1,OMEGA,INDEX))

&-1/DBLE(N(I+1,OMEGA,INDEX)))

PART3=PHAT(I+1,NU,K)*(1-PHAT(I,NU,K))*

&(N(I+1,OMEGA,INDEX)-RI1(I+1,OMEGA,INDEX))**2/DBLE(N(I+1,OMEGA

```

&,INDEX)*RI1(I+1,OMEGA,INDEX)*T(I+1,NU+1,K))
      PART4=(1-THETAHAT(I,NU,K))**2*(1/DBLE(RI2(I,NU,K))
&-1/DBLE(NN(I,NU,K)))
      IF(THETAHAT(I,NU,K).EQ.1)PART4=0.
      PART5=THETAHAT(I,NU,K)**2*(NN(I,NU,K)-RI2(I,NU,K))/
&DBLE(NN(I,NU,K))*(1/DBLE(R(I,NU,K)-OI(I,NU,K))-1/DBLE(R(I,NU,K)))
      IF(NN(I,NU,K).EQ.0)PART5=0.
      VSHAT(I,NU,K)=SHAT(I,NU,K)**2*(PART1+PART2+PART3+PART4
&+PART5)
40    CONTINUE
50    CONTINUE

200  RETURN
      END

```

Subroutine CONSTANT

```

      SUBROUTINE CONSTANT(M,n,nn,RI1,RI2,IAGES,INCOHT,INCLASS,
&IFTRAP,SUM)
C
C RETURNS THE MULTINOMIAL NORMALIZING CONSTANT FOR THE FULL MODEL
C WITH THE DATA IN M-ARRAY FORM RATHER THAN SUMMARIZED AS MSS
C
      IMPLICIT DOUBLE PRECISION (A-H,O-Z)
C
C COMPUTES THE RESIDUAL MULTINOMIAL TERM
C FOR THE UNPOOLED LIKELIHOOD
C
      INCLUDE 'MPAR'

      SUM=0.
      DO 50 NU=1,IAGES
        DO 50 K=1,IFTRAP+1
          DO 25 I=1,INCOHT
            TERM1=DLGAMA(DBLE(N(I,NU,K)+1))
            DO 15 J=I+1,INCOHT
15          TERM1=TERM1-DLGAMA(DBLE(M(I,J,1,1,NU,K)+1))

```

```

                DO 20 J=I,INCLASS
20             TERM1=TERM1-DLGAMA(DBLE(M(I,J,1,2,NU,K)+1))
                TERM1=TERM1-DLGAMA(DBLE(N(I,NU,K)-RI1(I,NU,K)+1))
25             SUM=SUM+TERM1
C
C NOW FOR C(I,2) COHORTS
C
                DO 40 I=1,INCLASS-1
                TERM2=DLGAMA(DBLE(NN(I,NU,K)+1))
                DO 30 J=I+1,INCOHT
30             TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,1,NU,K)+1))
                DO 35 J=I+1,INCLASS
35             TERM2=TERM2-DLGAMA(DBLE(M(I,J,2,2,NU,K)+1))
                TERM2=TERM2-DLGAMA(DBLE(NN(I,NU,K)-RI2(I,NU,K)+1))
40             SUM=SUM+TERM2
50 CONTINUE
                RETURN
                END

```

4. Programme CAPHIS

CAPHIS takes data in capture history format and converts it to the m-array format currently needed as input to JOLLYOBS. The input file for CAPHIS requires a capture history for each animal followed by a value for the age of the animal at first capture. The fictitious animal first captured at age 0 and with capture history 05013 has a line in the CAPHIS input file given by 05013 0 . The final figure indicates the animal was in age-class 0 when it was first captured in year 2.

