Approaches for the direct estimation of u , and demographic contributions to u , using capture-recapture data

James D. Nichols & James E. Hines

Approaches for the direct estimation of λ, and demographic contributions to λ, using capture-recapture data

JAMES D. NICHOLS & JAMES E. HINES, *US Geological Survey, Patuxent Wildlife Research Center, MD, USA*

ABSTRACT *We first consider the estimation of the finite rate of population increase or population growth rate, λ_i, using capture-recapture data from open populations. We review estimation and modelling of λ_i under three main approaches to modelling open-population data: the classic approach of Jolly (1965) and Seber (1965), the superpopulation approach of Crosbie & Manly (1985) and Schwarz & Arnason (1996), and the temporal symmetry approach of Pradel (1996). Next, we consider the contributions of different demographic components to λ_i using a probabilistic approach based on the composition of the population at time $i+1$ (Nichols et al., 2000b). The parameters of interest are identical to the seniority parameters, γ_i, of Pradel (1996). We review estimation of γ_i under the classic, superpopulation, and temporal symmetry approaches. We then compare these direct estimation approaches for λ_i and γ_i with analogues computed using projection matrix asymptotics. We also discuss various extensions of the estimation approaches to multistate applications and to joint likelihoods involving multiple data types.*

1 Introduction

Population size (N_i at time i) is the state variable of interest in most management and conservation programmes designed for animal populations. The expected rate of change in this state variable ($\lambda_i = E(N_{i+1}/N_i)$) is an important metric for judging population 'health' and assessing effects of management actions. A related topic is the relative contribution of different components of the population, or of different vital rates associated with these components, to population growth. Metrics reflecting such contributions can be useful in focusing investigative efforts and

Correspondence: J. D. Nichols, US Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, 20708-4017, USA.

management actions on components likely to produce the largest influence on population change. In this paper, we first discuss recently developed approaches for estimating λ_i and contributions to λ_i, from capture-recapture data. We then discuss the broader question of how these direct estimation approaches relate to other approaches designed to provide similar kinds of inferences. We also discuss the potential for combining these estimation approaches for capture-recapture data with other data sources in order to obtain better estimates and address interesting population-dynamic questions.

2 Estimation of λ_i

There are multiple, equivalent ways to write the likelihood for open model capture-recapture data (e.g. Williams *et al.*, in press), and these approaches differ in their treatment of abundance, N_i, and hence in the estimation of rate of change in abundance, λ_i. Here, we discuss estimation of λ_i under three general approaches to modelling capture-recapture data from open populations. We will devote most space to the temporal symmetry approach of Pradel (1996) that readily permits direct modelling of λ_i and is implemented in available computer software (White & Burnham, 1999). We focus on single-age populations at a single study location and note extensions in Section 4. Throughout this paper, we will view abundance, N_i, as a random variable determined by stochastic demographic processes. Although it is reasonable to consider both realized and expected population growth rate, here we will define λ_i as the expected rate of population growth, $\lambda_i = E(N_{i+1}/N_i)$.

2.1 *Jolly-Seber and robust design approaches*

Ever since the publication of the classic papers by Jolly (1965) and Seber (1965), it has been clear that λ_i can be estimated from capture-recapture data on open populations. Jolly (1965) and Seber (1965) showed how to estimate abundances N_2 through N_{K-1} for a K-period capture-recapture study. Population growth rate between successive periods can then be estimated as:

$$\hat{\lambda}_i = \frac{\hat{N}_{i+1}}{\hat{N}_i} \qquad i = 2, \ldots, K - 2 \tag{1}$$

where the $\hat{N}_i$ are the Jolly-Seber estimates for abundance. If Pollock's robust design is implemented (Pollock, 1982; Pollock *et al.*, 1990), with l_i secondary capture periods within each primary period, i, then closed-model estimators (e.g. Otis *et al.*, 1978) can be used to estimate N_i within each primary period. These closed-model estimates can be used in conjunction with equation (1) to estimate λ_i for periods $i = 1, \ldots, K - 1$.

The capture-recapture model developed by Jolly (1965) and Seber (1965) is parameterized only with survival, φ_i, and capture, p_i, probabilities. Abundance, N_i, and new recruits, B_i, are treated as unknown random variables to be estimated. The following assumptions typically are listed for the Jolly-Seber model (e.g. Seber, 1982; Pollock *et al.*, 1990) and are required for reasonable estimates of abundance, N_i, and thus λ_i.

