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A GENERAL APPROACH TO TEMPORARY EMIGRATION IN MARK–RECAPTURE ANALYSIS

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Abstract. During mark–recapture studies of open populations, animals often temporarily emigrate from study areas. Such temporary emigration can cause biased estimates of survival probabilities. We present a new statistical method to estimate survival probability from the capture histories of marked individuals in the presence of temporary emigration. This method uses stage-structured models that include one or more stages representing the individuals that have temporarily emigrated. Although not all parameters can be estimated in such stage structures, some important parameters are still estimable. Here, we determined the estimability of parameter values from the rank of the Jacobian of the likelihood function. We applied the temporary-emigration mark–recapture method to artificial data, representing various life histories and demonstrated consistency between actual and estimated values. As an example, we used the method to analyze data on reproductive female North Atlantic right whales. The method presented in this paper will be especially useful for studies of seabird, sea turtle, and marine-mammal populations where individuals are sampled only on their breeding grounds.

Key words: capture–recapture studies; multi-stage mark–recapture method; North Atlantic right whale; stage-structured models; survival probability; temporary emigration; transition probability.

Introduction

In mark–recapture studies, survival probability is estimated from capture histories of individually identified animals. Those histories contain information on whether or not each individual was captured at each sampling occasion. The analysis assumes that all individuals have identical capture probabilities. This assumption is violated when some individuals temporarily leave the sampling area and return during subsequent sampling occasions. We refer to this as ‘‘temporary emigration.’’ The capture probability of the individuals that have emigrated is zero, whereas the rest of the individuals that are alive have a nonzero capture probability. Therefore, assuming that all individuals have the same capture probability, regardless their location, results in under- and overestimation, respectively, of the capture probability for individuals inside and outside the sampling area. The biased capture probability estimate often biases survival probability estimates.

The temporary-emigration process that we consider in this paper is deterministic; i.e., we assume that all animals in the sampling area emigrate, with probability 1, before the next sampling occasion. This type of temporary-emigration process is common during immature stages and between reproductive events. We refer to these as the ‘‘immature-emigration process’’ and ‘‘inter-birth emigration process,’’ respectively. For example, albatrosses (Diomedeidae spp.) leave their breeding islands immediately after fledging (immature-emigration process) and do not return for 5–15 yr. Once they return, they are recaptured only when they breed (inter-birth emigration process; Weimerskirch et al. 1997). Similarly, grey seals (*Halichoerus grypus*) are marked when young, but cannot be recaptured before they mature (immature-emigration process; Schwarz and Stobo 2000). Right whales (*Eubalaena* sp.) are monitored at their calving ground; they leave this area after reproduction and return at intervals of several years for calving (inter-birth emigration process; Payne et al. 1990). Similarly, sea turtles are often individually identified only at their natal beach when they come back to lay their eggs (inter-birth emigration process).

Deterministic temporary emigration is different from permanent emigration and purely random temporary emigration, which are also common. Permanent emigration occurs when animals leave the sampling area and never come back. In the usual mark–recapture analyses, permanent emigration either is assumed to be a part of mortality as a loss from a population (e.g., Lebreton et al. 1992) or is assumed not to occur (e.g., Fujiwara and Caswell 2001). In purely random temporary emigration, individuals leave and return independently of their location at the previous sampling occasion. This type of temporary emigration occurs commonly when only a part of a habitat is sampled. When mark–recapture methods are applied to a population exhibiting purely random temporary emigration, the estimated capture probability is the product of the probability that individuals are in the sampling area and the probability that individuals within the sam-

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pling area are captured. However, survival probability is not affected by the emigration process (Brownie et al. 1993).

In this paper, we show how to estimate survival probability and other demographic transitions in the presence of deterministic temporary emigration. Our method includes location (temporarily emigrated or not) as a property of the individual, and uses a multi-stage mark–recapture method. Our approach is related to the methods used by Arnason (1972, 1973) and Hestbeck et al. (1991) to estimate movement rates, but applies to populations that exhibit temporary emigration. Because individuals that have emigrated are unobservable, the capture history data usually do not contain enough information to estimate all parameters separately. In order to add necessary information, we introduce constraints among the parameters. These constraints may be based on biologically reasonable models (e.g., that temporary emigration does not influence survival), or may be provided by independent estimates of some parameters from other data sets. The constraints reduce the number of parameters to be estimated and allow us to estimate all of the remaining parameter values separately. The possibility of modeling mark–recapture data with stage structures that contain unobservable stages was suggested by Lebreton (1995). Here, we apply the idea to populations that exhibit the two types of temporary emigration, and we analyze the estimability of parameters. Our results generalize those of Clobert et al. (1994), Lebreton et al. (1999), and Pradel and Lebreton (1999) in that we apply the method to inter-birth temporary emigration, analyze more general cases of immature temporary emigration, and use a formal method to determine estimable parameters.

As usual, estimating stage-specific transition and capture probabilities involves constructing an appropriate stage structure, expressing the likelihood function in terms of the parameters, and finding the best-fit parameter values using maximum likelihood (e.g., Nichols et al. 1992, Fujiwara and Caswell 2002). The likelihood function can be written down directly using Markov chains that specify transition probabilities among stages, assuming independence of fates among individuals, i.e., assuming that the number of outcomes falling into the possible capture history sequences is multinomial (Caswell 2001, Fujiwara and Caswell 2002). This likelihood can be maximized numerically to find the best-fit parameter values. This method allows simple programming using software such as MATLAB (MATLAB 1999). Alternatively, in many but not all cases, parameters can be estimated using software that is specifically designed for mark–recapture analyses, such as MARK (White and Burnham 1999), MSSURVIV (Hines 1994), and SURVIV (White 1983).

