

## A Theory for Combined Analysis of Ring Recovery and Recapture Data

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*Summary.* For capture-recapture studies the Jolly-Seber model theory for time-specific effects is well developed and established, as is the corresponding time-specific ring recovery model,  $M_1$  (Brownie et al. 1985). Many capture-recapture studies on birds will generate both live recaptures and rings reported from birds shot, or found dead, throughout the year. The purpose of this paper is to give the basic generalization of the Jolly-Seber and ring recovery model  $M_1$  for the simultaneous analysis of these recapture and recovery data. Under the generalized model, as under each model separately, the statistical distribution of the relevant data can be taken as a set of appropriately structured, independent, multinomial distributions but with response categories for two classes of events: (a) the first recapture after a known release of a live bird, and (b) ring recovery from a dead bird after a known release. These events can be considered a type of post-release stratification of the data. Moreover, these two types of events "interfere" (or compete) with each other, and it is that feature of the problem that causes the modeling difficulties here. Conditional on the known releases, these events are mutually exclusive and exhaustive (when considered together with the event, release and neither the bird nor its ring is ever encountered again). This paper gives the expanded multinomial representation of the correct statistical model for the combined data and gives alternative forms of the multinomial cell probabilities under two assumptions about emigration from the study area. Representation of some of these cell probabilities in the joint model is more complex than in either separate model. Finally, the abundance estimation part of the Jolly-Seber model derives from modeling the probability distribution of first captures; that model component is unaffected by the possibility of using recoveries as well as recaptures from the releases of ringed birds.

### 1. Introduction

Statistical theory for the analysis of data from bird ringing studies has been quite thoroughly developed for two seemingly distinct classes of studies: capture-recapture and ring recovery. In the former type of study, birds are repeatedly recaptured alive and then re-released, thus multiple encounters can occur after the initial ringing of a bird. The latter type of study typically applies to harvested or hunted species, such as game birds wherein re-encounters with rings come from dead birds, hence after ringing there is at most one re-encounter possible. However, in bird ringing studies we can expect both live recaptures (and re-releases) and reports of rings from dead birds. The purpose of this paper is to present basic statistical theory for the time-specific effects case when there are both live recaptures and dead recoveries resulting from a ringing study.

I assume the reader is familiar with the basic capture-recapture and ring-recovery statistical analysis literature. This literature includes such seminal publications as Cormack (1964), Jolly (1965) and Seber (1965, 1970). In particular, the reader should be familiar with the more recent comprehensive publications of Brownie et al. (1985), Burnham et al. (1987), Pollock et al. (1990) and Lebreton et al. (1992). Of the models considered in

these papers, I am only directly concerned here with the Cormack-Jolly-Seber capture-recapture model, the corresponding ring recovery model  $M_1$ , and their extension to joint recapture-recovery analysis.

The joint analysis of live recapture and ring-recovery data has not been much considered in the ringing analysis literature (cf, Clobert and Lebreton, 1991). When both types of data exist from one study, it has been common to just do the two separate analyses, see e.g., Anderson and Sterling (1974) and compare the results. Alternatives have been to force the live recapture data to "fit" into the dead recoveries framework (Mardekian and McDonald, 1981), or conversely, force the dead recoveries data component into the live capture-recapture framework (Buckland, 1980). Only recently have truly unified analysis methods been used for these type of "post-stratified" data (Szymczak and Rexstad, 1991; see also Schwarz et al., 1988) and the theory herein given for this analysis has not previously appeared.

One difficulty in producing a combined theory is the choice of notation. Theory for ring recovery and capture-recapture data have been developed separately. This has led to the two theories using very different notation and indexing over capture-release occasions. A large part of this difference stems from an historic emphasis in capture-recapture on estimation of population size rather than survival rate. The only parameter in common for recovery and recapture data is survival rate; thus a joint theory must focus on survival rate. With respect to survival rate, there is a basic statistical theory for time-specific release-resampling models that applies to both ring-recoveries and capture-recapture. This common theory is presented in Burnham et al. (1987), Lebreton et al. (1992) and given in detail in Burnham (1991). Burnham (1988) presents a very thorough theory development including a general notation for release-resampling that I will use here. Essentially, I choose to use capture-recapture type notation and multinomial modeling as the basis for a joint theory.

I will use here terminology and ideas of bird ringing studies with ringing done annually; the theory given here is, of course, more general and time intervals between capture occasions need not be equal. Ring recovery models have generally been developed in terms of known releases ( $R_i$ ) at the start of (study) year  $i$  with subsequent recoveries ( $m_{ij,d}$ , the  $d$  denotes "dead") during years  $j = i, i+1, \dots, t$  as being multinomially distributed events. By putting capture-recapture data in this same modeling framework (Burnham, 1991) we represent either type of data in a common framework.

Under the joint analysis we have releases,  $R_i$ , and *first* recaptures,  $m_{ij,l}$ , of live (denoted by the subscript  $l$ ) birds at times  $j = i+1, \dots, t$ , and ring recoveries,  $m_{ij,d}$ , from dead birds during yearly time periods  $i$  to  $i+1, i+1$  to  $i+2, \dots, t-1$  to  $t$ . Recaptures at year  $j$  are re-released as part of the  $R_j$  birds then known to be released (except losses on capture are allowed). Instead of only one type of re-sampling event under the separate theories, we have two types of events: if it is encountered again, the bird may be either alive (the  $m_{ij,l}$ ) or dead (the  $m_{ij,d}$ ). This can be thought of as post stratification of the encounter data, in the sense that at the time of release we cannot know which type of subsequent encounter will occur. (The subscripts  $l$  and  $d$  encoded the post stratification factor, hence are after the  $ij$  subscripts). In each cohort of releases (the  $R_i$ ) the subsequent encounter events are mutually exclusive. If we assume independent fates of individuals then the basic data have a multinomial distribution, independent over each of the released cohorts.

