

CAPTURE-RECAPTURE STUDIES FOR MULTIPLE STRATA  
INCLUDING NON-MARKOVIAN TRANSITION PROBABILITIES

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SUMMARY

We consider capture-recapture studies where release and recapture data are available from each of a number of strata on every capture occasion. Strata may, for example, be geographic locations or physiological states. Movement of animals among strata occurs with unknown probabilities, and estimation of these unknown transition probabilities is the objective. We describe a computer routine for carrying out the analysis under a model which assumes Markovian transitions and under reduced parameter versions of this model. We also introduce models which relax the Markovian assumption and allow “memory” to operate (i.e., allow dependence of the transition probabilities on the previous state). For these models, we suggest an analysis based on a conditional likelihood approach. Methods are illustrated with data from a large study on Canada geese (*Branta canadensis*) banded in 3 geographic regions. The assumption of Markovian transitions is rejected convincingly for these data, emphasizing the importance of the more general models which allow memory.

*Key Words:* Atlantic flyway, Canada geese, Conditional likelihood, Multi-state models, Reduced parameter models, Site fidelity.

## 1. Introduction

Tag-recapture studies and the statistical analysis of resulting data have become increasingly important tools for ecologists and wildlife biologists (Pollock et al., 1990). For example, the much-used Jolly-Seber method (e.g., Seber, 1982, Section 5.1) has provided estimates of abundance and survival from capture-recapture records from studies carried out on many different animal species. A limitation of the Jolly-Seber method, however, is that the tag-recapture data necessarily pertain to a homogeneous population segment. Interest in the relationships between survival and various demographic or environmental factors has consequently led to more complex data sets and corresponding generalizations of the Jolly-Seber model. Many of these generalizations are summarized by Lebreton et al. (1991), who describe state-of-the-art methodology for analyzing recapture records on animals classified at time of release according to factors such as sex, age, environment, and "treatment".

For studies where animals can be grouped into classes, it is important to distinguish at least two situations. In the first situation, information obtained at release (e.g., sex) determines the class or stratum to which an animal belongs for all subsequent periods of the study. In the second situation, animals may move among strata according to an unknown chance process. The methods described by Lebreton et al. (1991) apply to the first case, where an animal is either completely faithful to the stratum at release, or moves in an entirely predictable way among strata, as for example, when strata are age-classes. The second situation includes studies where the strata may be geographic locations, weight classes, or breeding status, so that stratum membership is unknown in any period when the animal is not captured. In this article we focus on this second type of study, which until recently has received little attention in the literature. Other situations such as "post-stratification" (Schwarz, Burnham, and Arnason, 1988) are not considered here.

Models for capture-recapture data from studies allowing movement between strata were considered by Arnason (1972, 1973) and also by Seber (1982, p. 555). These authors provided estimators of the probabilities of moving among strata that are inefficient if the number of capture occasions is greater than 3. Using matrix notation, Schwarz, Schweigert and Arnason (1991, Appendix B) provide the likelihood for Arnason's model, which we accordingly refer to as the Arnason-Schwarz model. Schwarz et al. (1991) also describe a computer program for calculating the maximum likelihood estimates (MLEs) of the movement or transition probabilities. This computer program was, however, derived for the analysis of recovery (i.e., single recapture) data and does not allow much

flexibility for handling data with multiple recaptures. Hilborn (1990) gives an alternative computational method for the analysis of band recovery data, which could, in theory, be adapted to handle multiple recapture data.

Hestbeck, Nichols and Malecki (1991) considered a study with multiple recapture data from Canada geese (Branta canadensis) banded in 3 geographic areas. They describe the biological importance of estimating the transition probabilities for movement between these 3 areas in the wintering grounds of the mid-Atlantic flyway. In addition to the Arnason-Schwarz model which assumes Markovian transitions, Hestbeck et al. (1991) propose a model where the transition probabilities depend on location in the previous period. Estimates were obtained using program SURVIV (White, 1983) though in a manner that is neither fully efficient nor easily generalized to more than 3 years of data. Nichols et al. (1991) consider a data set on meadow voles (Microtus pennsylvanicus), where the strata are body mass classes. Estimates were obtained (for the Markovian model) in a manner similar to that of Hestbeck et al.

The objectives of the present article are two-fold. We describe a conversion routine to be used with program SURVIV which allows easy implementation of the Arnason-Schwarz model, and of reduced parameter versions of this model (see Section 2). Secondly, we extend the work of Hestbeck et al. and provide a framework for models which allow simple non-Markovian transitions (Section 3). Computational routines for implementing these models which allow "memory", and for testing hypotheses concerning memory, are described. All models are illustrated using data from the Canada goose study described in Hestbeck et al. (1991). In Section 4, we conclude with a summary of the important biological applications of our methodology.

## 2. The Arnason-Schwarz Model

The experimental situation considered assumes that capture and release of uniquely marked animals occurs in each of  $a$  strata on each of  $k$  capture occasions. For simplicity, capture occasion  $i$  will often be referred to as time  $i$ , and animals referred to as birds. Except for multiple strata, the experimental situation is like that of the standard Jolly-Seber study. Thus a marked bird may be recaptured (resighted) more than once, and the complete capture history for each bird includes not only the time of each capture but also the stratum in which capture occurs. As customary, we assume there is no band loss, that bands are correctly identified, and birds behave independently (see Schwarz et al., 1991, for more detail).

We consider first the model of Arnason (1972, 1973) and Schwarz et al. (1991) which assumes Markovian transitions between strata. Let

$\phi_i^{rs}$ , be the probability of being alive and in stratum  $s$  at time  $i + 1$ ,  
for a bird alive and in stratum  $r$  at  $i$ , and let  
 $p_i^s$ , be the probability of capture at  $i$  for a bird in stratum  $s$  at  $i$ .

Thus it is assumed that  $\phi_i^{rs}$  and  $p_i^s$  do not depend on the stratum occupied by the bird at  $i - 1$  or before. Schwarz et al. develop the analogous model for band recovery data in detail and give the model for multiple recaptures in their Appendix B. We consider the multiple recapture situation only, and instead of repeating detail in Schwarz et al. we try to present the material in a different manner, where possible emphasizing readability. There is no way to avoid introducing a certain amount of notation, however, and we use notation more like that of Seber (1982, Section 13.4) instead of the band-recovery notation of Schwarz et al.

## 2.1 Notation

As the development in Schwarz et al. is completely general, for simplicity we assume  $a = 3$  strata with  $k = 4$  capture occasions. The basic Jolly-Seber parameters and data are now matrices with rows and columns indexing strata. In addition, matrix elements have superscripts that denote strata and subscripts that denote time or capture occasion.

Parameters.

With  $\phi_i^{rs}$  and  $p_i^s$  defined as above, the matrices of transition and capture probabilities are

$$\underline{\phi}_i = \begin{bmatrix} \phi_i^{11} & \phi_i^{12} & \phi_i^{13} \\ \phi_i^{21} & \phi_i^{22} & \phi_i^{23} \\ \phi_i^{31} & \phi_i^{32} & \phi_i^{33} \end{bmatrix}, \quad i = 1, 2, 3, \quad \text{and} \quad \underline{p}_i = \begin{bmatrix} p_i^1 \\ p_i^2 \\ p_i^3 \end{bmatrix}, \quad i = 2, 3, 4.$$

Also define  $D(\underline{p}_i)$  to be the diagonal matrix with diagonal elements equal to the elements  $p_i^s$  of the parameter vector  $\underline{p}_i$ . Similarly, let  $q_i^s = 1 - p_i^s$ , and define  $D(\underline{q}_i)$  to be the corresponding diagonal

matrix. Note that  $\phi_{k-1}^{rs} = \phi_3^{rs}$  and  $p_k^s = p_4^s$  are not separately identifiable, and the product  $\phi_3^{rs} p_4^s$  is treated as a single parameter, as in the single-stratum Jolly-Seber model.