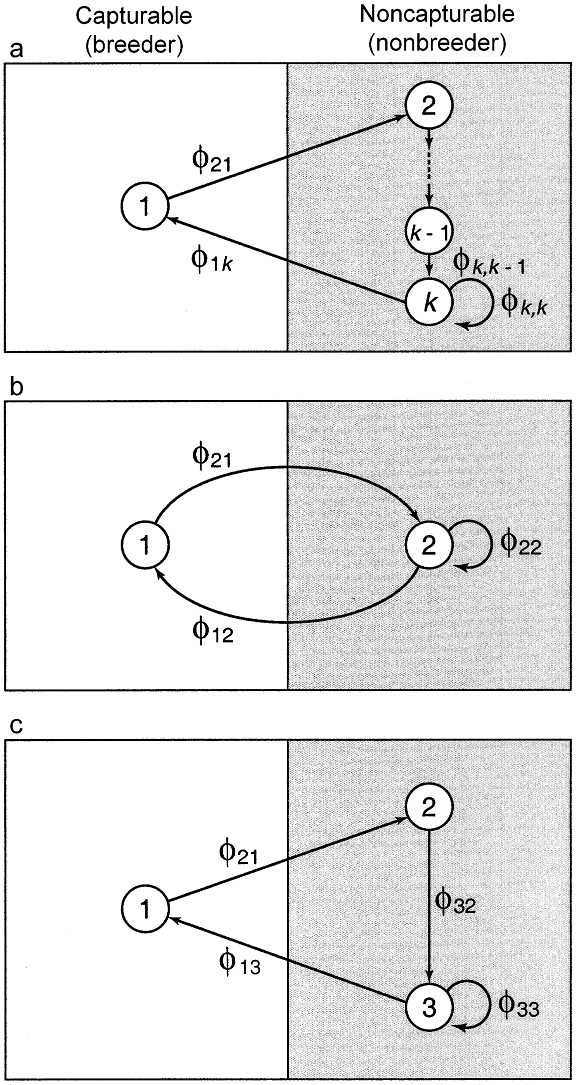

FIG. 1. Interbirth temporary-emigration stage structures. (a) General stage structure. (b) Stage structure with $k = 1$ (this represents the temporary emigration of Wandering Albatross [Models 1.1, 1.2, and 1.3]). (c) Stage structure with $k = 2$ (this represents the temporary emigration of the right whale [Models 2.1, 2.2, and 2.3]). Parameters for these stage structures are ϕ_{ji} (a transition probability from stage i to j) and p_1 (a capture probability of stage 1). Stages other than stage 1 have a zero recapture probability. Arrows indicate transitions from stage i to j with probabilities ϕ_{ji} over time t to $t + 1$. Stage 1 is a breeding adult; stage k is a mature stage. The value of k depends on the minimum inter-birth interval.

TEMPORARY-EMIGRATION STAGE STRUCTURES

Figs. 1 and 2 show examples of life cycle graphs including temporary emigration. Each arrow indicates a possible stage transition from time t to $t + 1$ and has a transition probability associated with it. We denote the transition probability from stage i to j by ϕ_{ji}. It should be noted that the subscripts for the transition probability are reversed from the traditional notation (e.g., Arnason 1973, Hestbeck et al. 1991) so that they indicate the entry in a matrix population model (e.g., Caswell 2001) and the column stochastic transition matrix used in Fujiwara and Caswell (2002). Individuals in a capturable stage have a nonzero probability of being recaptured. This probability is denoted by p_i for stage i.

The stage structure for the inter-birth emigration process (Fig. 1a) includes a breeding adult stage (stage 1) in which individuals can be recaptured with a probability p_1, and $k - 1$ adult stages between breeding events in which individuals cannot be recaptured. The value of k depends on the minimum inter-birth interval. For example, Wandering Albatrosses never breed successfully in two consecutive years (Weimerskirch et al. 1997). Those that give birth in one year will be missing from the breeding ground in the following year. After two years, they return to the breeding ground with some probability that is independent of age. Therefore, $k = 2$ for Wandering Albatross (Fig. 1b). Similarly, individual right whales do not give birth for at least two years after successful reproduction, so $k = 3$ for the right whale (Fig. 1c).

The stage structure for the immature-emigration process (Fig. 2a) contains a newborn stage (stage 0) in which individuals are first captured and marked, $k - 1$ immature stages (stage 1 through $k - 1$) in which individuals cannot be captured due to temporary emigration, and a mature stage (stage k) in which individuals can be captured with a probability p_k. If $k > 1$, the first $k - 1$ stages (i.e., newborn and the first $k - 2$ immature stages) represent individuals that cannot mature before the following sampling period, and these stages also correspond to ages of individuals. Stage $k - 1$ may mature (with probability $\phi_{k,k-1}$), remain immature (with probability $\phi_{k-1,k-1}$), or die (with probability $1 - (\phi_{k-1,k-1} + \phi_{k,k-1})$). For example, grey seals do not give birth before reaching age 4 years (Schwarz and Stobo 2000). Therefore, an appropriate stage structure for them is one with $k = 4$ (Fig. 2b). Similarly, albatrosses do not mature before reaching the age of 5 years (Weimerskirch et al. 1997); therefore, $k = 5$ in their stage structure (Fig. 2c). When $k = 1$, the stage structure does not contain a separate immature stage (i.e., newborn and immature stages are the same), and newborn individuals can mature directly or remain immature. In this stage structure, immature individuals can be marked but cannot be recaptured; therefore, they still exhibit temporary emigration. These stage structures include as special cases the model of Clobert 1994, but relax their assumption of a maximum age in the immature stage.