Completion of model specification now focuses on the functional form of the cell probabilities in the multiple-multinomial probability model for the recapture-recovery data. This paper gives a probability form that correctly generalizes Cormack-Jolly-Seber and Model  $M_1$ . The types of rate parameters in this model are survival probability,  $S$ , site fidelity,  $F$ , live capture probability,  $p$ , and ring recovery probability,  $f$  (the classical Jolly-Seber model assumes any emigration from the study area is permanent, hence only the

product  $\phi = SF$  is then estimable). The multinomial cell probabilities for the joint model are expressed as functions of these four types of parameters. However, some of the cell functional forms are more complex than for corresponding events in either marginal model. This is because the two types of resampling events (live or dead) compete (interfere) with one another for removal of a bird from its last release cohort. In particular, if a ring is known to have been recovered, then that bird is known to be unavailable for future live recapture.

In what follows I first summarize the basic theory for the Cormack-Jolly-Seber model and banding model  $M_1$  in a common notation (Section 2). Then Section 3 gives a theory of joint recapture-recovery data: Section 3.1 gives a multinomial model representation of the general probability model for the joint distribution of recapture and recovery data; Section 3.2 gives the specific form of the cell probabilities in this model under the usual permanent emigration assumption; Section 3.3 gives theory under the assumption that on any capture occasion it is an independent random event as to whether a live bird is in the subset of the population at risk of capture. To have a short way to refer to this later assumption, I will call it "random emigration."

## 2. Separate model theory summarized

### 2.1 Cormack-Jolly-Seber Probability Model

The basic notation needed for the survival component of the Cormack-Jolly-Seber model is defined below:

$R_i$       The number of ringed birds released at capture occasion  $i$ ; under the assumptions of the Jolly-Seber model these birds can be a mix of first captures and recaptures;  $i = 1, \dots, t-1$ .

$m_{ijt}$     The number of birds recaptured for the first time at occasion  $j$ , from those birds released at occasion  $i$ ;  $j = i+1, \dots, t$ ,  $i = 1, \dots, t-1$ .

I consider herein only the case of  $t$  capture and release occasions, hence  $t-1$  recapture occasions, and  $t-1$  time-intervals for recovery of rings from dead birds. Some derived statistics are also needed, in particular the total recaptures from the  $R_i$  releases,

$$r_{it} = \sum_{j=i+1}^t m_{ijt} \quad , \quad i = 1, \dots, t-1.$$

As given in much more detail in, e.g., Burnham (1987, 1988 or 1991) the probability model for these data is the product of  $t-1$  independent multinomial distributions:

$$\Pr\{\text{recaptures} \mid \text{releases}\} = \prod_{i=1}^{t-1} \Pr\{m_{i,i+1,t}, \dots, m_{it} \mid R_i\} = \prod_{i=1}^{t-1} \binom{R_i}{m_{i,i+1,t}, \dots, m_{it}, R_i - r_{it}} \left( \prod_{j=i+1}^t (\pi_{ijt})^{m_{ijt}} \right) (1 - \lambda_{it})^{(R_i - r_{it})} \quad (1)$$

with

$$\pi_{ijt} = \frac{E(m_{ijt} \mid R_i)}{R_i} = \begin{cases} \phi_i p_{i+1} & , j = i+1, \\ (\phi_i q_{i+1}) \cdots (\phi_{j-2} q_{j-1}) (\phi_{j-1} p_j) & , j > i+1. \end{cases} \quad (2)$$

For any definition of  $\pi_{ijt}$  (not just (2) above), define

$$\lambda_{it} = \sum_{j=i+1}^t \pi_{ijt}, \quad i = 1, \dots, t-1.$$

When (2) holds then there is a convenient recursive formula,

$$\lambda_{it} = \phi_i(p_{i+1} + q_{i+1}\lambda_{i+1,t}), \quad i = 1, \dots, t-1,$$

with boundary condition  $\lambda_{it} = 0$ .

The parameters in the Cormack-Jolly-Seber model are defined below:

- $p_i$  The probability of capture on occasion  $i$  given that the bird is still in the population at risk of capture on occasion  $i$ ,  $q_i = 1 - p_i$ ;  $i = 2, \dots, t$ .
- $\phi_i$  The probability of surviving in the subset of the population at risk of capture from occasion  $i$  to occasion  $i+1$  given that the bird is alive in the population at risk at the start of survival period  $i$ ,  $i = 1, \dots, t-1$ .

There are  $2t - 3$  identifiable parameters in this model:  $\phi_1, \dots, \phi_{t-2}, p_2, \dots, p_{t-1}$ , and the product  $\phi_{t-1}p_t$ . However, the parameter  $\phi_i$  is a product of two biologically interpretable parameters:  $\phi_i = S_i F_i$ . The probability of surviving between capture occasion  $i$  and  $i+1$  is  $S_i$ ; thus  $1 - S_i =$  probability of death. Given an animal is alive at occasion  $i+1$ , then  $F_i$  (fidelity) is the probability of it being in the study area at that time.

## 2.2 Ring Recovery Probability Model

Basic additional notation needed for the time-specific ring recovery model  $M_1$  in a form that will be compatible with capture-recapture data is below (still for  $t$  occasions):

- $m_{ijd}$  The number of rings recovered between ringing occasions  $j$  and  $j+1$ , from birds released on occasion  $i$ ,  $j = i, \dots, t$ ,  $i = 1, \dots, t$ .