Programme CAPHIS FORTRAN code

```

PROGRAM CAPHIS
C
C THIS PROGRAM READS IN THE DATA IN CAPTURE HISTORY FORMAT AND GENERATES
C THE REDUCED M-ARRAY - AT THE END OF EACH CAPTURE HISTORY THE AGE OF THE
C ANIMAL AT INITIAL CAPTURE NEEDS TO BE PROVIDED
C
IMPLICIT DOUBLE PRECISION (A-H,O-Z)

```

```
INCLUDE 'C:\JOLLYOBS\MPAR'
```

```
PARAMETER(MXRO=4000)
```

```
INTEGER CH(MXRO,MXCLAS),TYR,TCLASS(MXRO)
```

```
CHARACTER*12 FNAME,FNAME2
```

```
1 FORMAT(42I4)
```

```
2 FORMAT(20I6)
```

```
3 FORMAT(40I1)
```

```
4 FORMAT(5I3)
```

```
5 FORMAT(A12)
```

```
PRINT*, 'INPUT FILE NAME '
```

```
READ5,FNAME
```

```
PRINT*, 'OUTPUT FILE NAME '
```

```
READ5,FNAME2
```

```
PRINT*, 'NO. CAPTURE PERIODS '
```

```
READ*,INCOHT
```

```
PRINT*, 'NO. OBSERVATION PERIODS '
```

```
READ*,INCLASS
```

```
PRINT*, 'NO. AGE CLASSES '
```

```
READ*,IAGES
```

```
PRINT*, 'TRAP DEPENDENCE? (0 = NO, 1 = YES) '
```

```
READ*,IFTRAP
```

```
ICPOOL=0
```

```
C
```

```
C INITIALIZE DATA ARRAYS
```

```
C
```

```
DO 20 I=1,INCLASS
```

```
DO 20 NU=1,MXCLAS
```

```
DO 20 KK=1,2
```

```
N(I,NU,KK)=0
```

```
NN(I,NU,KK)=0
```

```

        NKILL(I,NU,KK)=0
        DO 20 J=1,INCLASS
            M(I,J,1,1,NU,KK)=0
            M(I,J,1,2,NU,KK)=0
            M(I,J,2,1,NU,KK)=0
20         M(I,J,2,2,NU,KK)=0

        OPEN(1,FILE=FNAME)
        DO 200 L=1,9999
            READ(1,1,END=205)(CH(L,J),J=1,INCLASS),JUNK,TCLASS(L)
            NU=TCLASS(L)
            DO 50 J=1,INCLASS
                IF(CH(L,J).NE.0) THEN
                    TYR=J
                    GOTO 55
50             ENDIF
55             CONTINUE
C
C ALL ANIMALS ARE FIRST RELEASED AS MEMBERS OF TRAP CLASS 1
C
        ISTATUS=1
        N(TYR,NU,1)=N(TYR,NU,1)+1
        I=TYR
        IC=1
        IF(CH(L,TYR).EQ.5) THEN
            M(TYR,TYR,1,2,NU,1)=M(TYR,TYR,1,2,NU,1)+1
            NN(TYR,NU,1)=NN(TYR,NU,1)+1
            IC=2
        ELSEIF(CH(L,TYR).EQ.6) THEN
            M(TYR,TYR,1,2,NU,1)=M(TYR,TYR,1,2,NU,1)+1
        ENDIF
C
C ISTATUS REMAINS AT 1 UNTIL THE ANIMAL IS RE-RELEASED
C WHEN INCLASS CHANGES TO 2