Statistics.

$$\text{Let } \underline{R}_i = \begin{bmatrix} R_i^1 \\ R_i^2 \\ R_i^3 \end{bmatrix}, \quad i = 1, 2, 3, \quad \text{and} \quad \underline{m}_{ij} = \begin{bmatrix} m_{ij}^{11} & m_{ij}^{12} & m_{ij}^{13} \\ m_{ij}^{21} & m_{ij}^{22} & m_{ij}^{23} \\ m_{ij}^{31} & m_{ij}^{32} & m_{ij}^{33} \end{bmatrix}, \quad i = 1, 2, 3, \quad j = i + 1, \dots, 4,$$

where  $R_i^r$  is the number of marked birds released in stratum  $r$  at time  $i$ ,  $i = 1, 2, 3$ ,  $r = 1, 2, 3$ , and  $m_{ij}^{rs}$  is the number of marked birds captured in stratum  $s$  at time  $j$  that were last captured in stratum  $r$  at time  $i$ ,  $i = 1, 2, 3$ ,  $j = i + 1, \dots, 4$ ;  $r, s = 1, 2, 3$ .

The release-recapture data are represented in detail in Table 1 where each row represents the distribution of the first recaptures of the  $R_i^r$  birds released in a given year  $i$  and stratum  $r$ . Note that, conditional on the number released,  $R_i^r$ , the recaptures  $(m_{i, i+1}^{r1}, \dots, m_{i, k}^{ra})$  in each row represent a multinomial random variable (provided, of course, that model assumptions are met). To present the cell probabilities for these multinomials, however, it is convenient to represent the data using the more compact matrix notation as indicated in Table 2 (see also Schwarz et al., 1991, Figure B.2). The cell probabilities are then also presented using matrix notation as shown in Table 2.

## 2.2 Computation of MLEs of $\phi$ and $p$ .

Although the multinomial structure of the recapture data in Table 1 leads readily to a product multinomial likelihood, the cell probabilities of the individual multinomials are not easily written down. As indicated in Table 2, these cell probabilities are generated by matrix multiplication of the parameter matrices, and calculation of ML estimates of the individual  $\phi_i^{rs}$  and  $p_i^s$  is just not possible without a specialized computer routine. Schwarz et al. describe a FORTRAN mainframe computer program developed for the analysis of analogous multi-stratum band recovery data. They indicate how to use the relationship between the band-recovery  $S$  and  $f$  and the multiple-recapture  $\phi$  and  $p$  (see Brownie et al., 1985, Section 8.2) to obtain MLEs for  $\phi$  and  $p$  from their program. However,

computation of variance estimates is not straightforward, and estimates under reduced parameter models, of say  $\phi_1^{rs} = \phi_2^{rs}$ , cannot be obtained from band-recovery estimates. This latter problem is a serious concern since the investigation of parsimonious models will be an important part of any analysis of multi-stratum recapture data, due to the potentially large number of parameters for the full model.

Simple to use computer routines are therefore essential if the biological potential of these multi-stratum models is to be realized. The user-friendly program SURVIV (White, 1983) may seem to be the obvious solution to this computing problem. SURVIV was developed specifically for use with product multinomial likelihoods, provides extensive output, has good numerical properties and runs on a PC. Closer inspection of the elements of Table 2 shows, however, that algebraic expressions for the multinomial cell probabilities will generally be too long to code in the usual SURVIV input format. Thus, with Gary White's permission, J. E. Hines has developed a conversion program, CNVMEMOV to be used with program SURVIV, that essentially automates the implementation of the Arnason-Schwarz model, and reduced parameter versions.

The modified SURVIV code, which we call MSSURVIV, was compiled (in FORTRAN77) on a PRIME minicomputer. Although MSSURVIV can be compiled and run on a PC, the 640K memory limitation of PC-DOS allows the analysis of only very small data sets. Larger data sets (3 or more strata and 3 or more years) will require a computer and operating system capable of addressing a much larger amount of memory (i.e., mainframes, minicomputers, Unix workstations or PC's with OS/2). The MSSURVIV code and the conversion program can be obtained by sending a tape or formatted diskette, and self-addressed return mailer, to authors J. E. Hines or J. D. Nichols.

The input to CNVMEMOV is a list of each observed capture history and the frequency with which it occurs. The conversion routine reads these records and generates the release and recapture statistics  $R_i^r$  and  $m_{ij}^{rs}$ , and the corresponding matrices in Table 2. In addition, the multinomial cell probabilities are generated via matrix multiplication as indicated in Table 2. The multinomial cohort data and cell probabilities are fed automatically to MSSURVIV. The required format for the capture history records is an obvious modification of the usual string of 1's and 0's, representing captured and not captured, respectively. Assuming strata are designated by integers 1, 2, . . . , a, then the integer corresponding to the stratum of capture replaces the customary "1" in the capture history record. For example, in a study with  $k = 6$  capture occasions, 012103 represents the history for a bird first captured at time 2 in stratum 1, then recaptured at time 3 in stratum 2, recaptured in stratum 1 at time 4 and

next recaptured in stratum 3 at time 6. At present, the conversion routine assumes no losses on capture, but should eventually allow for losses on capture by modifying the input capture history format as in Burnham et al. (1987, p. 28). We refer to this capture history format again in Section 3 where models allowing memory are considered.

### 2.3 Derived parameters

Schwarz et al. and Hestbeck et al. point out that the transition probabilities  $\phi_1^{rs}$  reflect both survival and movement (migration) rates. Unless strong assumptions are made about behavior it is not possible to separately estimate the components due to survival and movement. Nevertheless, certain functions of the  $\phi_1^{rs}$  (called derived parameters in Schwarz et al.) are of considerable biological interest. These include (for  $a = 3$  strata)

$\phi_1^r = \phi_1^{r1} + \phi_1^{r2} + \phi_1^{r3}$ , the total survival rate for birds in stratum  $r$  at time  $i$ , and

$\Psi_1^{rs} = \frac{\phi_1^{rs}}{\phi_1^r} =$  the probability of being in  $s$  at time  $i + 1$  for animals that were in  $r$  at  $i$  and have survived to  $i + 1$ .

When the strata are geographic locations, and movement occurs mainly just prior to capture, the  $\Psi_1^{rs}$  represent between-strata movement rates. The importance of these rates is described in Section 4, but for further discussion of the estimation and interpretation of the  $\Psi_1^{rs}$ , the reader is referred to Schwarz et al. and Hestbeck et al. We simply note here that implementing the Arnason-Schwarz model with MSSURVIV produces the estimated covariances needed to calculate standard errors for the  $\hat{\phi}_1^r$  and  $\hat{\Psi}_1^{rs}$  using a standard Taylor series approach. Alternatively, if the derived parameters are of primary interest, it is possible to implement MSSURVIV using a reparameterization in terms of  $\phi_1^r$ ,  $\Psi_1^{r1}$ ,  $\Psi_1^{r2}$  (for  $a = 3$  strata), and obtain estimates of these parameters directly.

### 2.4 Reduced parameter versions of the Arnason-Schwarz model

Versions of the Jolly-Seber model with survival or capture rates constant across time have proved useful for single-stratum studies (Jolly, 1982; Brownie, Hines, and Nichols, 1986). As noted above, motivation to consider parsimonious models is even greater for multi-stratum studies. Accordingly, as in Brownie et al. (1986), we consider a sequence of three models with increasingly restrictive assumptions about the time dependence of parameters. These models all assume stratum-specific parameters, and the assumptions concerning time-dependence are as follows.