The total number of rings recovered from released cohort  $i$  is

$$r_{id} = \sum_{j=i}^t m_{ijd}, \quad i = 1, \dots, t.$$

As shown in detail in Burnham (1988 or 1991) (see also Brownie et al., 1985) the probability model for these data is the product of  $t$  independent multinomial distributions:

$$\Pr\{\text{recoveries} \mid \text{releases}\} = \prod_{i=1}^t \Pr\{m_{i1d}, \dots, m_{itd} \mid R_i\} =$$

$$\prod_{i=1}^t \binom{R_i}{m_{i1d}, \dots, m_{itd}, R_i - r_{id}} \left( \prod_{j=i}^t (\pi_{ijd})^{m_{ijd}} \right) (1 - \lambda_{id})^{(R_i - r_{id})} \quad (3)$$

with

$$\pi_{ijd} = \frac{E(m_{ijd} \mid R_i)}{R_i} = \begin{cases} f_i & , j = i, \\ S_i \cdots S_{j-1} f_j & , j > i, \end{cases} \quad (4)$$

For any definition of  $\pi_{ij,d}$ , define

$$\lambda_{i,d} = \sum_{j=i}^t \pi_{ij,d}, \quad i = 1, \dots, t.$$

If (4) applies then there is a convenient recursive formula,

$$\lambda_{i,d} = f_i + S_i \lambda_{i+1,d}, \quad i = 1, \dots, t,$$

with boundary condition  $\lambda_{t+1,d} = 0$ .

The parameters in this ring recovery model are defined below:

- $f_i$       The probability of a ring being recovered between occasions  $i$  and  $i+1$  given that the bird is alive on occasion  $i$ ,  $i = 1, \dots, t$ .
- $S_i$       The probability of surviving from occasion  $i$  to occasion  $i+1$  given that the bird is alive at occasion  $i$ ,  $i = 1, \dots, t-1$ .

The above  $2t-1$  parameters are all identifiable (i.e.,  $S_1, \dots, S_{t-1}, f_1, \dots, f_t$ ).

### 2.3 Comments on Separate vs. Joint Models

The data representation used above is not minimal sufficient for either model; rather, in both cases a simply expressed, minimal sufficient statistic exists with a probability distribution representable by a product of binomials. The dimensionality of the minimal sufficient statistic is the same as the number of identifiable parameters ( $2t-3$  for the capture-recapture case as presented, and  $2t-1$  for the ringing case with  $t$  ringing occasions). In both cases, closed-form (if not restricted to the unit interval) maximum likelihood estimators exist. When the models are "merged" for joint analysis of recapture and recovery data, this simple reduction to a minimal sufficient statistic no longer seems to hold under the permanent emigration assumption of the Jolly-Seber model, hence I do not give the reduced probability models for these two above cases.

At first thought one might think to simply combine the multinomials and use, as the joint model for the  $i^{\text{th}}$  released cohort, the set of independent multinomials with cell probabilities as defined above in (2) and (4). Structurally this would be the set of cell probabilities

$$\pi_{i,i,d}, \pi_{i,i+1,t}, \pi_{i,i+1,d}, \pi_{i,i+2,t}, \dots, \pi_{i,t-1,d}, \pi_{i,t}, \pi_{i,t,d},$$

and a final cell probability of  $1 - \lambda_{i,d} - \lambda_{i,t}$ . This is correct in the context of this modeling approach *only* if some of the cell probabilities are appropriately redefined. Once a recapture at occasion  $j$  ( $> i$ ) occurs that bird is reassigned upon release to the  $j^{\text{th}}$  release cohort and hence is no longer available to become a dead recovery from the  $i^{\text{th}}$  release cohort after occasion  $j$ . Similarly, when a recovery is recorded in year  $j$ , that bird is known to be no longer available to become a live recapture in occasions beyond  $j$ . Thus, heuristically it should be clear that some modification to these sets of marginal cell probabilities (i.e., the  $\pi_{ij,t}$ , or the  $\pi_{ij,d}$ ) is needed in the joint model to adjust for the fact that the two possible types of re-encounters, after a known release, compete (as in competing risks) to remove birds from that release cohort. In the next section I consider a correct form of the joint cell probabilities.

There is also an issue here about whether to include or drop the final year of recovery data, the  $m_{i,t,d}$ ,  $i = 1, \dots, t$ . If we think of having a classical capture-recapture study and adding possible dead recoveries to the data during the study years, then the study ends at occasion  $t$  and we would do the data analysis without the  $m_{i,t,d}$  data. That is, we use ring recovery data  $m_{ij,d}$  only for

$i = 1, \dots, t-1, j = i, \dots, t-1$ . However, if the ring recovery process is independent of the capture process, then we will ultimately have not only the  $m_{itd}$  data, but also recoveries beyond capture occasion  $t$  (as in the models of Brownie et al., 1985):  $m_{ijd}, j = t, t+1, \dots, k, i = 1, \dots, t$ . It is beyond the scope of this paper to consider in detail the extension of theory to  $k > t$ .

### 3. A Probability Model for Joint Analysis of Recapture-Recovery Data

#### 3.1 The general model structure

The organization of the joint recapture and recovery data under the multinomial modeling framework used here is displayed in Table 1 for the case of no dead recoveries tabulated after the end of the last live capture occasion. Each of the  $t-1$  cohorts of releases, of size  $R_i$ , leads to a multinomial distribution for the counts of first recaptures and recoveries from that cohort. That this is so is a straightforward result of the usual assumptions of bird ringing studies (see e.g., Lebreton et al., 1992): the same parameters apply to each bird, independent fates of each bird and under the data summary form in Table 1, the possible fates (multinomial cells) within cohorts are mutually exclusive. Therefore, the probability model structure for these data is represented as below. Note that the cell probabilities ( $\pi_{ijd}$  and  $\pi_{ijt}$ ) in this joint model are not all identical to the forms given in (2) and (4), which are the marginal cell probabilities of the two data types separately. Two possible cell forms for the joint model are given in Sections 3.2 and 3.3; since (2) and (4) are special cases I do not use new notation here to denote the cell probabilities. The joint model is below:

$$\begin{aligned} & \Pr\{\text{recapture-recovery data up to occasion } t \mid \text{releases}\} = \\ & \prod_{i=1}^{t-1} \Pr\{m_{iid}, m_{i,i+1,t}, \dots, m_{i,t-1,d}, m_{itl} \mid R_i\} = \\ & \left[ \prod_{i=1}^{t-1} \binom{R_i}{m_{iid}, m_{i,i+1,t}, \dots, m_{i,t-1,d}, m_{itl}, R_i - r_{id} - r_{it}} \right] \times \\ & \left[ \prod_{i=1}^{t-1} \left\{ \prod_{j=i}^{t-1} (\pi_{ijd})^{m_{ijd}} (\pi_{i,j+1,t})^{m_{i,j+1,t}} \right\} (1 - \lambda_{id} - \lambda_{it})^{(R_i - r_{id} - r_{it})} \right]. \end{aligned} \quad (5)$$