Other population parameters (e.g., stage-specific survival probabilities, stage-specific probabilities of death, and probabilities of breeding) can be calculated from the ϕ_{ij}. For example, the stage-specific survival probability (s_i) is given by $\Sigma_j\ \phi_{ji}$ and the stage-specific probability of death is given by $1 - \Sigma_j\ \phi_{ji}$. In the immature-emigration model, the breeding probability, conditional on survival of individuals in stage $k - 1$ (we denote this probability by ψ), is

$$\psi = \frac{\phi_{k,k-1}}{\phi_{k,k-1} + \phi_{k-1,k-1}}. \qquad (1)$$

We will show how to calculate some other population indices in the section on right whales. More details can be found in (Caswell 2001).

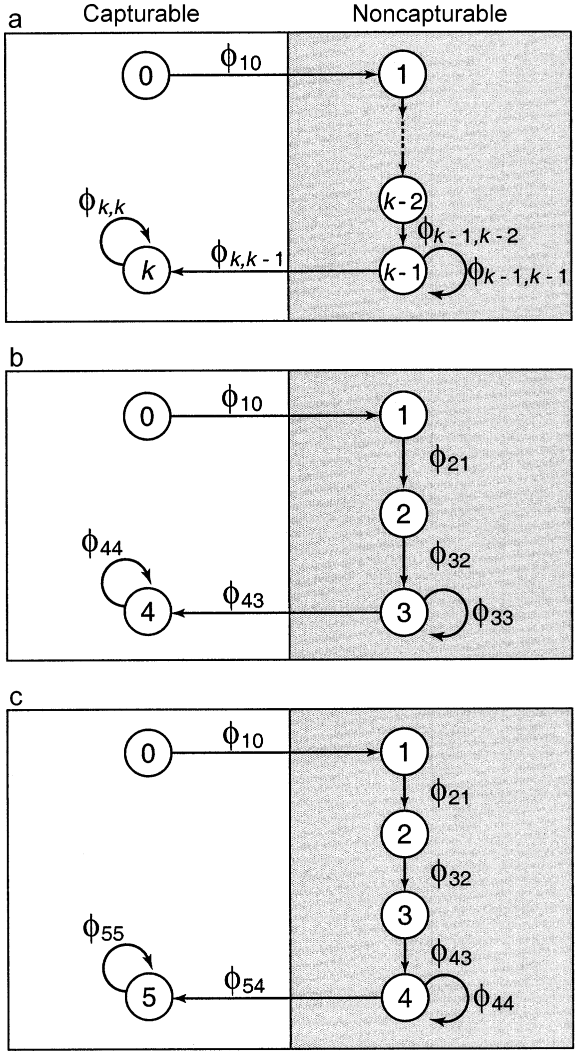

FIG. 2. Immature temporary-emigration stage structure. (a) General stage structure ($k = 0$ is the newborn stage; other stages and transition probabilities are defined in Fig. 1). (b) Stage structure with $k = 4$ (this represents the temporary emigration of the grey seal [Models 3.1, 3.2, 3.3, 3.4, and 3.5]). (c) Stage structure with $k = 5$ (this represents the temporary emigration of Wandering Albatross [Models 4.1, 4.2, 4.3, and 4.4]). Parameters for these stage structures are ϕ_{ji} (the transition probability from stage i to j) and p_k (the recapture probability of the mature stage). Stages other than stage k have a zero recapture probability.

ESTIMABILITY OF PARAMETERS

Unfortunately, some of the parameters in the stage structures for temporary-emigration processes may not be estimable, because of the lack of observations of the emigrated stages. In general, whether best-fit parameter values can be found uniquely or not depends on how the parameters appear in the likelihood function. If two or more parameters are confounded (i.e., they appear only in the same arithmetic form throughout the likelihood function), they cannot be estimated separately. The solution is to impose constraints on the parameters by specifying a model for the relationships among them.

Confounded parameters may result from model specification (intrinsic identifiability problem) or a lack of variation among observed data (extrinsic identifiability problem; McCullagh and Nelder 1989). When parameters are intrinsically confounded, the only way to eliminate the problem is to constrain parameters or modify the stage structure so that other useful parameters can be estimated separately. When parameters are confounded because of lack of variation among observed data, the solution is to constrain parameters, modify the stage structure, or increase the sample size. We will show how to determine whether or not a model has the intrinsic and extrinsic identifiability problems in the next section and give examples in the sections on *Estimable parameters in temporary-emigration models* and *Bias caused by temporary emigration*.

Determining estimability of parameters

Whether parameters are confounded in the likelihood function or not can be determined using the method of Catchpole and Morgan (1997). Their method uses the Jacobian matrix, which contains the derivatives of the likelihood functions with respect to parameters. If the rank of the Jacobian equals the number of parameters, then all parameters can be estimated separately. Here, we give a heuristic description of the method as it applies to temporary-emigration models; for details, see Catchpole and Morgan (1997).

We start with data consisting of capture histories of n individuals. The contribution of individual i to the likelihood function is proportional to the probability of its capture history. Let l_i be this contribution and assume that the model contains m parameters ($x_1, x_2, \ldots, x_m$). Then, l_i is a function of the parameters,

$$l_i = f_i(x_1, x_2, \ldots, x_m). \qquad (2)$$

Taking the partial derivatives of the function l_i with respect to the parameters results in

$$dl_i = \frac{\partial f_i}{\partial x_1}dx_1 + \frac{\partial f_i}{\partial x_2}dx_2 + \cdots + \frac{\partial f_i}{\partial x_m}dx_m. \qquad (3)$$