```

C

```
DO 110 J=TYR+1,INCLASS
  IF(CH(L,J).EQ.0)GOTO110
  IF(CH(L,J).EQ.1)THEN
    M(I,J,IC,1,NU,ISTATUS)=M(I,J,IC,1,NU,ISTATUS)+1
    ISTATUS=2
    NU=TCLASS(L)+J-TYR
    IF(NU.GT.4)NU=4
    N(J,NU,2)=N(J,NU,2)+1
    I=J
    IC=1
  ELSEIF(CH(L,J).EQ.5) THEN
    M(I,J,IC,1,NU,ISTATUS)=M(I,J,IC,1,NU,ISTATUS)+1
    ISTATUS=2
    NU=TCLASS(L)+J-TYR
    IF(NU.GT.4)NU=4
    N(J,NU,2)=N(J,NU,2)+1
    I=J
    IC=1
    M(J,J,IC,2,NU,2)=M(J,J,IC,2,NU,2)+1
    NN(J,NU,2)=NN(J,NU,2)+1
    IC=2
  ELSEIF(CH(L,J).EQ.6) THEN
    M(I,J,IC,1,NU,ISTATUS)=M(I,J,IC,1,NU,ISTATUS)+1
    ISTATUS=2
    NU=TCLASS(L)+J-TYR
    IF(NU.GT.4)NU=4
    N(J,NU,2)=N(J,NU,2)+1
    I=J
    IC=1
    M(J,J,IC,2,NU,2)=M(J,J,IC,2,NU,2)+1
  ELSEIF(CH(L,J).EQ.3)THEN
    M(I,J,IC,2,NU,ISTATUS)=M(I,J,IC,2,NU,ISTATUS)+1
    ISTATUS=2
    NU=TCLASS(L)+J-TYR
    IF(NU.GT.4)NU=4
```

```

        NN(J,NU,2)=NN(J,NU,2)+1
        I=J
        IC=2
    ELSEIF(CH(L,J).EQ.4) THEN
        M(I,J,IC,2,NU,ISTATUS)=M(I,J,IC,2,NU,ISTATUS)+1
        ISTATUS=2
    ENDIF
110 CONTINUE
200 CONTINUE
205 CONTINUE
    CLOSE(1)

    OPEN(2,FILE=FNAME2)
    WRITE(2,4)INCOHT,INCLASS,IAGES,IFTRAP,ICPOOL
    DO 400 NU=1,IAGES
        DO 400 KK=1,IFTRAP+1
            WRITE(2,2)(N(I,NU,KK),I=1,INCOHT)
            WRITE(2,2)(NN(I,NU,KK),I=1,INCLASS-1)
            DO 210 I=1,INCOHT
210  WRITE(2,3)(M(I,J,1,1,NU,KK),J=2,INCOHT),
                &(M(I,J,1,2,NU,KK),J=1,INCLASS)
                IMAX=INCOHT-1
                IF(INCLASS.GT.INCOHT)IMAX=INCLASS-1
                DO 220 I=1,IMAX
220  WRITE(2,3)(M(I,J,2,1,NU,KK),J=2,INCOHT),
                &(M(I,J,2,2,NU,KK),J=1,INCLASS)
400 CONTINUE
        CLOSE(2)
    END

```

5. Programmes used in conjunction with SURVIV

Two files facilitate use of programme SURVIV (White 1983) in fitting the models described in this thesis. The first programme, SVWRITE, takes the input file for JOLLYOBS and converts it into a SURVIV input file. The second file, ESTANCIL, provides the likelihood function for SURVIV. The compiled code from ESTANCIL

must be saved as EST.OBJ which is then linked with the other SURVIV components to form a new version of SURVIV incorporating the ESTANCIL likelihood. Before compiling ESTANCIL.FOR the number of age classes and whether a temporary trap response is to be fitted must be declared in ESTANCIL.

Programme SVWRITE

```

PROGRAM SVWRITE
  IMPLICIT DOUBLE PRECISION (A-H,O-Z)
  INCLUDE 'MPAR'
C
C LOCAL VARIABLES
C
  CHARACTER BANNER
  CHARACTER*12 FNAME,FNAME2

  PRINT*,'INPUT FILE? '
  READ9,FNAME
  PRINT*,'OUTPUT FILE? '
  READ9,FNAME2
  OPEN(1,FILE=FNAME)
  OPEN(2,FILE=FNAME2)
1  FORMAT(5I3)
2  FORMAT(20I6)
3  FORMAT(40I4)
8  FORMAT(A80)
9  FORMAT(A12)
  READ(1,8)BANNER
  READ(1,1)INCOHT,INCLASS,IAGES,IFTRAP,ICPOOL
  DO 20 NU=1,IAGES
    DO 20 OMEGA=1,IFTRAP+1
      READ(1,2)(N(I,NU,OMEGA),I=1,INCOHT)
      READ(1,2)(MN(I,NU,OMEGA),I=1,INCLASS-1)
      DO 10 I=1,INCOHT
10     READ(1,3)(M(I,J+1,1,1,NU,OMEGA),J=1,INCOHT-1),
&           (M(I,J,1,2,NU,OMEGA),J=1,INCLASS)