Also

$$\begin{aligned} \lambda_{it} &= \sum_{j=i+1}^t \pi_{ijt}, & i = 1, \dots, t-1, \\ \lambda_{id} &= \sum_{j=i}^{t-1} \pi_{ijd}, & i = 1, \dots, t-1. \end{aligned}$$

The number of releases,  $R_i$ , includes all newly ringed birds and all re-released live recaptures made on occasion  $i$ .

The probability model given in (5) is for the case where we do not have, or do not use, the recovery data  $m_{itd}$  obtained in time interval  $t$  to  $t+1$  (i.e., in year  $t$ ). If we include these data, then one more cell is added to each multinomial and a  $t^{\text{th}}$  multinomial (binomial, actually) distribution is added to the probability model. This probability model is given below:

Table 1. Symbolic cohort representation of joint recovery-recapture data,  $m_{ijv}$ , for  $t$  occasions with effort ending at the last recapture occasion;  $i$  denotes release occasion,  $j$  denotes the time interval for recoveries or the recapture occasion; post stratification is  $v = d$  (dead recoveries) or  $l$  (live recoveries).

i	Releases	j = 1	2	3	...	t - 1	t
1	$R_1$	$m_{11d}$	$m_{12l}$ $m_{12d}$	$m_{13l}$ $m_{13d}$	...	$m_{1,t-1,l}$ $m_{1,t-1,d}$	$m_{1td}$
2	$R_2$		$m_{22d}$	$m_{23l}$ $m_{23d}$	...	$m_{2,t-1,l}$ $m_{2,t-1,d}$	$m_{2td}$
3	$R_3$			$m_{33d}$	...	$m_{3,t-1,l}$ $m_{3,t-1,d}$	$m_{3td}$
⋮	⋮				⋮	⋮	⋮
t-1	$R_{t-1}$					$m_{t-1,t-1,d}$	$m_{t-1,td}$

$\Pr\{\text{recapture-recovery data through year } t \mid \text{releases}\} =$

$$\begin{aligned} & \left[ \prod_{i=1}^{t-1} \Pr\{m_{i1d}, m_{i,i+1,l}, \dots, m_{i,t-1,d}, m_{itl}, m_{itd} \mid R_i\} \right] \left[ \Pr\{m_{ttd} \mid R_t\} \right] = \\ & \left[ \prod_{i=1}^{t-1} \left( m_{i1d}, m_{i,i+1,l}, \dots, m_{i,t-1,d}, m_{itl}, m_{itd}, R_i - r_{id} - r_{il} \right) \right] \left( \frac{R_t}{m_{ttd}} \right) \times \\ & \left[ \prod_{i=1}^{t-1} \left[ \left\{ \prod_{j=i}^{t-1} (\pi_{ijd})^{m_{ijd}} (\pi_{i,j+1,l})^{m_{i,j+1,l}} \right\} (\pi_{itd})^{m_{itd}} (1 - \lambda_{id} - \lambda_{il})^{(R_i - r_{id} - r_{il})} \right] \right] \times \\ & \left[ (\pi_{ttd})^{m_{ttd}} (1 - \pi_{ttd})^{(R_t - m_{ttd})} \right]. \end{aligned} \quad (6)$$

Also

$$\begin{aligned} \lambda_{it} &= \sum_{j=i+1}^t \pi_{ijl}, & , i = 1, \dots, t-1, \\ \lambda_{id} &= \sum_{j=i}^t \pi_{ijd}, & , i = 1, \dots, t. \end{aligned}$$

Finally, note that cohort sums of re-encounters,  $r_{id}$  and  $r_{il}$ , mean the same thing for models (5) and (6) – separate sums of the  $m_{ijd}$  and  $m_{ijl}$  by cohort; I do not explicitly give their formulae under each model.

The correct cell probabilities for (5) and (6) can be given as formula (2) for the live (first) recapture-after-release probabilities,  $\pi_{ijl}$ . For the recoveries component we use (7) given below, which is a modified version of (4):

$$\pi_{ijd} = \frac{E(m_{ijd} \mid R_i)}{R_i} = \begin{cases} f_i & , j = i, \\ S_i \dots S_{j-1} \gamma_{ij} f_j & , j > i, \end{cases} \quad (7)$$

where  $\gamma_{ij}$  is the probability that a bird released at capture occasion  $i$  and still alive at occasion  $j$  will never have been removed from the  $i^{\text{th}}$  released cohort

by being captured on one of occasions  $i+1$  to, and including, occasion  $j$ . Such a removal from the cohort, and reassignment to a later released cohort, makes the bird (i.e., ring) not available to be recovered as a part of count  $m_{ij,d}$ . Rather, if that ring is then subsequently recovered in year  $j$ , that count becomes part of a different recorded  $m_{hjd}$  for  $i < h \leq j$ . This bookkeeping device allows us to formulate our model in terms of familiar multinomial distributions, for which much theory is known. If no live capture data are used (or recorded) then, in effect, all  $p_i = 0$  and as a result all  $\gamma_{ij} = 1$ . Similarly, if there are no recovery data collected or used, then all  $f_i = 0$ .