Model A — transition probabilities are stratum-specific and time-specific, capture probabilities are stratum-specific and time-specific. (This is the Arnason-Schwarz model.)

Model B — transition probabilities are stratum-specific but constant across time, capture probabilities are stratum- and time-specific.

Model D — transition probabilities and capture probabilities are stratum-specific but constant across time.

CNVMEMOV generates the PROC MODEL statements for the three Models A, B, and D in MSSURVIV. This means that a single MSSURVIV run can produce estimates of the  $\phi_i^{rs}$  and  $p_i^s$  under each of the models, a goodness of fit test for each model, and a sequence of likelihood ratio tests to distinguish between models.

Other reduced parameter models can be implemented using the CONSTRAINTS option in MSSURVIV. For example, to test equality of parameters across strata, the Arnason-Schwarz model would be fit first, followed by a model with the relevant  $\phi$  parameters set equal in the CONSTRAINTS statement. MSSURVIV will provide a likelihood ratio test of the equality of the parameters specified in the CONSTRAINTS statement with the Arnason-Schwarz model as the alternative model.

## 2.5 A Model with Capture Probabilities Dependent on the Previous Stratum.

When strata correspond to geographic regions, it seems biologically reasonable that if transition probabilities do not depend on the past, then capture probabilities should also be independent of the past. Thus, the Arnason-Schwarz model assumes that  $p_i^s$ , the probability of capture at time  $i$ , depends only on the stratum occupied at  $i$ , and not on strata occupied previously. It is possible, however, to construct a more general version of the Arnason-Schwarz model which assumes that the probability of capture at  $i$  depends on the strata occupied at  $i - 1$  and at  $i$ . We do not give any biological justification for this model, which we call Model JMV. The main reason for briefly describing Model JMV is that, from a statistical viewpoint, it is the natural generalization of the Jolly-Seber model to multiple strata. The Arnason-Schwarz model and Models B and D represent increasingly restrictive reduced-parameter versions of Model JMV.

To describe Model JMV it is necessary to introduce notation that is not used anywhere else in the article, and this section could easily be skipped at first reading. Assuming  $a = 3$  strata and  $k = 4$  occasions,

let  $p_{i-1, i}^{rs}$  = probability of capture at time  $i$ , for a bird in stratum  $s$  at  $i$ , that was also in stratum  $r$  at time  $i-1$ ,  $r, s = 1, 2, 3$ ,  $i = 2, 3, 4$ ,  $q_{i-1, i}^{rs} = 1 - p_{i-1, i}^{rs}$ ,

and by analogy to Seber (1982, p. 197),

$$\text{let } \underline{A}_i = \begin{bmatrix} \phi_i^{11} q_{i, i+1}^{11} & \phi_i^{12} q_{i, i+1}^{12} & \phi_i^{13} q_{i, i+1}^{13} \\ \phi_i^{21} q_{i, i+1}^{21} & \phi_i^{22} q_{i, i+1}^{22} & \phi_i^{23} q_{i, i+1}^{23} \\ \phi_i^{31} q_{i, i+1}^{31} & \phi_i^{32} q_{i, i+1}^{32} & \phi_i^{33} q_{i, i+1}^{33} \end{bmatrix},$$

$$\text{and } \underline{B}_i = \begin{bmatrix} \phi_i^{11} p_{i, i+1}^{11} & \phi_i^{12} p_{i, i+1}^{12} & \phi_i^{13} p_{i, i+1}^{13} \\ \phi_i^{21} p_{i, i+1}^{21} & \phi_i^{22} p_{i, i+1}^{22} & \phi_i^{23} p_{i, i+1}^{23} \\ \phi_i^{31} p_{i, i+1}^{31} & \phi_i^{32} p_{i, i+1}^{32} & \phi_i^{33} p_{i, i+1}^{33} \end{bmatrix}, \quad i = 1, 2, 3.$$

Model JMV has a product multinomial likelihood which is the same as the Arnason-Schwarz likelihood, *except* that the multinomial cell probabilities in Table 2 are replaced with expressions involving the matrices  $\underline{A}_i$  and  $\underline{B}_i$ . Specifically, the multinomial cell probabilities by release and recapture occasion, are defined by the following array:

	recapture		
release	2	3	4
1	$\underline{\mathbb{B}}_1$	$\underline{\mathbb{A}}_1 \underline{\mathbb{B}}_2$	$\underline{\mathbb{A}}_1 \underline{\mathbb{A}}_2 \underline{\mathbb{B}}_3$
2		$\underline{\mathbb{B}}_2$	$\underline{\mathbb{A}}_2 \underline{\mathbb{B}}_3$
3			$\underline{\mathbb{B}}_3$

Again, analogously to Jolly-Seber, we define row, column and block totals of the matrices  $\underline{m}_{ij}$  in the recapture array in Table 2. All summations are obtained by matrix addition.

$$\text{Let } \underline{m}_{.i} = \underline{m}_{i,i+1} + \dots + \underline{m}_{i,k}, \quad i = 2, \dots, k-1,$$

$$\underline{m}_{.i} = \underline{m}_{1i} + \dots + \underline{m}_{i-1,i}, \quad i = 2, \dots, k,$$

and

$$\underline{z}_1 = \underline{0}, \quad \underline{z}_i = \underline{z}_{i-1} + \underline{m}_{i-1} - \underline{m}_{.i}, \quad i = 2, \dots, k.$$

Equating these matrix totals to expectations leads to the following explicit expressions for MLEs

$$\hat{\underline{\mathbb{A}}}_i = \underline{\mathbb{R}}_i^{-1} \underline{m}_{.i} (\underline{m}_{.i+1} + \underline{z}_{i+1})^{-1} \underline{z}_{i+1} \underline{m}_{i+1}^{-1} \underline{\mathbb{R}}_{i+1}, \quad i = 1, \dots, k-2,$$

$$\hat{\underline{\mathbb{B}}}_i = \underline{\mathbb{R}}_i^{-1} \underline{m}_{.i} (\underline{m}_{.i+1} + \underline{z}_{i+1})^{-1} \underline{m}_{.i+1}, \quad i = 1, \dots, k-1.$$

[In this Section only,  $\underline{\mathbb{R}}_i$  represents a diagonal matrix with diagonal elements  $\underline{R}_i^S$ .]

Noting that  $\hat{\underline{\phi}}_i = \hat{\underline{\mathbb{A}}}_i + \hat{\underline{\mathbb{B}}}_i$  leads to

$$\hat{\underline{\phi}}_i = \underline{\mathbb{R}}_i^{-1} \underline{m}_{.i} (\underline{m}_{.i+1} + \underline{z}_{i+1})^{-1} (\underline{m}_{.i+1} + \underline{z}_{i+1} \underline{m}_{i+1}^{-1} \underline{\mathbb{R}}_{i+1}), \quad i = 1, \dots, k-2.$$

Estimates of the capture probabilities  $\hat{p}_{i-1,i}^{\text{rs}}$  are then obtained from the matrices  $\hat{\underline{\mathbb{B}}}_i$  and  $\hat{\underline{\phi}}_i$  via element by element division.

Comparison of the matrix expressions for  $\hat{\underline{\phi}}_i$  and  $\hat{\underline{\mathbb{A}}}_i, \hat{\underline{\mathbb{B}}}_i$  with corresponding estimators for the single-stratum Jolly-Seber model illustrates why Model JMV is said to be a generalization of Jolly-Seber to multiple strata. A GAUSS program which computes the estimates  $\hat{\phi}_i^{\text{rs}}$  and  $\hat{p}_{i-1,i}^{\text{rs}}$  for Model JMV can be obtained from authors J.E. Hines or J.D. Nichols. Model JMV is not included in the sequence of models which can be implemented with MSSURVIV, however, and at this time there is no software for computing variance estimates under Model JMV.