(1) Every animal (marked and unmarked) present in the population at sampling period i has the same probability p_i of being captured or sighted.

(2) Every marked animal present in the population immediately following the sampling in period i has the same probability φ_i of survival until sampling period $i + 1$.

(3) Marks are neither lost nor overlooked, and are recorded correctly.

(4) Sampling periods are instantaneous (in reality they are very short periods) and recaptured animals are released immediately.

(5) All emigration from the sampled area is permanent.

(6) The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

Discussion of the consequences of violating these assumptions for Jolly-Seber estimates can be found in various sources (e.g. Seber, 1982; Pollock *et al.*, 1990; Williams *et al.*, in press).

2.2 Superpopulation approach

The superpopulation approach (Crosbie & Manly, 1985; Schwarz & Arnason, 1996) to modelling capture-recapture data from open populations focuses on a parameter, N, denoting the total number of animals that are ever available for capture in the population of interest over the course of the study (it includes any animal available for capture at any sampling period, 1 through K). An alternative definition of superpopulation includes any animal that was a member of the sampled population during the course of the study, regardless of whether or not it was available on any sampling occasion. In terms of quantities defined by Jolly (1965) and Seber (1965, 1982), and using our initial definition of superpopulation, N can be written as:

$$N = \sum_{i=0}^{k-1} B_i \tag{2}$$

where B_i is defined as the number of new animals in the population at sampling period $i + 1$ that were not present in the population at i, with $B_0 = N_1$ (i.e. all animals in the population the first sampling period are 'new' with respect to sampling). The random variables B_i are viewed as following a multinomial distribution (see Schwarz & Arnason, 1996), with the members of the superpopulation entering the sampled population at the different sampling periods according to entry parameters, β_i; i.e. $\{B_0, \ldots, B_{K-1}\}$ is distributed as a multinomial with parameters $(N; \beta_0, \ldots, \beta_{k-1})$, where $\Sigma_{i=0}^{k-1} \beta_i = 1$.

Define per capita survival and recruitment rates as follows:

φ_i = survival probability, the probability that an animal alive at sampling period i is still alive and in the population at sampling period $i + 1$;

f_i = per capita recruitment rate, the expected number of new animals in the population at time $i + 1$ per animal in the population at time i ($f_i = E(B_i/N_i)$).

The likelihood used by Schwarz & Arnason (1996) for the superpopulation approach contains as parameters survival probabilities, φ_i, capture probabilities, p_i, and the entry probabilities, β_i. In the following development for estimation of λ_i, we assume the simple case of no losses on capture, for ease of presentation. The

per capita recruitment rate, f_i, is not a parameter of the superpopulation likelihood, but can be written in terms of these parameters as (Schwarz, 2001):

$$f_i = \frac{\beta_i}{\sum_{j=0}^{i-1}\left[\beta_j \prod_{l=j+1}^{i-1} \varphi_l \right]}. \tag{3}$$

The numerator of equation (3) is simply the probability that a member of N enters the sampled population between times i and $i+1$ and is available for capture at $i+1$. The denominator reflects the probability that a member of N was alive and in the population in period i.

The expected value for abundance at sampling period $i+1$, conditional on abundance at time i, can be written as:

$$E(N_{i+1}|N_i) = N_i(\varphi_i + f_i). \tag{4}$$

Equation (4) simply defines the expected population size in sampling period $i+1$ as the sum of expected survivors and new recruits, written as the product of abundance and the sum of survival probability and recruitment rate. Equation (4) can be rearranged, and population growth rate written as follows:

$$\lambda_i = \varphi_i + f_i. \tag{5}$$

Equation (5) expresses expected population growth rate intuitively, as the sum of survival and recruitment rates. Note that φ_i has been defined as a survival probability, and f_i as an expected recruitment rate; hence their sum equals the expected population growth rate. However, it is also true that the sum of the actual fraction of animals surviving from i to $i+1$ and the realized recruitment rate, B_i/N_i, equals the realized population growth rate.