### 3.2 Joint cell probabilities under permanent emigration

Previously ringed birds may still be alive at a later capture occasion but may have moved out of the area (i.e., subset of the population) in which birds are at risk of capture. This sort of "movement" may be accompanied by an intervening round trip migration, but that is not relevant per se. Such movements out of the subset of the population at risk of capture are said to be emigration, especially if these are permanent, i.e., the bird never returns to the subset of the population at risk of capture, at least at any time capture is occurring. Permanence of emigration movements (if any occur) is the usual assumption in capture-recapture. By making this additional assumption we can determine an explicit form for  $\gamma_{ij}$ :

$$\begin{aligned}\gamma_{jj} &= 1, \\ \gamma_{j-1,j} &= 1 - F_{j-1}(1 - q_j), \\ \gamma_{j-2,j} &= 1 - F_{j-2}(1 - q_{j-1}\gamma_{j-1,j}),\end{aligned}$$

or, in general

$$\gamma_{ij} = 1 - F_i(1 - q_{i+1}\gamma_{i+1,j}), \quad (8)$$

with boundary condition  $\gamma_{jj} = 1$  and indexed for  $i = 1, \dots, j-1$  and  $j = 1, \dots, t$ . To compute these parameters, do it for any given fixed  $j$  by iterating backwards from  $i = j-1, j-2, \dots$ , to 1. Written out in one long, awkward, form for  $j > i$ , we have

$$\gamma_{ij} = 1 - F_i(1 - q_{i+1}(1 - F_{i+1}(1 - q_{i+2}(1 - \dots - F_{j-1}(1 - q_j)\dots))))$$

and computation is from the inner-most component outward. Clearly, the probability  $\gamma_{ij}$  depends on only the parameters  $F_i, \dots, F_{j-1}, q_{i+1}, \dots, q_j$ ; of course  $q_i = 1 - p_i$ . Thus the  $\gamma_{ij}$ 's do not introduce any new parameters into the model.

The  $\gamma_{ij}$  probabilities adjust the cohort-specific ring recovery probabilities, in the multinomial approach, for the expected live capture rate after known releases. For releases at occasion  $j$  there are no recaptures before recoveries in time interval  $j$  to  $j+1$ , hence  $\gamma_{jj} = 1$ . Under the data representation scheme of Table 1, in order to be counted as a recovery in  $m_{j-1,j,d}$  a bird must first survive year  $j-1$  and then not be recaptured live at occasion  $j$ . This latter probability,  $\gamma_{j-1,j}$ , is the probability of two mutually exclusive events. Either the bird emigrates (note,  $E_i = 1 - F_i$ ) in year  $j-1$  or stays in the population at risk of capture but is not captured at occasion  $j$ . This probability is

$$\gamma_{j-1,j} = E_{j-1} + F_{j-1}q_j = 1 - F_{j-1}(1 - q_j).$$

In general for a bird released at occasion  $i$ , given that it is still alive at occasion  $j$ , to still be available to contribute a recovery from release cohort  $i$  in



year  $j$  to the count  $m_{ijd}$ , the bird must either emigrate in year  $i$  or stay in the population at risk of capture but not be caught at occasion  $i+1$  and then not be caught after occasion  $i+1$ . Translating this description to a mathematical formula we get the recursive definition of  $\gamma_{ij}$ :

$$\gamma_{ij} = E_i + F_i q_{i+1} \gamma_{i+1,j},$$

which is equal to form (8):  $1 - F_i(1 - q_{i+1}\gamma_{i+1,j})$ . This form for  $\gamma_{ij}$  is unique to the assumption of permanent emigration.

It is instructive to consider three special cases. If no emigration is possible, or if otherwise fidelity is perfect, then all  $F_i = 1$  and an explicit expression for  $\gamma_{ij}$  exists:

$$\gamma_{ij} = q_{i+1}q_{i+2}\cdots q_j.$$

If no recapture occurs, say because recaptures are ignored (i.e., not recorded), then all  $p_i = 0$ , hence all  $q_i = 1$  and this leads to all  $\gamma_{ij} = 1$ . This result is easily proven by induction on (8). If for a particular  $i$  and  $j$ ,  $\gamma_{ij} = 1$ , then from (8),  $\gamma_{i-1,j} = 1 - F_{i-1}(1 - q_i)$  and hence if all  $q_i = 1$  then  $\gamma_{i-1,j} = 1$ . But we already know that all  $\gamma_{ij} = 1$ , thus it follows that if all  $p_i = 0$ , then all  $\gamma_{ij} = 1$ .

If the adjustment entailed by  $\gamma_{ij}$  in (7) to the marginal recovery probabilities is not made and distribution (5) or (6) is erroneously used, the cell probability totals  $\lambda_{id} + \lambda_{il}$  can exceed 1. With the adjustment, these totals will never exceed 1. By way of example consider the case represented in Table 1 for  $t = 3$ , hence model (5), for  $F_i = 1$  and the extreme (but mathematically possible) case of  $f_i = 1 - S_i$  for  $i = 1, 2$ . For the proper model (multinomial cells defined by (2) and (7)), we have

$$\lambda_{1d} + \lambda_{1l} = 1 - (S_1 q_2 S_2 q_3),$$

which can never exceed 1. But with the cells as defined by (2) and (4) we have

$$\lambda_{1d} + \lambda_{1l} = 1 - S_1 S_2 + S_1(p_2 + q_2 S_2 p_3).$$

Let  $S_1 = S_2 = p_2 = p_3 = 0.9$  and the above is equal to 1.0729. This example is just to reinforce the point that in the joint analysis of recapture-recovery data the model must properly account for the fact that known recoveries cannot thereafter become live captures.

Under the case represented by model (5), permanent emigration and  $t$  occasions for capture and release with  $t-1$  ring recovery time intervals, there are  $4t-6$  identifiable parameters:  $S_1, \dots, S_{t-2}, p_2, \dots, p_{t-1}, f_1, \dots, f_{t-1}, F_1, \dots, F_{t-2}$ , and the product  $(S_{t-1} F_{t-1} p_t)$ . If we add to model (5) a  $t^{\text{th}}$  year of ring recovery data, thus we have model (6), there are  $4t-4$  identifiable parameters:  $S_1, \dots, S_{t-1}, p_2, \dots, p_{t-1}, f_1, \dots, f_t, F_1, \dots, F_{t-2}$ , and the product  $(F_{t-1} p_t)$ .