## 2.6 Example

Data from a study on Canada geese banded annually with individually coded neckbands in three wintering regions are used to illustrate the models in this article. The three regions are the mid-Atlantic, the Chesapeake, and the Carolinas, corresponding to strata 1, 2, and 3, respectively, and data are available for  $k = 6$  capture (i.e., banding/resighting) occasions. The study is described in more detail in Hestbeck et al. (1991). For illustrative purposes, different subsets of the data are used here and in Section 3.

Table 3 contains the release and recapture summary of the data required for analysis using the Arnason-Schwarz model. Data from 1989 have been omitted to reduce the dimensions of the table, so for this example  $a = 3$  and  $k = 5$ , and the number of parameters for the Arnason-Schwarz model is  $(k - 1)a^2 + (k - 2)a = 45$ . MSSURVIV was used to fit Models A (or Arnason-Schwarz), B, and D. To assess model adequacy, MSSURVIV produces a likelihood-ratio based goodness-of-fit  $G^2$  statistic (e.g., Moore, 1986) without pooling, and also a Pearson chi-square statistic ( $\chi^2$ ) calculated after pooling of cells within rows of the data array (to meet a “minimum expected value” criterion) with degrees of freedom (df) reduced accordingly. For sparse data, p-values for both statistics will be inaccurate, with the Pearson  $\chi^2$  p-values tending to be liberal where there is considerable pooling (e.g., Moore, 1986). Only minimal pooling was required for the data in Table 3, and results for both tests show important lack of fit for all 3 models (Pearson  $\chi^2$  values and df are  $\chi^2 = 128.55$ , df = 39 for Model A;  $\chi^2 = 245.05$ , df = 65 for Model B; and  $\chi^2 = 279.55$ , df = 77 for Model D). Likelihood ratio tests between models are not very meaningful given this lack of fit, but suggest Model A is preferred to both B and D.

Detailed output is not presented for Model A because of the poor fit, and reasons for this lack of fit are examined in Section 3.3. Allowing for possible biases due to model inadequacy, the estimated transition probabilities are nevertheless interesting. The estimates, averaged across years, are

$$\begin{array}{lll} \bar{\phi}_{11} = .49 & , & \bar{\phi}_{12} = .17 & , & \bar{\phi}_{13} = .004 & , \\ \bar{\phi}_{21} = .07 & , & \bar{\phi}_{22} = .58 & , & \bar{\phi}_{23} = .02 & , \\ \bar{\phi}_{31} = .02 & , & \bar{\phi}_{32} = .16 & , & \bar{\phi}_{33} = .47 & . \end{array}$$

Note that in each row the diagonal element  $\bar{\phi}_{ss}$  is the largest, suggesting that birds exhibit at least a type of short-term fidelity to the overwintering sites.

### 3. Models Allowing Memory

Of considerable interest to biologists studying large migratory species such as Canada geese is the question of fidelity to breeding or wintering sites. In the context of the Arnason-Schwarz model,  $\phi^{ss} > \phi^{st}$ , for  $t \neq s$ , is interpreted as evidence of "short-term" fidelity as in the example of Section 2.6. If, however, fidelity is more long-term in nature, the Markov assumption of the Arnason-Schwarz model will be violated. That is, if the probability of moving between two strata in  $i$  to  $i + 1$  depends on the stratum occupied at any time prior to  $i$ , then transitions are not "memory-less" and the Arnason-Schwarz model is incorrect. To obtain information on long-term fidelity, models allowing memory must be developed.

Following Hestbeck et al., we consider relaxing the Markovian assumption of Section 2 to allow transition probabilities for period  $i$  to depend on the stratum occupied at  $i - 1$ . For  $a = 2$  and  $a = 3$  strata, respectively, this results in  $a^3 = 8$  and  $a^3 = 27$  transition probabilities, respectively, per period. The number of parameters for the Memory model is potentially very large, and as for the Arnason-Schwarz model we assume that the probability of capture at  $i$  depends only on the stratum occupied at time  $i$ . This assumption seems biologically reasonable for most examples and, data permitting, can be relaxed (see Section 2.5). For new releases (newly banded birds) no information on stratum in the previous year can be assumed, and so another set of transition probabilities must be defined for new releases. The parameters of the Memory model are

$\phi_{i-1, i}^{rst}$  = probability of being present in stratum  $t$  at time  $i + 1$  for a bird that was in  $r$  at time  $i - 1$  and is in  $s$  at time  $i$ .

$p_i^s$  = probability of capture at  $i$  for a bird present in  $s$  at time  $i$ ,

and  $\phi_{i-1, i}^{+st}$  = probability of transition from  $s$  to  $t$  in  $i$  to  $i + 1$  for new releases at  $i$ .

As usual  $\phi_{k-2, k-1}^{rst}$  and  $p_k^t$  are not separately identifiable, and the product  $\phi_{k-2, k-1}^{rst} p_k^t$  is regarded as a single parameter.

The full likelihood under the Memory model for multiple recapture data from  $a > 2$  strata and  $k > 3$  capture occasions is hard to write down in a compact and general form. Conditioning on releases in a given stratum does not lead to a product multinomial likelihood because stratum  $i - 1$  is not

known for all releases at  $i$ . Hence, MSSURVIV is not applicable, and computation of MLEs is even more difficult than for the Arnason-Schwarz model. In theory, one possibility is to list every single capture history for every cohort of new releases, and write out the multinomial cell probabilities for every history. MLEs would then be obtained using program SURVIV in the usual way (i.e., without the conversion routine). Hestbeck et al. used this approach for data from  $a = 3$  strata and  $k = 3$  occasions, with separate analyses for cohorts released in different years. Extending this approach to simultaneously analyze releases from more than one year with  $k > 3$  occasions is a formidable task. The expressions for cell probabilities become so long that using SURVIV in the standard way to obtain MLEs is hardly feasible.

A second possibility is to use the “simulation and numerical optimization” approach of Hilborn (1990). Implementing this procedure with the multinomial likelihood (or even with the approximate Poisson likelihood) for  $a > 2$  strata and  $k > 3$  capture occasions is likely to be prohibitively difficult or time consuming for most data analysis situations.

We suggest a third approach that is not fully efficient but has the advantage that it can be readily implemented using a conversion routine with program MSSURVIV similar to that described in Section 2. Our approach is based on a conditional likelihood which is also a “partial likelihood,” in the sense of Cox (1975). This conditional (or partial) likelihood contains much of the information in the data relevant to the estimation of the  $\phi_{i-1, i}^{\text{rst}}$ , and fits nicely into the product multinomial framework given for the Arnason-Schwarz model. As in other situations, the use here of a partial likelihood is motivated by the advantages of tractability and computational ease (achieved by eliminating nuisance parameters) weighed against minor loss in information.

In constructing the conditional likelihood (CL), we condition on the numbers of releases at  $i$  for which stratum at  $i - 1$  is known,  $i = 2, \dots, k - 1$ . Attention is therefore restricted to histories containing at least one set of captures in consecutive years. To illustrate, recall the modified capture history representation introduced in Section 2.2 and consider the two histories 012103 and 010030 for a study with  $k = 6$  capture occasions. The history 012103 contains 2 sets of consecutive captures, at times 2 and 3, and at times 3 and 4. The second history 010030 does not contain any consecutive captures. Only histories with consecutive nonzero digits contribute to the conditional likelihood, so, for example, birds with history 010030 are ignored in constructing the CL.

Having restricted attention to histories with consecutive captures, the CL can be written in

product multinomial form. This is done, as for the Arnason-Schwarz model, by identifying release cohorts and for each cohort tabulating the next recaptures by time and stratum. The difference is that for the Memory model, release cohorts consist of birds seen in consecutive years, and are defined by the strata occupied in each of these years. Thus in year  $i$  ( $i = 2, \dots, k-1$ ), there are  $a^2$  release cohorts, corresponding to the  $a \times a$  'stratum at  $i-1$ ' by 'stratum at  $i$ ' combinations, and  $a^2$  multinomials or rows in the data array.