Regarding estimation, the φ_i and β_i are estimated numerically using maximum likelihood (Schwarz & Arnason, 1996), and the f_i can then be estimated by substituting the $\hat{\beta}_i$ and $\hat{\phi}_i$ into equation (3). Estimates of φ_i and f_i are then substituted into equation (5) to estimate λ_i. The full, time-specific model (φ_i, p_i, β_i) presents identifiability problems that must be overcome through constraints such as $p_1 = p_K = 1$, or perhaps $p_1 = p_2, p_{K-1} = p_K$ (see Schwarz & Arnason, 1996). Estimation under superpopulation models is accomplished using POPAN5 (Arnason & Schwarz, 1999).

All the assumptions required under the Jolly-Seber model (Section 2.1) are required by the superpopulation approach as well. The primary distinction between the Jolly-Seber and superpopulation approaches to modelling involves the unmarked animals that are caught during the study. The new parameters required under the superpopulation approach are the entry probabilities, β_i, i.e. the probabilities that members of the superpopulation are unavailable for capture (e.g. not previously present on the study area) until after sampling period i, and then enter the study population and are exposed to sampling efforts at period $i+1$. The multinomial modelling assumes homogeneity of these entry probabilities. Thus, all members of the superpopulation N that have not yet become available for potential capture as of sampling period $i-1$, are assumed to exhibit the same probability of being in the group of animals exposed to sampling efforts at period i.

2.3 Pradel's temporal symmetry approach

2.3.1 Reverse-time modelling. Survival rate estimation under capture-recapture models for open populations such as the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) proceeds by conditioning on releases in earlier time periods and following the fates of these animals in later time periods. Pollock *et al.* (1974) noted that if the capture history data are considered in reverse time order, conditioning on animals caught in later time periods and observing their captures in earlier occasions, then inference can be made about the recruitment process. Specifically, 'a backward process with recruitment and no mortality is statistically equivalent to a forward process with mortality and no recruitment' (Pollock *et al.*, 1974, pp. 85-86). This reverse-time approach was used by Nichols *et al.* (1986) and then developed independently by Pradel (1996), who also developed a full likelihood that simultaneously incorporates survival and recruitment parameters and thus permits the direct modelling of population dynamics.

The standard, CJS approach to modelling capture-history data is based on survival (φ_i) and capture (p_i) probability parameters. In addition, define χ_i parameters that specify the probability that an animal alive and in the study population just following sampling period i is not caught or observed again at any sampling period after period i. For a K-period study, $\chi_K = 1$ and values for other sampling periods ($i < K$) can be computed recursively as functions of the survival and capture probability parameters:

$$\chi_i = (1 - \varphi_i) + \varphi_i(1 - p_{i+1})\chi_{i+1}.$$

Consider the probability associated with the capture history 011010, indicating capture in periods 2, 3, and 5 of a 6-period study:

$$Pr\{011010 | \text{release at period } 2\} = \varphi_2 p_3 \varphi_3 (1 - p_4)\varphi_4 p_5 \chi_5.$$

The statistical model for this history requires conditioning on the initial capture in sampling period 2, and then proceeds by modelling the events in the remainder of the capture history.

The conditional, reverse-time models of Pradel (1996) require the following parameters:

- γ_i the probability that an animal present just before sampling occasion i was present in the sampled population just after sampling at occasion $i - 1$;
- p_i' the probability that an animal present just after sampling at time i was captured at i;
- ξ_i the probability of not being seen at sampling periods before i for an animal present immediately before i.

The γ_i, p_i', ξ_i are the reverse-time analogue of the φ_i, p_i, χ_i used in standard CJS modelling. As with the forward-time χ_i, the reverse-time ξ_i can be computed recursively, as

$$\xi_i = (1 - \gamma_i) + \gamma_i(1 - p_{i-1}')\xi_{i-1}$$

for $i = 2, \ldots, K$, and $\xi_1 = 1$. Again consider history 011010. For reverse-time modelling, we condition on the final capture and model prior events in the capture history:

$$Pr\{011010 | \text{last capture at period } 5\} = \gamma_5(1 - p_4')\gamma_4 p_3' \gamma_3 p_2' \xi_2.$$

The temporal symmetry models of Pradel (1996) essentially use both forward- and reverse-time modelling simultaneously (see below).

The parameter definitions above make reference to times just before and just after sampling, as this separation becomes important for the modelling when there are losses on capture. Define N_i^- and N_i^+ respectively as abundance just before and after sampling period i. Defining d_i as the number of animals that are caught at i and not released back into the population following sampling, we can write $N_i^+ = N_i^- - d_i$. We denote as η_i the probability that an animal captured in period i survives trapping and handling and is released back into the population.