```

```

DO 20 I=1,INCLASS-1
20   READ(1,3)(M(I,J+1,2,1,NU,OMEGA),J=1,INCOHT-1),
&      (M(I,J,2,2,NU,OMEGA),J=1,INCLASS)

      NPAR=(INCOHT-1)*5+1
      IF(INCLASS.GT.INCOHT)NPAR=NPAR+1+(INCLASS-INCOHT)*(1+(INCLASS
- INCOHT-1)/2)
      NPAR=IAGES*(IFTRAP+1)*NPAR
      WRITE(2,*)'PROC TITLE ;'
4   FORMAT(A16,I3,A1)
5   FORMAT(A7,I5,A1)
6   FORMAT(A2,I3,A2)
7   FORMAT(I3,A2)
      WRITE(2,4)'PROC MODEL NPAR=',NPAR,',';
      DO 50 NU=1,IAGES
        DO 50 KK=1,IFTRAP+1
          DO 42 I=1,INCOHT
            WRITE(2,5)'COHORT:',N(I,NU,KK),',';
            DO 41 J=I+1,INCOHT
41          WRITE(2,7)M(I,J,1,1,NU,KK),':;'
            DO 42 J=I,INCLASS
42          WRITE(2,7)M(I,J,1,2,NU,KK),':;'
          DO 46 I=1,INCLASS-1
            WRITE(2,5)'COHORT:',NN(I,NU,KK),',';
            DO 45 J=I+1,INCOHT
45          WRITE(2,7)M(I,J,2,1,NU,KK),':;'
            DO 46 J=I+1,INCLASS
46          WRITE(2,7)M(I,J,2,2,NU,KK),':;'
50 CONTINUE
      WRITE(2,*)'PROC ESTIMATE MAXFN=32000 NSIG=6 NOVAR NAME=M1;'
      WRITE(2,*)'INITIAL;'
      DO 60 I=1,NPAR
60   WRITE(2,6)'S(',I,')='
      WRITE(2,*)'PROC STOP;'
      END

```

SURVIV subroutine ESTANCIL

```
      SUBROUTINE EST(NP,PPAR,XLL)
C
C      Estimation routine for a multi-age study with recaptures
C      and resightings
C
      IMPLICIT DOUBLE PRECISION (A-H,O-Z)
      include 'MODEL.C'
C
C      local parameters
C
      PARAMETER (mxage=3,mtrap=2)
C
C LOCAL VARIABLES
C
      INTEGER OMEGA
C
      DOUBLE PRECISION F(MAXPAR,mxage,mtrap),S(MAXPAR,mxage,mtrap),
&PP(MAXPAR,mxage,mtrap),
&FF(MAXPAR,mxage,mtrap),THETA(MAXPAR,MXAGE,mtrap),GAMMA,
&PIE(MXCLAS,MAXCHT,MXAGE,mtrap),xi(mxclas,mxage,mtrap),
&zeta(maxcht,mxclas,mxage,mtrap),mu(mxage,2),lam(mxage,2)
&,rho(mxclas,mxage,mtrap)
C
      CALL MOVFLT(PPAR,PAR,NEST)
C
C NB: the data must be arranged in the form: Age-class 0  trap-class 0
C
C      Age-class 0  trap-class 1
C
C      Age-class 1  trap-class 0
C
C      Age-class 2  trap-class 1
C
C      .
C
C      .
C
C      .
C
C      Age-class 1  trap-class 0
C
C      Age-class 1  trap-class 1
```

```

c
c initialise : nch = the number of C(i,1) cohorts
c             n1  = the number of years of resighting
c             iages = the number of age classes
c             IMODEL = 0 permanent emigration model
c                   = 1 random emigration model
c             iftrap = 0 no temporary trap response
c                   = 1 temporary trap response model
c
c
c     nch=4
c     n1=5
c     iages=1
c     iftrap=1
c     IMODEL=1
c     nsig=6
c     small=1.D1**(-NSIG)
c
c initialise the values of rho(i) - the following are for Lake Brunner males
c one age with marking effect
c
c     rho(1,1,1)=0.0416667
c     rho(2,1,1)=0.0666667
c     rho(3,1,1)=0.1052632
c     rho(4,1,1)=0.3870968
c     rho(5,1,1)=1.
c     rho(1,1,2)=small
c     rho(2,1,2)=small
c     rho(3,1,2)=0.1666667
c     rho(4,1,2)=0.1500000
c     rho(5,1,2)=1.
c
c 1 format(5(f8.4))
c     indx=0
c     jmp=5*nch-4
c     if(n1.gt.nch)jmp=jmp+1+(n1-nch)*(1+(n1-nch-1)/2)
c     do 8 nu=1,iages