Extending the notation of Section 2, let

$$R_{i-1,i}^{rs} = \text{the number of releases in stratum } s \text{ at } i, \text{ that were also seen in stratum } r \text{ at } \\ i-1, i = 2, \dots, k-1; r, s = 1, \dots, a,$$

$$\text{and } m_{i-1,i,j}^{rst} = \text{the number of birds in release cohort } R_{i-1,i}^{rs} \text{ that are next captured in stratum } \\ t \text{ at time } j, i = 2, \dots, k-1, j = i+1, \dots, k; r, s, t = 1, \dots, a.$$

The corresponding release and recapture matrices, for  $a = 2$  strata, are

$$\tilde{R}_{i-1,i} = \begin{bmatrix} R_{i-1,i}^{11} \\ R_{i-1,i}^{12} \\ R_{i-1,i}^{21} \\ R_{i-1,i}^{22} \end{bmatrix}, i = 2, \dots, k-1, \text{ and}$$

$$\tilde{m}_{i-1,i,j} = \begin{bmatrix} m_{i-1,i,j}^{111} & m_{i-1,i,j}^{112} \\ m_{i-1,i,j}^{121} & m_{i-1,i,j}^{122} \\ m_{i-1,i,j}^{211} & m_{i-1,i,j}^{212} \\ m_{i-1,i,j}^{221} & m_{i-1,i,j}^{222} \end{bmatrix}, i = 2, \dots, k-1, j = i+1, \dots, k.$$

To illustrate computation of  $R_{i-1, i}^{\text{fs}}$  and  $m_{i-1, i, j}^{\text{fst}}$ , note that  $R_{23}^{12}$  is the number of histories with 2nd and 3rd digits equal to 1 and 2 respectively, and  $m_{234}^{121}$  is the number of histories with 2nd, 3rd, and 4th digits equal to 1, 2, and 1, respectively. Thus a bird with history 012103 will contribute to releases  $R_{23}^{12}$  and  $R_{34}^{21}$ , and to recapture statistics  $m_{234}^{121}$  and  $m_{346}^{213}$ . This description assumes no losses on capture but may be modified to allow for losses on capture, as in Burnham et al. (1987, p. 28).

The data for the Memory model CL can now be represented in tables like those presented in Section 2.1 for the Arnason-Schwarz model. Thus Table 4 gives the symbolic representation using compact matrix notation for a study with  $k = 6$  capture occasions, and Table 5 contains the actual data array for a subset of the Canada goose data with  $a = 2$  strata and  $k = 6$  occasions. Note that there are  $(k - 2) \times a^2 = 16$  rows in the data array, corresponding to 16 multinomials in the CL. The data in Table 5 will be used to illustrate the Memory model in Section 3.3.1.

Having identified the multinomial cohorts, in order to construct the Memory model CL we must now define the corresponding multinomial cell probabilities. Again, this is best done using matrix notation with appropriately defined matrices of transition and capture probabilities. For  $a = 2$  strata, these parameter matrices are

$$\phi_{i-1, i} = \begin{bmatrix} \phi_{i-1, i}^{111} & \phi_{i-1, i}^{112} & 0 & 0 \\ 0 & 0 & \phi_{i-1, i}^{121} & \phi_{i-1, i}^{122} \\ \phi_{i-1, i}^{211} & \phi_{i-1, i}^{212} & 0 & 0 \\ 0 & 0 & \phi_{i-1, i}^{221} & \phi_{i-1, i}^{222} \end{bmatrix}, i = 2, \dots, k-1,$$

$$p_i = \begin{bmatrix} p_i^1 & 0 \\ 0 & p_i^2 \\ p_i^1 & 0 \\ 0 & p_i^2 \end{bmatrix}, \text{ and } D(q_i) = \begin{bmatrix} q_i^1 & 0 & 0 & 0 \\ 0 & q_i^2 & 0 & 0 \\ 0 & 0 & q_i^1 & 0 \\ 0 & 0 & 0 & q_i^2 \end{bmatrix}, i = 3, \dots, k,$$

where  $q_i^s = 1 - p_i^s$ .

Some explanation of these matrices seems necessary. For  $a$  strata there are transitions between  $a^2$  ‘states’ at each period, so the transition matrix has dimension  $a^2 \times a^2$ . By definition, however, only the fraction  $1/a$  of the transitions are possible so many of the entries of the matrix are 0. For example, with  $a = 2$ , the elements in row 1 of  $\phi_{i-1, i}$  correspond to transitions from state “1 in  $i - 1$  and 1 in  $i$ ” to the states defined by strata occupied at  $i$  and at  $i + 1$ . The first 2 elements relate to transitions to “1 in  $i$  and 1 in  $i + 1$ ”, and to “1 in  $i$  and 2 in  $i + 1$ ”, respectively. The 3rd and 4th are for transitions to “2 in  $i$  and 1 in  $i + 1$ ”, and to “2 in  $i$  and 2 in  $i + 1$ ”, respectively. These latter two transitions cannot occur as they require presence in both strata 1 and 2 at  $i$ , hence the last 2 elements of row 1 are 0.

In the matrices  $\underline{p}_i$  and  $D(\underline{q}_i)$ , the number of different nonzero elements is  $a = 2$ , because we have assumed capture rates do not depend on the past. If this assumption seems too restrictive, the nonzero elements in rows 3 and 4 can be made different from those in rows 1 and 2, respectively.

The multinomial cell probabilities for the CL are now defined in Table 6 in terms of the parameter matrices, for the data of Table 5. Note that the parameters  $\phi_{i-1, i}^{+st}$  defined for new releases do not enter into the CL. Under the Memory model the  $\phi_{i-1, i}^{+st}$  are nuisance parameters which provide no information on “non-Markovian” or long term fidelity, and so their omission is of no concern. For completeness, the Memory model CL is given in the Appendix.

### 3.1 Computation of parameter estimates for the Memory model.

Comparison of Tables 4 and 6 with Table 2 shows the close analogy between the structure of the Memory model CL and the likelihood for the Arnason-Schwarz model. MSSURVIV can therefore be used to compute estimates of the Memory model transition probabilities  $\phi_{i-1, i}^{rst}$  and capture rates  $p_i^t$ . Input and output are analogous to that for the Arnason-Schwarz model. Note however, that although estimates  $\widehat{\phi}_{i-1, i}^{rst}$  and  $\widehat{p}_i^t$  are obtained by maximizing the CL, they are not MLEs because they are not based on the complete data likelihood. From a purely computational viewpoint, using MSSURVIV to implement the CL makes it possible to include in the analysis a larger number of capture occasions and/or strata than is possible with any other easily implemented method.

### 3.2 Reduced parameter versions of the Memory model.

Again the potentially large number of parameters for the Memory model means that it will be

important to investigate various parsimonious models. Two types of reduced parameter models which are easily implemented using MSSURVIV need to be distinguished. The first type are Memory models where transition rates depend on stratum in the present and immediate past, but where these rates, or capture rates, may be constant across time. These models are analogous to models B and D of Section 2.4.