### 3.3 Cell probabilities under random emigration

The permanent emigration assumption is not the only assumption under which the time-specific models remain structurally valid. As given in Burnham (1988) an alternative parameterization of the Jolly-Seber model cells given in (2) is possible. Specifically, the "location" of a live bird during a capture occasion could be random with regard to whether or not it is in the sub-population (area) at risk of capture. Now the parameter  $F_i$  is the probability at occasion  $i$  that the bird is at risk of capture given it is alive;  $p_i$  is the probability of capture given the bird is alive and at risk of capture. The structure of  $\pi_{ijl}$  remains as in (2) however, we must now interpret  $\phi_i$  as in fact being true survival rate,  $S_i$ , and  $p_i$  is actually the product of  $F_i$  and the traditional conditional capture probability.

To avoid confusion I will explicitly give cell probabilities appropriately reparameterized under this "random emigration" assumption. For live captures we have

$$\pi_{ijl} = \frac{E(m_{ijl} | R_i)}{R_i} = \begin{cases} S_i p_{i+1}^* & , j = i+1, \\ (S_i q_{i+1}^*) \cdots (S_{j-2} q_{j-1}^*) (S_{j-1} p_j^*) & , j > i+1. \end{cases} \quad (9)$$

The model structure, under this assumption, for the recovery cell probabilities under the joint analysis model is given by (7) with

$$\begin{aligned} \gamma_{ij} &= 1 & , j = i, \\ \gamma_{ij} &= q_{i+1}^* q_{i+2}^* \cdots q_j^* & , j > i. \end{aligned}$$

Here we have  $p_i^* = F_{i-1} p_i$  and  $q_i^* = 1 - F_{i-1} p_i$ . One can think of this model as one wherein the birds have fidelity  $F_i = 1$ , capture probability  $p_i^*$ , and  $\phi_i \equiv S_i$ . The separate  $F_{i-1}$  and  $p_i$  are confounded, hence not estimable; only their product,  $p_i^* = F_{i-1} p_i$  is estimable.

As a consequence of the multiplicative structure on the  $\gamma_{ij}$ , we have for this model

$$\pi_{ijd} = \frac{E(m_{ijd} | R_i)}{R_i} = \begin{cases} f_i & , j = i, \\ (S_i q_{i+1}^*) \cdots (S_{j-1} q_j^*) f_j & , j > i. \end{cases} \quad (10)$$

Thus under the random emigration assumption, the model for joint recapture-recovery data is the probability distribution in (5), or (6), with cell probabilities as given in (9) and (10).

Under the case represented by model (5) with  $t$  occasions for capture and release,  $t-1$  ring recovery time intervals, random emigration and with full time-specificity of parameters there are  $3t-4$  identifiable parameters:  $S_1, \dots, S_{t-2}, f_1, \dots, f_{t-1}$ , and the products  $p_2^*, \dots, p_{t-1}^*$ ,  $(S_{t-1} p_t^*)$  where  $p_i^* = (F_{i-1} p_i)$ . If we add to this model a  $t^{\text{th}}$  year of ring recovery data, then there are  $3t-2$  identifiable parameters:  $S_1, \dots, S_{t-1}, f_1, \dots, f_t$ , and the products  $p_2^*, \dots, p_t^*$ .

#### 4. Direct Construction of the Likelihood

The approach used here to give a probability model for capture-recapture and recovery data separately or jointly is not unique. This is because there are other approaches to the capture-recapture aspect of the problem, e.g., hypergeometric models (Pollock, 1975), Poisson models (Cormack and Jupp, 1991), log-linear models (Cormack, 1989) and capture history based models (Crosbie and Manly, 1985, Lebreton et al., 1992). All these approaches to capture-recapture give either the same or almost the same likelihood (the differences relate to what parameters are the focus of the model). The most flexible approach to creating likelihoods for bird ringing data, as regards inference on survival rates, is the encounter history approach. The data are represented as the ordered sequence of all possible encounters (captures, recoveries, etc.) coded 1 for encounter, 0 otherwise. For an encounter history,  $h$ , let  $X_h$  be the count of birds having this history and let  $Y_h = 1$  if at the last recorded encounter the bird is re-released;  $Y_h = 0$  if the bird is not re-released on last encounter. Trailing zeros in  $h$  are used for convenience after a ring recovery.

Under the encounter history formulation the likelihood contribution of each observed encounter history is first computed; some examples are given in Table 2 wherein  $t = 5$  and  $j =$  the capture occasion, or the between-occasion interval during which ring recoveries are made. The first encounter is a live capture at which time the bird is ringed. Thereafter potential dead and live encounters alternate. Assuming the usual Cormack-Jolly-Seber model with

Table 2. Examples of the probabilities of specific encounter histories (h) assuming the Cormack-Jolly-Seber model (with permanent emigration);  $t=5$ , the study ends at occasion 5,  $j$  = the capture occasion or the between-occasion interval during which ring recoveries are made (live, or dead);  $X_h$  = number of birds with history, h;  $Y_h = 0$  if the bird is not re-released at its last encounter; probabilities are conditional on first capture.