```

```

do 8 kk=1,iftrap+1
  it=indx*jump
  indx=indx+1
  DO 4 I=1,NCH-1
4    PP(I,nu,kk)=SS(I+it)
  jump=nch-1
  do 5 i=1,nch-1
    S(I,nu,kk)=SS(I+jump+it)
    FF(I,nu,kk)=SS(I+2*jump+it)
c
c if fitting the markov emigration model assign the first two fidelity
c parameters to mu and lambda - constrain the others to zero
c
    if(imodel.eq.3)then
      mu(nu,kk)=ss(1+2*jump+it)
      lam(nu,kk)=ss(2+2*jump+it)
    endif
    THETA(I,NU,kk)=SS(I+3*jump+IT)
5    F(I,NU,kk)=SS(I+4*jump+IT)
  jump=5*(nch-1)
  f(nch,nu,kk)=ss(jump+1+IT)
  jump=jump+1
  if(n1.eq.nch)goto 8
  theta(nch,nu,kk)=ss(jump+1+it)
  jump=jump+1
  do 6 i=nch+1,n1
    k=i-nch
6    xi(i,nu,kk)=ss(jump+k+it)
  jump=jump+n1-nch
  index=1
  do 7 i=nch+1,n1-1
    do 7 j=i+1,n1
      zeta(i,j,nu,kk)=ss(jump+index+it)
7    index=index+1
  ix=n1-nch
  jump=jump+((ix-1)*ix)/2

```

```

      8 continue

c      do 10 nu=1,iages
c      do 10 kk=1,iftrap+1
c      do 9 i=1,nch-1
c      9   print1,pp(i,nu,kk),s(i,nu,kk),ff(i,nu,kk),theta(i,nu,kk),
c      &f(i,nu,kk)
c      print1,f(nch,nu,kk),theta(nch,nu,kk)
c      print*,xi(5,nu,kk)
c      print*,xi(5,nu,kk),xi(6,nu,kk),xi(7,nu,kk)
c      print*,zeta(5,6,nu,kk),zeta(5,7,nu,kk),zeta(6,7,nu,kk)
c      10 print*,'      '

C
C AIJ = PR(ANIMAL CAPTURED AT I IS NEXT CAPTURED AT J BUT NOT CAPTURED
C      BETWEEN I AND J)
C BIJ = PR(ANIMAL CAPTURED AT I NOT IN STUDY AREA AT J AND
C      NOT CAPTURED BEFORE J)
C GAMMA(I,J) = PR(ANIMAL LAST CAUGHT AT I IS NOT CAPTURED BY J)
C
      k2=iftrap+1
      DO 140 NU=1,IAGES
      do 140 kk=1,iftrap+1

c
c First compute cell probs for M(i,j,1,1)'s
c
c
c
c NB to fit the random emigration model use pp(nu) not pp(omega)
C
      DO 18 I=kk,NCH
      GAMMA=1.
      OMEGA=NU+1
      IF(NU.EQ.IAGES)OMEGA=IAGES
      if(IMODEL.EQ.1)omega=nu