Because the data consist of n captured individuals, n such functions exist. In a vector notation, they are:

$$d\mathbf{l} = \mathbf{J}d\mathbf{x} \qquad (4)$$

where

$$d\mathbf{l} = (dl_1 \quad dl_2 \quad dl_3 \quad \cdots \quad dl_n)^{\mathsf{T}}$$

$$d\mathbf{x} = (dx_1 \quad dx_2 \quad \cdots \quad dx_m)^{\mathsf{T}}$$

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_m} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_m} \\ \frac{\partial f_3}{\partial x_1} & \frac{\partial f_3}{\partial x_2} & \cdots & \frac{\partial f_3}{\partial x_m} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_m} \end{pmatrix}.$$

Here, **J** is the Jacobian matrix of the likelihood function with respect to the parameters. Eq. 4 is a system of linear equations with **J** as a coefficient matrix. For **x** to be estimated uniquely, the Jacobian matrix must map $d\mathbf{x}$ to $d\mathbf{l}$ uniquely. This requires that the rank of the Jacobian matrix be m (i.e., columns of the Jacobian matrix must be independent). Therefore, if the rank of **J** is equal to the number of parameters, values for the parameters can be estimated separately using the maximum likelihood method. Otherwise, some parameters cannot be estimated separately, and the number of parameters that can be estimated separately is given by the rank of **J**.

If multiple individuals have the same capture history sequence, the likelihoods associated with their capture histories are the same. Therefore, only one such copy needs to be included in the likelihood vector, and the duplicated likelihoods can be eliminated. If we do the analysis assuming that every possible capture history is observed at least once for each stage structure, then this analysis can be used to detect intrinsic identifiability problems. On the other hand, if we use likelihood associated with the available capture history sequences, the analysis can be used to detect extrinsic identifiability problems.

An example of the Jacobian method

As an example, we apply the method just described to the inter-birth emigration model with $k = 2$ (Fig. 1b). We assume that all individuals are marked at the first sampling occasion and that there are four subsequent sampling occasions for recaptures (i.e., five capture occasions). Under these assumptions, there are five possible capture histories:

$$h_1 = 10101 \qquad h_2 = 10100 \qquad h_3 = 10001$$

$$h_4 = 10010 \qquad h_5 = 10000$$

where 1 indicates that an individual was captured and 0 indicates that it was not captured.

TABLE 1. Parameter constraints, number of parameters, and the rank of the Jacobian matrix for the 15 temporary emigration models.

Species and model	Constraints on survival probabilities	Parameters set to known values	No. parameters	Rank of Jacobian
Albatross (Fig. 1b)				
Model 1.1	none	none	4	3
Model 1.2	none	p_1	3	2
Model 1.3†	$\phi_{21} = \phi_{12} + \phi_{22}$	none	3	3
Right whale (Fig. 1c)				
Model 2.1	none	none	5	3
Model 2.2	none	p_1	4	2
Model 2.3†	$\phi_{21} = \phi_{32} = \phi_{13} + \phi_{33}$	none	3	3
Grey seal (Fig. 2b)				
Model 3.1	none	none	6	3
Model 3.2†	$\phi_{10} = \phi_{21} = \phi_{32} = (\phi_{33} + \phi_{43}) = \phi_{44}$	none	3	3
Model 3.3†	$\phi_{10} = \phi_{21} = \phi_{32} = (\phi_{33} + \phi_{43})$	p_4	3	3
Model 3.4†	$\phi_{21} = \phi_{32} = (\phi_{33} + \phi_{43}) = \phi_{44}$	p_4	3	3
Albatross (Fig. 2c)				
Model 4.1	none	none	7	3
Model 4.2†	$\phi_{10} = \phi_{21} = \phi_{32} = \phi_{43} = (\phi_{44} + \phi_{54}) = \phi_{55}$	none	3	3
Model 4.3†	$\phi_{10} = \phi_{21} = \phi_{32} = \phi_{43} = (\phi_{44} + \phi_{54})$	p_5	3	3
Model 4.4†	$\phi_{21} = \phi_{32} = \phi_{43} = (\phi_{44} + \phi_{54}) = \phi_{55}$	p_5	3	3
Model 4.5†	logistic model‡	p_5	3	3

Note: Definitions: ϕ_{ji} is the transition probability from stage i to stage j; p_i is the capture probability for stage i.

† Values of all of the free parameters are estimable.

‡ See Eqs. 10–17.

The likelihood functions corresponding to these capture histories are:

$$l_1 = p_1^2\phi_{21}^2\phi_{12}^2 \tag{5}$$

$$l_2 = p_1\phi_{21}\phi_{12} - p_1^2\phi_{21}^2\phi_{12}^2 \tag{6}$$

$$l_3 = [\phi_{21}^2\phi_{12}(1 - p_1) + \phi_{21}\phi_{22}^2]\phi_{12}p_1 \tag{7}$$

$$l_4 = p_1\phi_{21}\phi_{22}\phi_{12}[\phi_{21} + (1 - \phi_{21})] \tag{8}$$

$$l_5 = 1 - l_1 - l_2 - l_3 - l_4. \tag{9}$$

A likelihood function can be determined by creating a list of event sequences that could lead to the capture history, calculating the probability of the sequences, and then summing the probabilities. For example, h_1 can only arise for an animal that makes the transition back to stage 1 immediately after each observation occasion in stage 2, and is observed on each occasion when it is in stage 1. The corresponding likelihood function (Eq. 5) is simply the product of this unique sequence of transition and recapture probabilities, with some collection of terms. Likelihood functions l_2 through l_4 are more complicated because more than one sequence of events can lead to the observation sequence h_2 through h_4. For example, h_3 could arise from an animal that remained in stage 2 during sampling occasions 2–4 and then made the transition to stage 2 for sampling occasion 5 and was recaptured. However, this sequence could also arise if the animal went through the same stage transitions that produced h_1, but was not recaptured during sampling occasion 3. We calculate l_5 simply as the probability that capture histories h_1 through h_4 do not occur.