$j = 112233445$ $h = \underline{ldldldldld}$	$X_h$	$Y_h$	Pr(h   first capture)
100010001	3	1	$\phi_1 q_2 \phi_2 p_3 \phi_3 q_4 \phi_4 p_5$
100010010	2	1	$\phi_1 q_2 \phi_2 p_3 S_3 \gamma_{34} f_4$
100100000	9	0	$S_1 \gamma_{12} f_2$
100000010	9	0	$S_1 S_2 S_3 \gamma_{14} f_4$
100000000	44	1	$1 - (\lambda_{1l} + \lambda_{1d})$
101010000	11	1	$\phi_1 p_2 \phi_2 p_3 (1 - (\lambda_{3l} + \lambda_{3d}))$
101010000	1	0	$\phi_1 p_2 \phi_2 p_3$
001000100	6	1	$\phi_2 q_3 \phi_3 p_4 (1 - (\lambda_{4l} + \lambda_{4d}))$
001010010	6	0	$\phi_2 p_3 S_3 \gamma_{34} f_4$
000010110	2	0	$\phi_3 p_4 f_4$

permanent emigration, each  $\text{Pr}(h | \text{first capture})$  is easily written, as has been done in Table 2. The full likelihood is then

$$\mathcal{L} = \prod_h \left[ \left\{ \text{Pr}(h | \text{first capture}) \right\}^{X_h} \right].$$

Numerical-based likelihood inference is feasible as the "rules" for constructing  $\text{Pr}(h | \text{first capture})$  can be encoded in a computer program. Technically,  $Y$  enters the model (or likelihood) via the form

$$\text{Pr}(h | \text{first capture}) = \text{Pr}(\text{first to last encounter events of } h | \text{first capture}) \times [\text{Pr}(\text{never encountered again} | \text{final encounter of } h)]^Y$$

This formalism is hardly needed as  $Y = 0$  denotes that the probability is 1 that the bird will never be encountered again.

If the last encounter is a live capture, the form of  $\text{Pr}(h | \text{first capture})$  up to that last occasion,  $j$  (i.e., the first symbolic component above), is well known from capture-recapture theory. The remaining multiplicative component of the probability for that encounter history is  $1 - (\lambda_{jl} + \lambda_{jd})$  if the bird was released, and is 1 otherwise (bird not released). If the last encounter was a ring recovery (hence the bird is dead) the (first component) probability of  $h$  is more complex and we must partition the encounter history into two parts: from the first capture occasion (i) to last live recapture occasion (o); then from that last recapture to the next encounter (j) which is the ring recovery event. Symbolically the probability is  $P_{io} P_{oj}$ . If  $i = o$ , then  $P_{io} = 1$ . For  $o > i$  the probability terms in  $P_{io}$  are just the usual Cormack-Jolly-Seber product  $\phi_i \cdots \phi_{o-1} p_o$ , and the corresponding product of  $p_w$  or  $q_w$  for  $w = i+1$  to  $o-1$ , according to whether capture occurred or not at occasion  $w$ . The second

multiplicative component is

$$\begin{aligned} P_{oj} &= f_o, & , j = 0, \\ &= S_o \cdots S_{j-1} \gamma_{oj} f_j, & , j > 0, \end{aligned}$$

for  $\gamma_{oj}$  as given in (8). Several examples of  $\Pr(h | \text{first capture})$  are in Table 2.

Using this encounter history approach the models for joint analysis of recapture-recovery data can be generalized to include factors such as age, control-treatment, sex, capture-history dependencies, and so forth, such as the models discussed in Lebreton et al. (1992). Also, it is clearly possible to use multinomial models (or explicit estimators) for inference and then construct estimated expected counts for any encounter histories; this is important for some types of model goodness of fit testing. This direct approach of getting  $\Pr(h | \text{first capture})$  is not as convenient for theory development because there are a very large number of histories to consider, much more than  $2^t$  and  $t > 10$  is not uncommon.

## 5. Discussion

The purpose of this paper is to give a form of the correct joint sampling probability distribution for recapture and recovery data arising from the same set of released ringed birds. Moreover, this is herein done mostly in terms of extending the Cormack-Jolly-Seber model for survival estimation to include the ring recoveries, assuming such recoveries would have a marginal probability distribution as in the Brownie et al. (1985) time-specific model  $M_1$ . There are easy extensions or special cases possible for this joint recapture-recovery model, in particular to the use of ring recoveries from years beyond year  $t$ .

If the same ring recovery process continues in years beyond capture occasion  $t$ , then there are also recovery data  $m_{ijd}$  for  $j = t + 1, \dots, k$ . These counts just extend the number of mutually exclusive cells in the underlying multinomial models. The corresponding cell probabilities in model (6) for these extended ring recovery process counts is a generalization of (7):

$$\pi_{ijd} = S_i \cdots S_{t-1} \gamma_{it} S_t \cdots S_{j-1} f_j, \quad , t + 1 \leq j \leq k .$$

Because the live capture process ends at occasion  $t$ , birds are no longer subject to cohort reassignment after occasion  $t$ ; therefore, the role of the  $\gamma_{ij}$ -parameters ends after occasion  $t$ .

These additional ring recovery data (i.e., having  $k > t$ ) can increase the precision of some parameter estimators, such as  $S_i$ ; however, no additional parameters of real interest become identifiable by this extension. Rather, this model extension adds to the parameters the  $k - t$  identifiable *products*  $(S_t f_{t+1})$ ,  $(S_t S_{t+1} f_{t+2})$ , ...,  $(S_t \cdots S_{k-1} f_k)$ .

Other assumptions about the recovery process can be made which lead to different forms for the  $\gamma_{ij}$ , in particular, the assumption that birds are not hunted, but rather recoveries come from birds found dead. The nature of the model then depends on the spatial area and time interval over which rings are found and reported. One restricted case is that only the area in which captures occur is examined for dead birds. This case is further restricted if the searches for dead birds occur only during the time of live capture effort. For such a situation we take  $m_{ijd}$  to be the number of rings recovered at occasion  $i + 1$  from birds ringed at occasion  $i$  and not live captured at occasion  $i + 1$ . In general, now the time interval for recoveries is the limiting case of "time" being  $j - \epsilon$  to  $j$ . Then the survival parameter in (7) is really  $\phi_i$ , not  $S_i$ . Under permanent emigration and the recovery process limited to the capture area and to the capture occasions, (7) becomes

$$\pi_{ijd} = \frac{E(m_{ijd} | R_i)}{R_i} = \begin{cases} \phi_i f_i & , j = i, \\ \phi_i q_{i+1} \cdots \phi_{j-1} q_j \phi_j f_j & , j > i. \end{cases} \quad (11)$$

There are  $3t - 4$  identifiable parameters in this model:  $\phi_1, \dots, \phi_{t-2}, p_2, \dots, p_{t-1}, f_1, \dots, f_{t-2}$  and the products  $(\phi_{t-1} p_t)$  and  $(\phi_{t-1} f_{t-1})$ .