```

```

IF(I.LE.NCH-1) then
  AIJ=FF(I,NU,KK)
  BIJ=1-FF(I,NU,KK)
  IF(IMODEL.EQ.3) THEN
    AIJ=MU(NU,KK)
    BIJ=1-MU(NU,KK)
  ENDIF
  GAMMA=AIJ
ENDIF

ALPHA1=S(I,NU,kk)*THETA(I,NU,kk)*PP(I,OMEGA,kk)
BETA=S(I,NU,kk)*THETA(I,NU,kk)
SUM=ALPHA1*GAMMA
PRD=BETA
PIE(1,I,NU,kk)=SUM
omega=nu+1
if(nu.eq.iages) omega=nu
iom=omega
if(IMODEL.EQ.1) iom=nu

DO 16 J=I+1,NCH-1
  K=J-I+1
  IK=IFTRAP+1
  IF(J.EQ.I+1) IK=KK
c
c update aij and bij and gamma
c
  if(imodel.ne.3)then
    mu(omega,k2)=ff(J,omega,k2)
    lam(omega,k2)=0.
  endif
  OLDA=AIJ
  OLDB=BIJ
  AIJ=OLDA*(1-PP(J-1,iOM,ik))*mu(OMEGA,k2)+olddb*lam(omega,k2
&)
  BIJ=OLDA*(1-PP(J-1,iOM,ik))*(1-mu(OMEGA,k2)) + OLDB*

```

```

&(1-lam(omega,k2))
      GAMMA=AIJ
      iom=iom+1
      if(iom.gt.iages)iom=iages
      omega=omega+1
      if(omega.gt.iages)omega=iages

      IT=NU+J-I
      IF(IT.GT.IAGES)IT=IAGES

      ALPHA1=S(J,IT,k2)*THETA(J,IT,k2)*PP(J,iom,k2)
      BETA=S(J,IT,k2)*THETA(J,IT,k2)
      PIE(K,I,NU,kk)=PRD*ALPHA1*GAMMA
      SUM=SUM+PIE(K,I,NU,kk)
16      PRD=PRD*BETA
c
c compute cell probabilities for M(i,j,1,2)'s
c
      ALPHA2=F(I,NU,kk)
      PIE(NCH-I+1,I,NU,kk)=ALPHA2
SUM=SUM+alpha2
c
c if i = nch prd and beta must be set to 1
c
      beta=1.
      prd=1.
      gamma=1.
      if(i.ne.nch)BETA=S(I,NU,kk)*THETA(I,NU,kk)
      if(i.ne.nch)PRD=BETA

      IF(I.LE.NCH-1) then
      AIJ=FF(I,NU,KK)
      BIJ=1-FF(I,NU,KK)
      IF(IMODEL.EQ.3) THEN
      AIJ=MU(NU,KK)
      BIJ=1-MU(NU,KK)

```

```

        ENDIF
    ENDIF

    omega=nu+1
    if(nu.eq.iages)omega=nu
        iom=omega
    if(IMODEL.EQ.1)iom=nu

    it=nu
    DO 17 J=I+1,N1
        K=(NCH-I) + (J-I+1)
        if(j.le.nch)then
            ik=iftrap+1
            if(j.eq.i+1)ik=kk
            GAMMA=AIJ*(1-PP(J-1,iom,ik)) + BIJ
c
c now update aij and bij
c
            if(imodel.ne.3)then
                mu(omega,k2)=ff(J,omega,k2)
                lam(omega,k2)=0.
            endif
            OLDA=AIJ
            OLDB=BIJ
            AIJ=OLDA*(1-PP(J-1,iOM,ik))*mu(OMEGA,k2)+oldb*lam(omega,k2
&)
            BIJ=OLDA*(1-PP(J-1,iOM,ik))*(1-mu(OMEGA,k2)) + OLDB*
&(1-lam(omega,k2))

            iom=iom+1
            if(iom.gt.iages)iom=iages
            OMEGA=OMEGA+1
            IF(OMEGA.GT.IAGES)OMEGA=IAGES

            if(it.eq.iages)it=it-1
            ALPHA2=F(J,it+1,k2)