There are four parameters (p_1, ϕ_{21}, ϕ_{22}, and ϕ_{12}) and five likelihoods; therefore, the Jacobian is a 5 × 4 matrix. Its rank is the number of independent columns in **J**. The Jacobian and its rank can be found easily using software for symbolic calculations; we used the SYMBOLIC MATH TOOLBOX in MATLAB (MATLAB 1999). The rank of the Jacobian is 3, so only three of the four parameters can be estimated separately; therefore, this model has an intrinsic identifiability problem. This does not necessarily imply that any three parameters can be estimated; we include a discussion on which three parameters can be estimated in the next section.

ESTIMABLE PARAMETERS IN TEMPORARY-EMIGRATION MODELS

To evaluate the estimability of parameters in selected temporary-emigration models, we applied the Jacobian method to 15 models based on the four stage structures in Figs. 1b, c and 2b, c. Table 1 lists the models and also shows (1) constraints on transition probabilities, (2) parameters with values that are assumed to be known, (3) the number of parameters to be estimated, and (4) the rank of the Jacobian matrix. After we impose constraints and eliminte known parameters, all of the remaining parameters become estimable in some models.

Consider the inter-birth emigration model of Wandering Albatross (Fig. 1b; $k = 2$). Adults can be captured on the breeding grounds, but then disappear until they next breed. If no constraints are placed on the parameters (Model 1.1), the rank of the Jacobian is 3, so we can estimate at most only three of the four parameters. However, this does not imply that any three parameters can be estimated. For example, if p_1 is known independently (Model 1.2), the number of parameters is reduced to 3, but the rank of the Jacobian is reduced to 2. On the other hand, we can fit a model that assumes that survival probability of breeding and nonbreeding adults is the same, which implies the constraint $\phi_{21} = \phi_{12} + \phi_{22}$ (Model 1.3). In this model, both the number of parameters and the rank of the Jacobian are 3, indicating that all three parameters can be estimated.

For the inter-birth emigration model of the right whale without constraints (Model 2.1), the rank of the Jacobian is 3, whereas the number of parameters is 5. If we assume that survival probability is unaffected by reproduction ($\phi_{21} = \phi_{32} = \phi_{13} + \phi_{33}$; Model 2.3), both the rank of the Jacobian and the number of parameters become 3, indicating that all of the three remaining parameters (ϕ_{13}, ϕ_{33}, and p_1) can be estimated.

For the immature-emigration model of the grey seal without constraints (Model 3.1), the rank of the Jacobian is 3, whereas the number of parameters is six. While keeping the rank of the Jacobian at 3, we can reduce the number of parameters to three in several ways, depending on assumptions on how mortality varies among the emigrated stages. Here, we show some specific examples. Model 3.2 assumes that survival probabilities of all stages are the same. Under this assumption, the three parameters ϕ_{33}, ϕ_{43}, and p_4 can be estimated separately, which also provides estimates of the survival of other stages (ϕ_{21}, ϕ_{32}, and ϕ_{44}). The next two models use an independent estimate of the capture probability of stage 4 (p_4). This permits estimation of an extra survival probability. For example, Model 3.3 assumes that all immature stages (0, 1, 2, and 3) have the same survival probability, which may differ from that of adults (stage 4). Model 3.4 assumes that the survival of newborn individuals (stage 0) may differ from that of all other stages.

The capture probability p_4 required for Models 3.3 and 3.4 could be obtained using Pollock's robust design (Pollock 1982) if multiple samples of the mature individuals are collected within each primary sampling occasion, or by using a Cormack-Jolly-Seber type mark–recapture method (e.g., Burnham et al. 1987, Lebreton et al. 1992) if capture histories of the mature individuals over multiple sampling occasions are available. The latter method is used by Clobert et al. (1994) to estimate survival probability and age-specific breeding probability. This method also provides a separate survival probability estimate for the mature stage (ϕ_{44}). This survival probability could also be provided in these models, reducing both the number of parameters and the rank of the Jacobian by one.

The situation for the immature temporary-emigration models for Wandering Albatross is the same as the grey seal models. After reducing the number of parameters by assuming that survival probabilities of all stages are the same ($\phi_{21} = \phi_{32} = \phi_{43} = \phi_{44} + \phi_{54} = \phi_{55}$; Model 4.2), we can estimate all remaining parameters (ϕ_{44}, ϕ_{54}, p_5). Alternatively, different distributions of survival probability during temporary emigration can be used. Model 4.3 assumes that survival probability is the same for the first four stages ($\phi_{21} = \phi_{32} = \phi_{43} = \phi_{44} + \phi_{54}$), and a separately estimated capture probability (p_5) is provided. Then we can estimate the remaining three parameters (ϕ_{44}, ϕ_{54}, and ϕ_{55}). Similarly, Model 4.4 assumes that survival probability is the same for the last four stages ($\phi_{32} = \phi_{43} = \phi_{44} + \phi_{54} = \phi_{55}$) and p_5 is provided. Then we can estimate ϕ_{21}, ϕ_{44}, and ϕ_{54} separately. This result suggests that the length of temporary emigration in our immature-emigration model does not change the number and types of parameters that can be estimated.

Another approach to constraining parameters in the immature-temporary-emigration models is to write the survival probability as a parametric function of the stage and estimate the parameters in that function. For example, with the stage structure of Wandering Albatross, we might model the survival probability as a logistic function of age with the last immature stage and mature stage having the same survival probability. In many organisms, survival probability increases with age; therefore, this model may be realistic in many cases. Let s_i be the survival probability of individuals in stage i; then:

$$s_i = \frac{\exp(\gamma + \delta i)}{1 + \exp(\gamma + \delta i)} \quad \text{for } i = 0, \ldots, 4 \tag{10}$$

where γ and δ are intercept and slope parameters. From the survival probability, transition probabilities can be calculated as:

$$\phi_{01} = s_0 \tag{11}$$

$$\phi_{21} = s_1 \tag{12}$$

$$\vdots \tag{13}$$

$$\phi_{43} = s_3 \tag{14}$$

$$\phi_{44} = (1 - \psi)s_4 \tag{15}$$

$$\phi_{54} = \psi s_4 \tag{16}$$

$$\phi_{55} = s_5 \tag{17}$$

where ψ is the probability of transition from stage 4 to stage 5 conditional on survival. If p_5 is known, the rank of the Jacobian is 3, permitting estimation of γ, δ, and ψ separately.