The second type of reduced parameter model is obtained by eliminating some, or all, of the dependence on the past of the transition rates. Hestbeck et al. considered one such model (called Model MV2). For  $a = 3$  strata they assumed that the probability of going from stratum  $s$  in  $i$  to stratum  $t$  in  $i + 1$  depended on whether or not the stratum occupied at time  $i - 1$  was stratum  $t$ . Thus  $\phi_{i-1, i}^{rst} = \phi_{i-1, i}^{sst}$ , but  $\phi_{i-1, i}^{rst} \neq \phi_{i-1, i}^{tst}$ , and  $\phi_{i-1, i}^{sst} \neq \phi_{i-1, i}^{tst}$ , reducing the number of different transition rates per period from 27 to 18. For  $a = 3$  strata, dependence on the past is removed entirely by setting  $\phi_{i-1, i}^{1st} = \phi_{i-1, i}^{2st} = \phi_{i-1, i}^{3st}$  for all  $s, t$ . This produces a model with Markovian transitions. A real advantage of using MSSURVIV, is that having fit the full Memory model any of these reduced parameter models are easily fitted also.

In addition to achieving parsimony, a reason for investigating reduced parameter models is to obtain answers to questions about behavior or other biological issues. Comparisons between models with different degrees of “memory”, for example, can provide information about fidelity. For  $a = 2$  strata, if a test of the Arnason-Schwarz model against the full Memory model rejects the simpler model, then there may be evidence of non-Markovian or long term fidelity (or possibly “avoidance”). For  $a = 3$  strata, a sequence of tests of interest would be to test the Arnason-Schwarz model against Model MV2 of Hestbeck et al., followed by Model MV2 against the full Memory model.

To perform the tests between these nested models, computational limitations are again an issue. Likelihood ratio tests cannot be carried out if it is prohibitively difficult to maximize the complete likelihood for the Memory model with existing software. One approach is to carry out analogous tests based on the Memory model CL and the output from MSSURVIV. Due to the product multinomial structure of the CL, p-values for both goodness-of-fit tests and tests between models can be obtained using the usual large-sample  $\chi^2$  approximation.

### 3.3 Examples based on the Memory model

#### 3.3.1 Mid Atlantic and Chesapeake regions, 1984 - 1989.

All recapture records which include capture (i.e., banding or resighting) in stratum 3 (the Carolinas) were deleted for this first illustration of the Memory model. This was partly because the transition from 1 to 3 was rare and consequently a substantial number of the  $m_{i-1, i, j}^{rst}$  are 0 if stratum 3 is included. The data required for the Memory model CL are displayed in Table 5. MSSURVIV was used to fit the Memory model and a second model with  $\phi_{i-1, i}^{1st} = \phi_{i-1, i}^{2st}$ ,  $i = 2, \dots, k-1$ ;  $s, t = 1, 2$ . This second model assumes no memory as does the Arnason-Schwarz model, but note that for estimation purposes this second model is not equivalent to applying the Arnason-Schwarz model to data obtained from Table 3 by deleting all histories with a capture in stratum 3. This is because histories without consecutive recaptures are included in Table 3 but not in Table 5. In addition, the data in Tables 3 and 5 also differ for purposes of assessing model adequacy because Table 5 represents a finer partitioning of the capture history information than does Table 3. To avoid confusion the second model is therefore referred to as the "No Memory" model, even though assumptions concerning transition probabilities are the same as for Arnason-Schwarz.

Results from MSSURVIV for assessing model adequacy are given in Table 7. The Memory model is clearly superior to the model which assumes Markovian transitions. The small p-value for goodness-of-fit probably overstates lack of fit for the Memory model as df were reduced from 42 to 21 by pooling. In addition, cohort to cohort, fit is generally reasonable for the Memory model except for a single cell in each of cohorts 7 and 10. Estimates of the transition probabilities (see Table 8) provide strong evidence that inadequacy of the model with Markovian transitions is due to "long-term" fidelity or a tendency to return to sites occupied in previous years. That is, birds present in stratum 1 at time  $i-1$  are more likely to be found in stratum 1 at time  $i+1$  than are birds that were in stratum 2 at time  $i-1$ . In each row of Table 8, the estimate in column (a) (stratum at  $i-1 =$  stratum at  $i+1$ ) is greater than that in column (b) (stratum at  $i-1 \neq$  stratum at  $i+1$ ). Results in Table 8 add substantially to similar conclusions concerning fidelity in Hestbeck et al. which, due to computational limitations, were based on estimates of the products  $\phi_{12}^{rst} p_3^t$ .

### 3.3.2 All three regions, 1986 - 1989.

Additional information about fidelity is obtained if data from all 3 regions are analyzed using the Memory model and reduced parameter versions. To illustrate, we use data from years 1986-1989 (i.e., capture occasions 3 to 6), shown summarized in the appropriate form in Table 9. There are  $a^2 = 9$  release cohorts in each of the years 1987 and 1988, 18 multinomials in the CL, and 57

parameters for the full Memory model. The data are sparse in places (transitions from 1 to 3 were rare) and estimates under the full Memory model of certain  $\phi_{i-1, i}^{rst}$  were 0. In this situation, the standard errors produced by MSSURVIV may not be accurate, and p-values for the goodness-of-fit statistics are suspect. Accordingly, we highlight results relating to comparisons between models, where as outlined in Section 3.2, the 3 models of interest are the full Memory model, Model MV2, and the No Memory model.

Again the assumption of memory-less or Markovian transitions is rejected convincingly on the basis of results for both goodness-of-fit and comparisons against the more general MV2 and Memory models (see Table 7). In contrast, the intermediate model MV2 compares more favorably with the full Memory model ( $p = .13$  for the test of MV2 vs. Memory in Table 7). Examination of test results and estimates (not shown) under both the full Memory and MV2 models suggests that “memory” results in the chance of a bird overwintering in a particular site in 1988 being greater if the bird had occupied that site in 1986 than if it had not ( $\hat{\phi}^{tst} > \hat{\phi}^{rst}$ ,  $r \neq t$ , in all but one instance). However, the fact that tests (and estimates) demonstrate little difference between MV2 and the full Memory model may be due partly to the limited amount of data from stratum 3 (the Carolinas). We hesitate to conclude, therefore, that the behavior mechanism corresponding to the reduced parameterization of model MV2 is in fact a biological reality.

#### 4. Applications

The biological potential of the statistical methods introduced here is enormous. To emphasize this point, we conclude with a summary of some of the more important applications of the methodology.

The general class of field situations to which these models apply is large and includes a number of important ecological problems. Of the three determinants of population change (survival, reproduction, movement), movement is the least understood for animal populations. Movement is a central mechanism in several hypotheses about animal population regulation, but the inability to properly estimate rates of movement has prevented rigorous testing of these hypotheses. Among migratory species, fidelity to breeding and wintering areas is predicted to vary by age and sex in different ways by competing hypotheses about the evolution of animal social systems. Adequate tests of these hypotheses have not been possible, but should become feasible with the availability of these multi-stratum models that include memory. Worldwide increases in habitat fragmentation have led to

substantial interest in metapopulation models in which animals are restricted to patches of suitable habitat. Dynamics of such populations are determined not only by within-patch birth and death processes, but also by between-patch movements. The models described here provide the appropriate framework for estimating parameters of interest for populations structured in this way.

As previously noted, the models described here are also applicable to situations where animals are stratified based on individual attributes that may change over time. These applications are likely to be of special interest to evolutionary ecologists interested in the influence of such attributes on animal fitness. Strata can be based on morphological, physiological or behavioral characteristics, and multi-stratum models can then be used to test for and estimate associated differences in survival probabilities. The idea of a "cost of reproduction" is an important component of models used to investigate the optimality of different life history patterns. Multi-state models permit the estimation of survival rate differences between animals that do and do not breed in a particular season. In addition, the series of memory models permits tests of hypotheses about the influence of past reproductive history on present reproductive status. Multi-stratum models permit direct estimation of the transition probabilities of stage-based population projection models (Nichols et al., 1991).