The need for different capture probability parameters for forward-time (p_i) and reverse-time (p_i') modelling also stems from losses on capture. The simultaneous use of reverse-time and forward-time modelling requires a relationship between the two capture probability parameters (Focusing on the capture probability for forward-time modelling, the relationship between N_i^- and N_i^+ can be written as:

$$N_i^+ = N_i^-[1 - p_i(1 - \eta_i)]. \tag{6}$$

Equation (6) simply indicates that a member of N_i^- must survive the possibility of being caught and removed from the population in order to become a member of N_i^+. Thus, the probability that a member of N_i^+ was captured in sampling period i is

$$p_i' = \frac{p_i\eta_i}{1 - p_i(1 - \eta_i)}$$

Note that when all animals are released following capture ($\eta_i = 1$), the forward- and reverse-time capture probabilities are equal, $p_i' = p_i$.

2.3.2 Temporal symmetry models: development. Simultaneous forward-time and reverse-time modelling proceeds by conditioning on the number of animals in the population at the initiation of the study, $N_1^- = B_0$. The expected number of animals in the population at later times is determined by considering the rate of population growth between successive sampling occasions. Expressions for population growth rate can be obtained by considering two alternative ways of writing the expected number of animals alive in two successive sampling occasions. Based on forward-time and reverse-time model we can write this expectation as $N_i^+\varphi_i = N_{i+1}^-\gamma_{i+1}$. Solving this approximate equality yields an expression for population growth rate:

$$\lambda_i = E(N_{i+1}^-/N_i^+) \approx \varphi_i/\gamma_{i+1}. \tag{7}$$

Equation (7) is relevant to biological changes in the population, but does not account for animals that are captured and not released back into the population. To account for animals not released, we can write the expectation for a modified rate of population change (λ_i') that also incorporates losses of animals during sampling:

$$\lambda_i' = E(N_{i+1}^-/N_i^-) \approx \lambda_i E(N_i^+/N_i^-) \approx \frac{\varphi_i(1 - p_i[1 - \eta_i])}{\gamma_{i+1}}. \tag{8}$$

The λ_i of equation (7) thus reflects the growth rate that would presumably have occurred in the absence of sampling (and associated trap mortality), whereas the λ_i' defined in equation (8) reflects the expected growth in the presence of sampling and trap mortality.

The expected number of animals exhibiting capture history 011010 under Pradel's (1996) temporal symmetry model can now be written as:

$$E(x_{011010}|N_1^-) = N_1^- \lambda_1' \xi_2 p_2 \eta_2 \varphi_2 p_3 \eta_3 \varphi_3 (1 - p_4) \varphi_4 p_5 \eta_5 \chi_5 \tag{9}$$

The term, $N_1^- \lambda_1'$ gives the expected number of animals in the population just before sampling period 2, and ξ_2 is the probability that an animal in this group was not caught prior to sampling period 2 (i.e. was not caught at 1). The animals exhibiting this history were caught at period 2, and the associated probability is p_2. They survived the sampling of period 2 to be released again (we know this because they were seen in subsequent periods), and the probability associated with surviving sampling is η_2. The subsequent (for sample periods > 2) modelling is similar to that of the CJS model (e.g. Lebreton *et al.*, 1992), except that survival probabilities for the sampling process now are incorporated into the model. Thus, every capture event requires both a capture probability p_i, and a probability η_i, of surviving the sampling process.

Equation (9) does not lead directly to a probability distribution, because the expectation contains the initial population size, N_1^-, an unknown random variable. Let x_h be the number of animals exhibiting capture history h, and M denote the total number of animals caught in the entire study:

$$M = \sum_h x_h.$$

The expected number of animals caught during a study can be written as the sum of the expected number of animals seen for the first time at each sampling occasion:

$$E(M) = \sum_{i=1}^{K} \xi_i N_i^- p_i$$

$$= N_1^- \sum_{i=1}^{K} \xi_i p_i \left(\prod_{j=1}^{i-1} \lambda_j' \right). \tag{10}$$

Finally, the conditional probability (conditioned on the total M of animals caught) associated with a particular capture history (denote as $P(h)$) can be obtained by dividing the expected number of animals with that history (e.g. as in equation (9)) by the expected number of total individual animals caught during the study (as in equation (10)):

$$P(h) = \frac{E(x_h)}{E(M)}. \tag{11}$$

From equations (9) and (10) the initial population sizes in the numerator and denominator of equation (11) cancel, leaving the conditional probabilities of interest expressed in terms of estimable model parameters. Then the likelihood L for the set of animals observed in a study can be written generally as the product of the conditional probabilities associated with all the individual capture histories:

$$L = \prod_h P(h)^{x_h}. \tag{12}$$

Pradel (1996) rewrites this likelihood in more detail in terms of the model parameters and sufficient statistics.