TABLE 2. Actual and mean of estimated parameters for models 1.3, 2.3, 3.4, 4.2, and 4.5.

Model and parameter	Actual value	Mean estimate (1 SD)
Model 1.3		
p_1	0.80	0.79 (0.09)
ϕ_{22}	0.40	0.38 (0.08)
ϕ_{12}	0.50	0.52 (0.08)
Model 2.3		
p_1	0.90	0.90 (0.06)
ϕ_{33}	0.30	0.30 (0.06)
ϕ_{13}	0.60	0.60 (0.05)
Model 3.4		
p_4	0.90	known
ϕ_{10}	0.50	0.50 (0.10)
ϕ_{33}	0.40	0.40 (0.08)
ϕ_{43}	0.50	0.51 (0.08)
Model 4.2		
p_5	0.80	0.80 (0.02)
ϕ_{44}	0.45	0.45 (0.06)
ϕ_{54}	0.50	0.50 (0.06)
Model 4.5		
p_5	0.80	known
γ	1.3863	1.40 (0.36)
δ	0.3895	0.39 (0.13)
ψ	0.4737	0.46 (0.07)

Note: Results are based on simulating 1000 replicate data sets.

BIAS CAUSED BY TEMPORARY EMIGRATION

To examine the bias of the estimates, we applied Models 1.3, 2.3, 3.4, 4.2, and 4.5 (shown in Table 1) to simulated data. Each simulated data set contained 75 individuals marked at the first sampling occasion. For each individual, the stage at the next sampling occasion was selected at random from the possible states (including death), with probabilities given by the column of the transition matrix corresponding to the current stage. An individual in a capturable stage was captured randomly with a probability equal to the capture probability of that stage. For Models 1.3 and 2.3, the data sets consisted of nine resampling occasions; for Models 3.4, 4.2, and 4.5, sequences of 19 resampling occasions were generated.

From the data, we estimated the parameters in the corresponding model. This process was repeated to obtain 1000 sets of parameter estimates. From the same data, we also estimated survival probability under the erroneous assumption that there was no temporary emigration, using the Cormack-Jolly-Seber method (Cormack 1964, Jolly 1965, Seber 1965) with constant survival and capture probabilities.

Table 2 compares the values of parameters that were used to generate data and the means of 1000 estimates for the five models. Biases in both capture probability and transition probability are very small. Model 1.3 performs most poorly, but even here, the survival probability ($\phi_{22} + \phi_{12}$) appears to be without bias. On the other hand, Table 3 compares actual values and the means of 1000 estimates under the false assumption that there was no temporary emigration. Assuming that there was no temporary emigration while there was, in fact, temporary emigration caused overestimations of survival probability for Models 1.3 and 2.3 and underestimations for most stages in Models 3.4 and 4.2, showing that these biases are a serious problem.

In the preceding parameter estimation processes, we were not always able to estimate parameters. Under Models 1.3 and 2.3 with 75 marked individuals, ~14% and 9%, respectively, of the numerical optimization failed to converge. These appear to be primarily caused by extrinsic identifiability problems as repeating the analysis with 150 marked individuals reduced the incidence of nonconvergence to 5% and 1%, respectively.

AN EXAMPLE: THE RIGHT WHALE

As an example, we apply our method to data on the North Atlantic right whale (*Eubalaena glacialis*). This is one of the most endangered mammal populations in

TABLE 3. Estimated capture and survival probabilities wrongly assuming no temporary emigration (simple Cormack-Jolly-Seber model with constant capture and survival probability).

Model and parameter	Actual value	Mean estimate (1 SD)
Model 1.3		
Capture probability (p)	0.80 for stage 1	0.20 (0.02)
Survival probability (s)	0.90	0.94 (0.02)
Model 2.3		
Capture probability (p)	0.90 for stage 1	0.14 (0.01)
Survival probability (s)	0.90	0.98 (0.01)
Model 3.4		
Capture probability (p)	0.90 for stage 4	0.52 (0.05)
Survival probability (s)	0.5 for stage 0; 0.9 for stage > 0	0.83 (0.03)
Model 4.2		
Capture probability (p)	0.80 for stage 5	0.63 ($<$0.01)
Survival probability (s)	0.95	0.72 ($<$0.01)

Notes: Data were generated assuming models 1.3, 2.3, 3.4, and 4.2. Results are based on simulating 1000 replicate data sets.

the world, currently consisting of fewer than 300 individuals. There is evidence to suggest that this number is in slow decline because of declining survival probability (Caswell et al. 1999, Fujiwara and Caswell 2001). Right whales are found along the east coast of the United States. In summer, they feed in the northwest Atlantic, including Massachusetts Bay, Great South Channel, Bay of Fundy, and Brown's Bank. In winter, some females migrate to the coast of Florida and Georgia for calving. Their inter-birth interval is 3–5 yr.