```

```

        PIE(K,I,NU,kk)=PRD*ALPHA2*GAMMA
c
c now compute beta(j) and update prd
c
        IT=NU+J-I
        IF(IT.GT.IAGES)IT=IAGES
c
c only update prd and beta if j < nch, otherwise they will be zero
c
        if(j.lt.nch) then
            BETA=S(j,IT,k2)*THETA(j,IT,k2)
            PRD=PRD*BETA
        endif
    else
        it2=nu+nch-i
        if(it2.gt.iages)it2=iages
        ik2=iftrap+1
        if(i.eq.nch)ik2=kk
        PIE(K,I,NU,kk)=PRD*GAMMA*xi(j,it2,ik2)
    endif
17     SUM=SUM+PIE(K,I,NU,kk)
18     PIE(NCH-i+n1-i+2,I,NU,kk)=1.-SUM
        if(kk.eq.2)PIE(NCH-1+n1-1+2,1,NU,kk)=1.

C
C NOW REPEAT FOR C(I,2) COHORTS
C First for M(i,j,2,1)'s
c
        imax=nch-1
        if(n1.gt.nch)imax=n1-1
        DO 110 I=kk,imax
            delta=1.
            if(i.gt.nch)goto 95
            beta=1.
            prd=1.

```

```

gamma=1.
OMEGA=NU+1
IF(NU.EQ.IAGES)OMEGA=IAGES
if(IMODEL.EQ.1)omega=nu

IF(I.LE.NCH-1)then
  AIJ=FF(I,NU,KK)
  BIJ=1-FF(I,NU,KK)
  IF(IMODEL.EQ.3) THEN
    AIJ=MU(NU,KK)
    BIJ=1-MU(NU,KK)
  ENDIF
  GAMMA=AIJ
ENDIF

ALPHA1=S(I,NU,kk)*THETA(I,NU,kk)*PP(I,OMEGA,kk)
if(i.lt.nch)BETA=S(I,NU,kk)*THETA(I,NU,kk)

if(kk.eq.2 .and. i.eq.1)then
  delta=0.
else
  DELTA=(1-THETA(I,NU,kk))/(THETA(I,NU,kk)*F(I,NU,kk)*
&rho(i,nu,kk))
endif

PRD=BETA
SUM=DELTA*ALPHA1*gamma
PIE(1,nch+I,NU,kk)=SUM
omega=nu+1
if(nu.eq.iages)omega=nu
iom=omega
if(IMODEL.EQ.1)iom=nu
DO 90 J=I+1,NCH-1
  K=J-I+1
  IK=IFTRAP+1
  IF(J.EQ.I+1)IK=KK

```

```

        if(imodel.ne.3)then
            mu(omega,k2)=ff(J,omega,k2)
            lam(omega,k2)=0.
        endif
        OLDA=AIJ
        OLDB=BIJ
        AIJ=OLDA*(1-PP(J-1,iOM,ik))*mu(OMEGA,k2)+olddb*lam(omega,k2)
        BIJ=OLDA*(1-PP(J-1,iOM,ik))*(1-mu(OMEGA,k2)) + OLDB*
&(1-lam(omega,k2))
        GAMMA=AIJ
        iom=iom+1
        if(iom.gt.iages)iom=iages
        omega=omega+1
        if(omega.gt.iages)omega=iages

        IT=NU+J-I
        IF(IT.GT.IAGES)IT=IAGES
        ALPHA1=S(J,IT,k2)*THETA(J,IT,k2)*PP(J,IOM,k2)
        BETA=S(J,IT,k2)*THETA(J,IT,k2)
        PIE(K,nch+I,NU,kk)=PRD*DELTA*ALPHA1*gamma
        SUM=SUM+PIE(K,nch+I,NU,kk)
90     PRD=PRD*BETA
95     continue

c
c compute cell probs for M(i,j,2,2)'s
c

        beta=1.
        prd=1.
        gamma=1.
        if(i.gt.nch)goto 105
        if(i.lt.nch)BETA=S(I,NU,kk)*THETA(I,NU,kk)
        PRD=BETA

        IF(I.LE.NCH-1)then
            AIJ=FF(I,NU,KK)