Finally, we note that multi-stratum models would be useful even if the biologist had no interest in the questions listed above but wanted only to estimate animal abundance and survival. Heterogeneity in survival and capture probabilities is one of the most pervasive problems in applying capture-recapture models to animal populations (Seber 1982, Pollock et al., 1990). The multi-stratum models described here provide a means of dealing with such heterogeneity in situations where it is associated with characteristics that can be identified or measured on capture. When viewed in this way, these methods simply represent another attempt to introduce biological realism into capture-recapture models.

APPENDIX

By matching up the elements of corresponding matrices in Tables 4 and 6, let  $\theta_{i-1, i, j}^{rst}$  be the multinomial cell probability from Table 6 which corresponds to the element  $m_{i-1, i, j}^{rst}$  in the recapture matrix  $\underline{m}_{i-1, i, j}$ ,  $i = 2, \dots, k-1$ ,  $j = i+1, \dots, k$ ;  $r, s, t = 1, \dots, a$ . Also, let  $r_{i-1, i}^{rs}$  be the total number of birds subsequently recaptured from the release cohort  $R_{i-1, i}^{rs}$ , i.e.,

$$r_{i-1, i}^{rs} = \sum_{j=i+1}^k \sum_{t=1}^a m_{i-1, i, j}^{rst}$$

Similarly, let  $\theta_{i-1, i}^{rs.} = \sum_{j=i+1}^k \sum_{t=1}^a \theta_{i-1, i, j}^{rst}$ .

The likelihood under the Memory model of Section 3.1 for the data  $\{m_{i-1, i, j}^{rst}\}$  conditional on the releases  $\{R_{i-1, i}^{rs}\}$ , is

$$\begin{aligned} \text{CL} = & \prod_{i=2}^{k-1} \prod_{r=1}^a \prod_{s=1}^a \left\{ \frac{(R_{i-1, i}^{rs})!}{(R_{i-1, i}^{rs} - r_{i-1, i}^{rs})!} (1 - \theta_{i-1, i}^{rs.})^{(R_{i-1, i}^{rs} - r_{i-1, i}^{rs})} \right. \\ & \left. \times \prod_{j=i+1}^k \prod_{t=1}^a \frac{(\theta_{i-1, i, j}^{rst})^{m_{i-1, i, j}^{rst}}}{(m_{i-1, i, j}^{rst})!} \right\}. \end{aligned}$$

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Table 1.

Symbolic representation, in the format required for the Arnason-Schwarz model, of release-recapture data for a study with  $k = 4$  capture occasions and  $a = 3$  strata.

Year of release	Stratum of release	Number released	Year of recapture (Stratum of recapture)								
			2			3			4		
			( 1	2	3 )	( 1	2	3 )	( 1	2	3 )
1	1	$R_1^1$	$m_{12}^{11}$	$m_{12}^{12}$	$m_{12}^{13}$	$m_{13}^{11}$	$m_{13}^{12}$	$m_{13}^{13}$	$m_{14}^{11}$	$m_{14}^{12}$	$m_{14}^{13}$
1	2	$R_1^2$	$m_{12}^{21}$	$m_{12}^{22}$	$m_{12}^{23}$	$m_{13}^{21}$	$m_{13}^{22}$	$m_{13}^{23}$	$m_{14}^{21}$	$m_{14}^{22}$	$m_{14}^{23}$
1	3	$R_1^3$	$m_{12}^{31}$	$m_{12}^{32}$	$m_{12}^{33}$	$m_{13}^{31}$	$m_{13}^{32}$	$m_{13}^{33}$	$m_{14}^{31}$	$m_{14}^{32}$	$m_{14}^{33}$
2	1	$R_2^1$				$m_{23}^{11}$	$m_{23}^{12}$	$m_{23}^{13}$	$m_{24}^{11}$	$m_{24}^{12}$	$m_{24}^{13}$
2	2	$R_2^2$				$m_{23}^{21}$	$m_{23}^{22}$	$m_{23}^{23}$	$m_{24}^{21}$	$m_{24}^{22}$	$m_{24}^{23}$
2	3	$R_2^3$				$m_{23}^{31}$	$m_{23}^{32}$	$m_{23}^{33}$	$m_{24}^{31}$	$m_{24}^{32}$	$m_{24}^{33}$
3	1	$R_3^1$							$m_{34}^{11}$	$m_{34}^{12}$	$m_{34}^{13}$
3	2	$R_3^2$							$m_{34}^{21}$	$m_{34}^{22}$	$m_{34}^{23}$
3	3	$R_3^3$							$m_{34}^{31}$	$m_{34}^{32}$	$m_{34}^{33}$

Table 2

Symbolic representation of recapture data of Table 1 and corresponding multinomial cell probabilities, both using compact matrix notation. Release and recapture matrices  $\underline{R}_i$  and  $\underline{m}_{ij}$ , and parameter matrices  $\underline{\phi}_i$ ,  $D(\underline{p}_i)$  and  $D(\underline{q}_i)$ , are defined in Section 2.1.

Year of release	Number released	<u>Recapture Array</u>		
		Year of Recapture		
		2	3	4
1	$\underline{R}_1$	$\underline{m}_{12}$	$\underline{m}_{13}$	$\underline{m}_{14}$
2	$\underline{R}_2$		$\underline{m}_{23}$	$\underline{m}_{24}$
3	$\underline{R}_3$			$\underline{m}_{34}$

Year of release	<u>Multinomial Cell Probabilities</u>		
	Year of recapture		
	2	3	4
1	$\underline{\phi}_1^{D(\underline{p}_2)}$	$\underline{\phi}_1^{D(\underline{q}_2)}\underline{\phi}_2^{D(\underline{p}_3)}$	$\underline{\phi}_1^{D(\underline{q}_2)}\underline{\phi}_2^{D(\underline{q}_3)}\underline{\phi}_3^{D(\underline{p}_4)}$
2		$\underline{\phi}_2^{D(\underline{p}_3)}$	$\underline{\phi}_2^{D(\underline{q}_3)}\underline{\phi}_3^{D(\underline{p}_4)}$
3			$\underline{\phi}_3^{D(\underline{p}_4)}$

Table 3

Release-recapture data from the Canada goose study (Hestbeck et al., 1991) in the format required for the Arnason-Schwarz model. Data from 1989 have been omitted to simplify presentation, resulting in  $a = 3$  strata and  $k = 5$  occasions (years 1984-1988). Release cohorts are defined by year and stratum of release.

Year of Release	Number Released	Number of recaptures by year (and stratum)												Not seen again
		1985			1986			1987			1988			
		(1	2	3)	(1	2	3)	(1	2	3)	(1	2	3)	
1984	$R_1^1 = 2082$	491	134	0	149	71	3	51	42	3	21	13	0	1104
	$R_1^2 = 3918$	159	869	15	63	335	10	41	164	3	18	74	2	2165
	$R_1^3 = 1098$	14	101	158	8	47	48	7	16	18	1	14	11	655
1985	$R_2^1 = 2666$				564	200	8	150	116	5	52	46	2	1523
	$R_2^2 = 4026$				125	1017	36	53	325	14	29	146	6	2275
	$R_2^3 = 911$				7	45	178	11	27	39	1	21	26	556
1986	$R_3^1 = 1952$							404	175	5	121	58	0	1189
	$R_3^2 = 3507$							132	843	42	64	264	14	2148
	$R_3^3 = 1345$							19	89	196	12	70	99	860
1987	$R_4^1 = 1291$										271	99	2	919
	$R_4^2 = 2887$										137	654	18	2078
	$R_4^3 = 992$										18	105	168	701

Table 4

Symbolic representation, using compact matrix notation, of the recapture data from a study with  $k = 6$  occasions, in the format required for the Memory model CL. Release and recapture matrices  $\mathbb{R}_{i-1, i}$  and  $\mathbb{m}_{i-1, i, j}$  are defined in Section 3.