The capture-history data that we use here are based on photographs taken by members of the North Atlantic right whale consortium during annual surveys along the east coast of the United States. Because right whales have unique markings called callosity patterns on their heads, individuals can be identified from photographs. Based on these photographs, the New England Aquarium has been accumulating capture history data of individuals since 1980. Here, we use only sightings of mothers (i.e., females with their calf). We consider individuals to have been marked on the occasion of their first identification as mothers, and to have been recaptured when they were resighted with a calf during a subsequent year. If the data had actually been collected in this way, females would exhibit an inter-birth temporary emigration with an interval of at least three years. This corresponds to the data structure in the ongoing study of southern right whales (*Eubalaena australis*) in their breeding ground off Peninsula Valdes, Argentina (Payne et al. 1990).

We use the stage structure shown in Fig. 1c. This stage structure is consistent with the fact that right whales do not give birth for at least two years after successful reproduction. Because previous analyses have detected time variation in survival and transition probabilities (Caswell et al. 1999, Fujiwara and Caswell 2001), we divided the data into two periods, 1980–1988 ($t = 1$) and 1989–1997 ($t = 2$). Transition and survival probabilities are assumed to be constant within each period. We further assume that the survival probabilities are the same for all stages (Model 2.3). The Jacobian indicates that this model, given the available data, is identifiable. Because individuals in stage 3 have three possible fates (remaining in stage 3, moving to stage 1, and death), the probability of which must sum to 1, the transition probabilities (ϕ_{13} and ϕ_{33}) in each period ($t = 1, 2$) were modeled with polychotomous logistic equations:

$$\phi_{13}^{(t)} = \frac{\exp(\alpha_t)}{1 + \exp(\alpha_t) + \exp(\beta_t)} \tag{18}$$

$$\phi_{33}^{(t)} = \frac{\exp(\beta_t)}{1 + \exp(\alpha_t) + \exp(\beta_t)} \tag{19}$$

where α_t and β_t are the parameters to be estimated. Because the model assumes that survival probabilities of all stages are the same, $\phi_{21}^{(t)} = \phi_{32}^{(t)} = \phi_{13}^{(t)} + \phi_{33}^{(t)}$. We expressed the likelihood associated with the data using the method of Fujiwara and Caswell (2002), and the negative log of the likelihood was numerically minimized using MATLAB function "fminu()" to estimate the six parameters (p_1, p_2, α_1, α_2, β_1, and β_2).

To compare the estimated parameters between the two periods, in terms of demographic context, we calculated survival probability as:

$$s^{(t)} = \phi_{13}^{(t)} + \phi_{33}^{(t)}. \tag{20}$$

We also calculated the number of reproductive events, based on Markov chain theory:

$$\hat{\mathbf{R}}^{(t)} = \mathbf{F}(\mathbf{I} - \hat{\mathbf{A}}^{(t)})^{-1} \tag{21}$$

where

$$\hat{\mathbf{A}}^{(t)} = \begin{pmatrix} \hat{\phi}_{13}^{(t)} & 0 & 0 \\ \hat{\phi}_{21}^{(t)} & 0 & 0 \\ 0 & \hat{\phi}_{32}^{(t)} & \hat{\phi}_{33}^{(t)} \end{pmatrix} \tag{22}$$

$$\mathbf{F} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \tag{23}$$

and $\mathbf{I}$ is the identity matrix. The value r_{11} gives the expected number of future reproductive events from a female that has just given a birth. More details of this calculation can be found in Caswell (2001: Chapter 5).

Fig. 3 compares survival probability and the expected number of reproductive events between the two periods. Error bars in the figures are point-wise 95% CIS based on a parametric bootstrap sampling procedure. We drew bootstrap samples of the four parameters $\hat{\alpha}^{(1)}$, $\hat{\alpha}^{(2)}$, $\hat{\beta}^{(1)}$, and $\hat{\beta}^{(2)}$ from a multivariate normal distribution, with mean vector equal to the maximum likelihood estimates and covariance matrix calculated from the inverse of the last Hessian matrix obtained during model fitting. We generated 1000 bootstrap samples and, for each bootstrap sample of the parameters, the survival probabilities and expected number of reproductive events were calculated. The 95% confidence intervals for these parameters were defined by the 2.5 and 97.5 percentiles of the simulated distributions.

As expected, Fig. 3 shows wide confidence intervals for survival and reproductive events because of the small sample size. However, the results suggest that both survival and the expected number of reproductive events have declined. This result is consistent with the previous finding in Fujiwara and Caswell (2001), although the declines revealed by the analysis of the full data set are greater than those found here.

DISCUSSION

Temporary emigration causes an extreme case of heterogeneity in capture probability. Temporarily emigrated individuals have zero capture probability, whereas the rest of the individuals have a nonzero capture probability. Ignoring temporary emigration when it exists leads to biased estimates of survival proba-

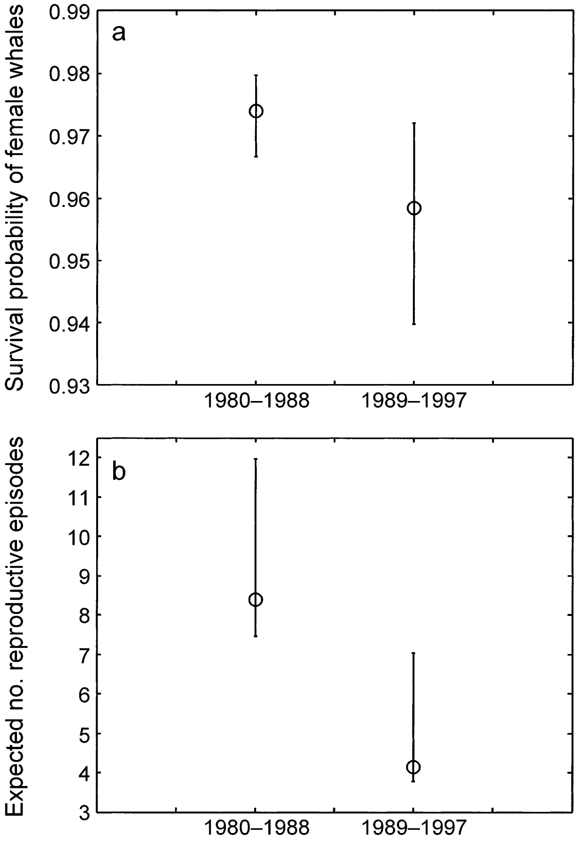

FIG. 3. Analyses of North Atlantic right whale data. (a) Survival probability of females that previously have given birth at least once during periods between 1980 and 1988 and between 1989 and 1997. (b) Expected number of future reproductions during the lifetime of females that have given birth at least once. Error bars indicate 95% confidence intervals.

bility. By explicitly modeling the emigration process, the method presented in this paper eliminates this bias.