```

```

BIJ=1-FF(I,NU,KK)
IF(IMODEL.EQ.3) THEN
  AIJ=MU(NU,KK)
  BIJ=1-MU(NU,KK)
ENDIF
GAMMA=AIJ
ENDIF

omega=nu+1
if(nu.eq.iages)omega=nu
iom=omega
if(IMODEL.EQ.1)iom=nu
it=nu

DO 100 J=I+1,N1
  K=(NCH-I) + (J-I)
  if(j.le.nch)then
    ik=iftrap+1
    if(j.eq.i+1)ik=kk
    GAMMA=AIJ*(1-PP(J-1,iOM,ik)) + BIJ
c
c now update aij and bij
c
    if(imodel.ne.3)then
      mu(omega,k2)=ff(J,omega,k2)
      lam(omega,k2)=0.
    endif
    OLDA=AIJ
    OLDB=BIJ
    AIJ=OLDA*(1-PP(J-1,iOM,ik))*mu(OMEGA,k2)+oldb*lam(omega,k2
&)
    BIJ=OLDA*(1-PP(J-1,iOM,ik))*(1-mu(OMEGA,k2)) + OLDB*
&(1-lam(omega,k2))
    iom=iom+1
    if(iom.gt.iages)iom=iages
    OMEGA=OMEGA+1

```

```

IF(OMEGA.GT.IAGES)OMEGA=IAGES

if(it.eq.iages)it=it-1
ALPHA2=F(J,it+1,k2)
PIE(K,nch+I,NU,kk)=PRD*DELTA*ALPHA2*GAMMA

c
c now update beta(j) and prd
c

IT=NU+J-I
IF(IT.GT.IAGES)IT=IAGES
if(j.ne.nch)BETA=S(j,IT,k2)*THETA(j,IT,k2)
if(j.ne.nch)PRD=PRD*BETA
else
it2=nu+nch-i
if(it2.gt.iages)it2=iages
ik2=iftrap+1
if(i.eq.nch)ik2=kk
PIE(K,nch+I,NU,kk)=PRD*delta*GAMMA*xi(j,it2,ik2)
endif
100 SUM=SUM+PIE(K,nch+I,NU,kk)
goto 110

c
c now compute pie(i,j,k,l) for additional C(i,2) cohorts if there are
c observations beyond the final capture period
c
105 continue
sum=0.
do 107 j=i+1,n1
K=J-I
pie(k,nch+i,nu,kk)=zeta(i,j,nu,kk)
107 sum=sum+pie(k,nch+i,nu,kk)
110 PIE(k+1,nch+I,NU,kk)=1.-SUM
if(kk.eq.2)PIE(nch-1+n1,nch+1,NU,kk)=1.
140 CONTINUE

c
c now reshape pie(j,i,nu,k) to p(j,i)

```

c

```
index=0
do 210 nu=1,iages
  do 210 kk=1,iftrap+1

    it=index*(nch+n1-1)
    index=index+1
    do 170 i=1,nch
      do 150 k=1,nch-i
150      p(k,i+it)=pie(k,i,nu,kk)
      do 160 k=nch-i+1,nch-i+n1-i+1
160      p(k,i+it)=pie(k,i,nu,kk)
170      p(nch-i+n1-i+2,i+it)=pie(nch-i+n1-i+2,i,nu,kk)
    do 200 i=1,nch
      do 180 k=1,nch-i
180      p(k,nch+i+it)=pie(k,nch+i,nu,kk)
      do 190 k=nch-i+1,nch-i+n1-i+1
190      p(k,nch+i+it)=pie(k,nch+i,nu,kk)
200      p(nch-i+n1-i+2,nch+i+it)=pie(nch-i+n1-i+2,nch+i,nu,kk)
    do 205 i=nch+1,n1-1
      do 202 k=1,n1-nch-i+nch
202      p(k,nch+i+it)=pie(k,nch+i,nu,kk)
205      p(n1-nch-i+nch+1,nch+i+it)=pie(n1-nch-i+nch+1,nch+i,nu,kk)
210 continue
    XLL=0.
    DO 300 I=1,NCOHT
      DO 300 J=1,NCLASS(I)
c      print*,i,j,p(j,i),obs(j,i)
300      XLL=XLL-DBLE(OBS(J,I))*LOG(MAX(SMALL,P(J,I)))
    Return
  end
```