Year of release	Number released	Year of Recapture			
		3	4	5	6
2	$\mathbb{R}_{12}$	$\mathbb{m}_{123}$	$\mathbb{m}_{124}$	$\mathbb{m}_{125}$	$\mathbb{m}_{126}$
3	$\mathbb{R}_{23}$		$\mathbb{m}_{234}$	$\mathbb{m}_{235}$	$\mathbb{m}_{236}$
4	$\mathbb{R}_{34}$			$\mathbb{m}_{345}$	$\mathbb{m}_{346}$
5	$\mathbb{R}_{45}$				$\mathbb{m}_{456}$

Table 5

Release-recapture data from the Canada goose study (Hestbeck et al., 1991) in the format required for the Memory Model CL. Data from the Carolinas (stratum 3) have been excluded. Data utilized represent  $a = 2$  strata (the mid-Atlantic and Chesapeake regions, respectively) and  $k = 6$  occasions (years 1984 - 1989). Release cohorts are defined by stratum in the year prior to, and in the year of, release, and recaptures are tabulated by year and stratum of recapture (see Section 3).

Year of Release	Release Cohort	Number Released	Number of recaptures by year (and stratum)								Not seen again
			3		4		5		6		
			(1	2)	(1	2)	(1	2)	(1	2)	
2	R <sub>12</sub> <sup>11</sup>	239	75	3	21	4	5	2	1	0	128
2	R <sub>12</sub> <sup>12</sup>	53	11	5	2	1	0	1	0	1	32
2	R <sub>12</sub> <sup>21</sup>	84	18	6	4	3	0	2	1	3	47
2	R <sub>12</sub> <sup>22</sup>	610	15	145	8	68	7	22	1	16	328
3	R <sub>23</sub> <sup>11</sup>	483			159	13	48	7	9	2	245
3	R <sub>23</sub> <sup>12</sup>	132			10	25	3	6	3	3	82
3	R <sub>23</sub> <sup>21</sup>	156			30	20	5	17	2	3	79
3	R <sub>23</sub> <sup>22</sup>	856			15	245	4	80	4	39	469
4	R <sub>34</sub> <sup>11</sup>	561					183	37	40	15	286
4	R <sub>34</sub> <sup>12</sup>	197					25	42	11	14	105
4	R <sub>34</sub> <sup>21</sup>	121					19	16	7	3	76
4	R <sub>34</sub> <sup>22</sup>	975					19	270	15	75	596
5	R <sub>45</sub> <sup>11</sup>	400							127	15	254
5	R <sub>45</sub> <sup>12</sup>	172							21	32	119
5	R <sub>45</sub> <sup>21</sup>	128							16	22	90
5	R <sub>45</sub> <sup>22</sup>	817							24	225	568

Table 6

Multinomial cell probabilities under the Memory model CL for the recapture data in Table 5, presented using the compact matrix notation. Parameter matrices  $\phi_{i-1, i}$ ,  $\underline{p}_i$ , and  $D(q_i)$ , are defined in Section 3.

Year of release	Year of recapture			
	3	4	5	6
2	$\phi_{12} \underline{p}_3$	$\phi_{12}^{D(q_3)} \phi_{23} \underline{p}_4$	$\phi_{12}^{D(q_3)} \phi_{23}^{D(q_4)} \phi_{34} \underline{p}_5$	$\phi_{12}^{D(q_3)} \phi_{23}^{D(q_4)} \phi_{34}^{D(q_5)} \phi_{45} \underline{p}_6$
3		$\phi_{23} \underline{p}_4$	$\phi_{23}^{D(q_4)} \phi_{34} \underline{p}_5$	$\phi_{23}^{D(q_4)} \phi_{34}^{D(q_5)} \phi_{45} \underline{p}_6$
4			$\phi_{34} \underline{p}_5$	$\phi_{34}^{D(q_5)} \phi_{45} \underline{p}_6$
5				$\phi_{45} \underline{p}_6$

Table 7

Goodness-of-fit chisquare values and LogCL values from MSSURVIV for the data in Examples 3.3.1 and 3.3.2 under various Memory models. Note that because of pooling or sparse data, goodness of fit p-values are approximate.

## Example 3.3.1 (2 regions, 1984-1989)

Model	Number of Parameters	Pearson Goodness-of-fit		p-value	LogCL
		$\chi^2$	df		
Nomemory	22	350.708	44	.000	-315.457
Memory	38	45.12	21	.002	-193.437

## Example 3.3.2 (3 regions, 1986-1989)

Model	Number of Parameters	Likelihood-ratio Goodness-of-fit		p-value	LogCL
		$G^2$	df		
Nomemory	21	297.96	60	.00	-258.695
MV2	39	59.35	42	.04	-139.387
Memory	57	34.45	24	.08	-126.936

Table 8

Annual transition probabilities estimated under the Memory model for the data of Table 5, and grouped according to whether or not transition in  $i$  to  $i + 1$  represents a "return" to the stratum occupied at  $i - 1$ . Approximate standard errors are given in parentheses.

Year = $i$	Transition made in $i$ to $i + 1$	estimated transition probability if	
		(a): stratum at $i + 1$ = stratum at $i - 1$	(b): stratum at $i + 1$ $\neq$ stratum at $i - 1$
1985	11	.57 (.05)	.38 (.07)
	12	.22 (.07)	.04 (.02)
	21	.34 (.09)	.05 (.01)
	22	.66 (.04)	.21 (.09)
1986	11	.58 (.04)	.31 (.05)
	12	.37 (.06)	.06 (.02)
	21	.13 (.04)	.03 (.01)
	22	.67 (.03)	.42 (.06)
1987	11	.54 (.04)	.27 (.05)
	12	.31 (.06)	.14 (.02)
	21	.22 (.04)	.03 (.01)
	22	.59 (.03)	.51 (.06)

Table 9

Release-recapture data from the Canada goose study, for all 3 regions and years 1986-1989, in the format required for the Memory model CL. Release cohorts are defined by strata occupied in the year before, and in the year of release.

Year of Release	Release Cohort	Number Released	Number of recaptures by year (and stratum)						Not seen again
			1988			1989			
			(1	2	3)	(1	2	3)	
1987	R <sub>34</sub> <sup>11</sup>	564	184	37	0	40	15	0	288
1987	R <sub>34</sub> <sup>12</sup>	200	26	42	1	11	14	0	106
1987	R <sub>34</sub> <sup>13</sup>	8	2	0	0	1	1	0	4
1987	R <sub>34</sub> <sup>21</sup>	125	21	17	1	7	3	0	76
1987	R <sub>34</sub> <sup>22</sup>	1017	21	276	8	16	78	0	618
1987	R <sub>34</sub> <sup>23</sup>	36	0	5	4	0	0	1	26
1987	R <sub>34</sub> <sup>31</sup>	7	0	0	0	0	1	0	6
1987	R <sub>34</sub> <sup>32</sup>	45	0	8	5	0	5	0	27
1987	R <sub>34</sub> <sup>33</sup>	178	0	5	47	3	3	29	91
1988	R <sub>45</sub> <sup>11</sup>	404				129	19	0	256
1988	R <sub>45</sub> <sup>12</sup>	175				21	32	1	121
1988	R <sub>45</sub> <sup>13</sup>	5				1	3	0	1
1988	R <sub>45</sub> <sup>21</sup>	132				16	23	0	93
1988	R <sub>45</sub> <sup>22</sup>	843				25	230	2	586
1988	R <sub>45</sub> <sup>23</sup>	42				1	7	4	30
1988	R <sub>45</sub> <sup>31</sup>	19				1	0	2	16
1988	R <sub>45</sub> <sup>32</sup>	89				4	13	3	69
1988	R <sub>45</sub> <sup>33</sup>	196				1	16	68	111