The temporary-emigration problem is often encountered in sampling large animals such as seabirds, sea turtles, and marine mammals. When the same problem is encountered with smaller organisms such as fish or insects, researchers may be able to eliminate the temporary-emigration problem by experimental manipulation. For example, it has been suggested that when organisms can be marked and released into unobservable stages in the inter-birth temporary-emigration stage structures (e.g., Models 3.1 and 4.1), all of the parameters may be estimated separately (G. White, *personal communication*). In such cases, the methods outlined here to determine the estimability of parameters are still useful.

Our results are complementary to the approach of Kendall et al. (1997) and Kendall (1999), who use Pollock's (1982) robust design method to deal with temporary emigration. In their method, a closed-population model is used to estimate capture probabilities, which are incorporated into an open-population model to estimate survival probabilities. This method has an advantage over our method in that it permits estimation of survival probabilities that vary freely from one sampling occasion to the next. The robust design method, however, requires multiple secondary samplings within each primary sampling period in order to obtain information on the capture probability. The method presented here does not require secondary sampling, although it can be combined with the robust design method when such samples are available.

In this paper, we focused on two stage structures, representing two different emigration processes, and considered only selected constraints on the parameters. We emphasize that the method can be applied to any biologically interesting age- or stage-classified life cycle, with any pattern of observed and unobserved stages. Each such structure may admit several choices for constraining parameters to make estimation possible. Choosing biologically relevant constraints is part of the data analysis process. We are certain that many useful stage structures and parameter constraints exist and are yet to be discovered.

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LITERATURE CITED

Arnason, A. 1972. Parameter estimates from mark–recapture experiments on two populations subject to migration and death. Research on Population Ecology **13**:97–113.

Arnason, A. M. 1973. The estimation of population size, migration rates, and survival in a stratified population. Research in Population Ecology **15**:1–8.

Brownie, C., J. E. Hines, J. D. Nichols, K. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics **49**: 1173–1187.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Maryland, Monograph 5.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H., M. Fujiwara, and S. Brault. 1999. Declining survival probability threatens the North Atlantic right whale. Proceedings of the National Academy of Sciences (USA) **96**:3308–3313.

Catchpole, E., and B. Morgan. 1997. Detecting parameter redundancy. Biometrika **84**:187–196.

Clobert, J., J. Lebreton, D. Allainé, and J. Gaillard. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. Biometrics **50**:375–387.

Cormack, R. 1964. Estimates of survival from the sighting of marked animals. Biometrika **51**:429–438.

Fujiwara, M, and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. Nature **414**:537–541.

Fujiwara, M. and H. Caswell. 2002. Estimating population projection matrices from multi-stage mark–recapture data. Ecology **83**:3257–3265.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. Ecology **72**:523–533.

Hines, J. 1994. MSSURVIV user's manual. National Biological Service, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Jolly, G. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. Biometrika **52**:225–247.

Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology **80**:2517–2525.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology **78**:563–578.

Lebreton, J.-D. 1995. The future of population dynamic studies using marked individuals: a statistician's perspective. Journal of Applied Statistics **22**:1009–1030.

Lebreton, J., T. Almeras, and R. Pradel. 1999. Competing events, mixture of information and multistratum recapture models. Bird Study **46**(Supplement):S39–46.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. Ecological Monographs **62**:67–118.

MATLAB. 1999. MATLAB version 5.3, release 11. MathWorks, Natick, Massachusetts, USA.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Monographs on Statistics and Applied Probability 37. Second edition. CRC Press, Boca Raton, Florida, USA.

Nichols, J. D., J. R. Sauer, K. H. Pollock, and J. B. Hestbeck. 1992. Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. Ecology **73**:306–312.

Payne, R., V. Rowntree, J. S. Perkins, J. G. Cooke, K. Lankester, P. S. Hammond, and S. A. Mizroch. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. Pages 271–278 *in* G. P. Donovan, editor. Conference Symposium and Workshop on Individual Recognition and the Estimation of Cetacean Population Parameters. Report of the International Whaling Commission (Special Issue), Number 12. International Whaling Commission, La Jolla, California, USA.

Pollock, K. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management **46**:757–760.

Pradel, R., and J. Lebreton. 1999. Comparison of different approaches to the study of local recruitment of breeders. Bird Study **46**(Supplement):74–81.

Schwarz, C., and W. Stobo. 2000. Estimation of juvenile survival, adult survival, and age-specific pupping probabilities for the female grey seal (*Halichoerus gryprus*) on Sable Island from capture–recapture data. Canadian Journal of Fisheries and Aquatic Sciences **57**:247–253.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika **52**:249–259.

Weimerskirch, H., N. Brothers, and P. Jouventin. 1997. Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-time fisheries: conservation implications. Biological Conservation **79**:257–270.

White, G. C. 1983. Numerical estimation of survival rates from band recovery and biotelemetry data. Journal of Wildlife Management **47**:716–728.

White, G., and K. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study **46**(Supplement):120–138.