The integrity of the notation is retained in this special case even though a different indexing ( $j+1$  in place of  $j$ ) would make sense and be easier to understand for this case because the counts  $m_{ijd}$  are now actually obtained on occasion  $j+1$ . This shows the difficulty of finding a general, logical notation that would cover all special cases. Note that fidelity is not an estimable parameter in this model.

If we reparameterized (11) to have  $\phi_i f_i = f_i^*$  then (11) is *structurally* identical to (10). Hence, heuristically this case of all dead recoveries being from the capture area on the capture occasions is structurally like the joint model with all  $F_i = 1$ . A conclusion I draw here is that if one caught and released a bird on occasion  $j$  and then found it dead very soon afterwards, that bird could be treated as a loss on (live) capture. However, birds only found dead on occasion  $j$  should not be considered a loss on capture because that will bias the estimators of  $p_i$ . This is because the encounter probabilities are different for live recapture (or resighting) vs. for dead birds.

Closed-form maximum likelihood estimators and their variances do not seem possible for the joint recapture-recovery model under permanent emigration. Nor does it seem possible to get explicit probability distributions for a reduced dimension sufficient, or minimal sufficient, statistic under this assumption. However, under the assumption of random emigration the multiplicative nature of all the cell probabilities  $\pi_{ijd}$  and  $\pi_{ijl}$  allows determination of a full rank minimal sufficient statistic and its distribution and closed-form maximum likelihood estimators and their sampling variances. Those results require far too much space to be given here, but have been derived by the author.

Numerical likelihood-based estimation and inference for joint recapture-recovery data in the model given by (5) or (6) under cell structures given by (2), (7) and (8) is straightforward because this is a standard multinomial-based model. The model can be, for example, implemented in program SURVIV (White, 1983). This has been done recently by Szymczak and Rexstad (1991) for some gadwall (*Anas strepera*) data. Alternatively, the method presented in Burnham (1989) can be implemented using SAS PROC NLIN to achieve convenient and flexible data analysis of joint recapture and recovery data. Also, methods of parsimonious model construction and selection as presented in Lebreton et al. (1992) and Burnham and Anderson (1992) are directly applicable to this extended general model. In fact, Szymczak and Rexstad (1991) used these analysis methods, such as AIC (Akaike, 1985) based model selection, for the gadwall recapture-recovery data; their paper provides the interested reader with an example of this "joint" analysis theory.

The Jolly-Seber model includes components for the estimation of population abundance parameters,  $N_i$ 's and  $B_i$ 's. As shown in Burnham (1991) the additional model component needed is  $\Pr(u_1, \dots, u_t)$ , the probability distribution of the first captures of birds. At first-capture birds are not ringed;  $u_i$  denotes the number of unringed birds caught at occasion  $i$ . All or most of these birds would be ringed and released, hence contribute to  $R_i$ . The  $\Pr(u_1, \dots, u_t)$  is not effected by whether or not there are dead recoveries augmenting the usual live recaptures of the Jolly-Seber model. Also, the sets of random variables  $\{m_{ijd}, m_{ijl} | R_i\}$  and  $\{u_i\}$  are independent, hence the models given here can be extended to include abundance estimation by just including the component for  $\Pr(u_1, \dots, u_t)$  from Burnham (1991) with the recapture-recoveries likelihood. This added theory is too extensive to repeat here.

Basically, however, abundance estimation under the Jolly-Seber model is the same regardless of whether or not any ring recovery data are used.

There are additional theoretical models that should be developed for the joint analysis of recapture-recovery data, in particular extensions to age-specific models. However, I think the most pressing need now is to try the existing (above) theory on a wide variety of adult data to find out if this theory is useful: is the inclusion of recapture data with recovery data (in what are meant to be ring recovery studies) worthwhile, and conversely in recapture studies is the inclusion of any recovery data worthwhile? Calculation of theoretical efficiencies will also be a useful research direction and it could be done using Monte Carlo simulation.

*Acknowledgments.* The author's initial work on this problem (some years ago) produced the results for random emigration and was reviewed by Cavell Brownie who pointed out that those results did not apply under permanent emigration. I thank Dr. Brownie for first noting the form of (8) as being correct for the permanent emigration model and in general for discussions and help on some aspects of this work. Helpful review comments on drafts of this paper were supplied by David Anderson, whose questions caused me to discover and correct several errors, Gary White who reviewed the final draft, allowing me to improve it some more, and an anonymous reviewer, who made some appreciated, helpful comments.

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A CIP catalogue record for this book is available from the Library of Congress,  
Washington D.C., USA

**Deutsche Bibliothek Cataloging-in-Publication Data**

**Marked individuals in the study of bird population** / ed. by J.-D. Lebreton ; Ph. M. North.

– Basel ; Boston ; Berlin : Birkhäuser, 1993

(Advances in life sciences)

ISBN 3-7643-2780-4 (Basel...)

ISBN 0-8176-2780-4 (Boston)

NE: Lebreton, Jean-Dominique [Hrsg.]

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PO. Box 133  
CH-4010 Basel  
Switzerland  
FAX: (+ +41) 61 271 76 66

Camera-ready copy prepared by the authors  
Printed on acid-free paper produced from chlorine-free pulp  
Printed in Germany  
ISBN 3-7643-2780-4  
ISBN 0-8176-2780-4

9 8 7 6 5 4 3 2 1



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Birkhäuser Verlag  
Basel · Boston · Berlin