2.3.3 Temporal symmetry models: alternative parameterizations. Pradel (1996) suggested three different parameterizations for the above likelihood, each of which might be useful in addressing specific questions, and all of which retain capture (p_i) and survival (φ_i) probabilities. Of these, we believe that the most natural parameterization incorporates the reverse-time parameters γ_i. Thus, equation (8) is substituted into the capture history expectations (equations (9) and (10)), so that all probabilities (P_h) are written in terms of p_i, φ_i and γ_i.

A second parameterization uses population growth rate λ_i as a model parameter. Based on the definition in equation (7), the following expression is substituted for the γ_i of the original parameterization:

$$\gamma_i = \frac{\varphi_{i-1}}{\lambda_{i-1}}. \tag{13}$$

A third parameterization is based on a measure f_i of recruitment rate, defined above as the expected number of recruits to the population at time $i+1$ per animal present in the population at i. Substituting expression (5) into equation (13), it is seen that a model with f_i can be obtained by substituting

$$\gamma_i = \frac{\varphi_{i-1}}{\varphi_{i-1}+f_{i-1}} \tag{14}$$

for γ_i of the original parameterization.

Maximum likelihood estimates can be obtained for the likelihood of equation (12), or its analogue based on sufficient statistics (Pradel, 1996). In Pradel's (1996) initial implementation of this model, he used a logit transform for φ_i and γ_i as a means of constraining these parameters to the interval [0, 1]. For the λ_i parameterization, Pradel (1996) used a log transform for population growth rate (λ_i), in order to constrain it to be positive. All three parameterizations ($[\varphi_t, p_t, \gamma_t]$, $[\varphi_t, p_t, \lambda_t]$, $[\varphi_t, p_t, f_t]$, where t denotes time-specificity) described above have been implemented in program MARK (White & Burnham, 1999). The implementation in MARK appears to provide approximately unbiased estimates for the case of no losses on capture, but not for the case of losses on capture. The magnitude of the bias is a function of magnitude of η_i, the probability of surviving trap mortality, and if this probability is very high, then the estimates provided by MARK will not exhibit large bias (Hines & Nichols, this issue). The GAUSS program written by Hines and described by Pradel (1996) does provide approximately unbiased estimates of λ_i and λ_i' for the full temporal symmetry model even when there are losses on capture.

Pradel's temporal symmetry models are relatively new and have seen only limited use. It appears that the numerical optimization algorithms may sometimes perform better (e.g. fewer convergence problems) with the γ-parameterization than with the other two parameterizations.

If primary interest is in population growth rate, it may be reasonable to fit model (φ_t, p_t, γ_t) to data, and then estimate population growth rate by substitution using equation (7) or (8). This estimator (7) is also computed in program MARK (White & Burnham, 1999). The parameter f_i can be estimated in a similar manner, based

on estimates from model $(\varphi_t, p_t, \gamma_t)$ and a rearrangement of equation (14):

$$\hat{f}_i = \frac{\hat{\varphi}_i (1 - \hat{\gamma}_{i+1})}{\hat{\gamma}_{i+1}}$$

for $i = 2, \ldots, K - 2$.

Future work on the models of Pradel (1996) should include detailed investigations of the identifiability of parameters under the different model parameterizations. The approach of Catchpole *et al.* (1998), based on the rank and eigenstructure of the matrix of derivatives of expectations of the data with respect to the parameter vector under the model, should be especially useful in such investigations. Under the time-specific model with γ-parameterization $(\varphi_t, p_t, \gamma_t)$ the parameters

$$\varphi_1, \varphi_2, \ldots, \varphi_{K-2}; p_2, p_3, \ldots, p_{K-1}; \gamma_3, \gamma_4, \ldots, \gamma_K; \gamma_2 p_1; \varphi_{K-1} p_k$$

can be estimated. Note that the list includes $K - 2$ survival parameters, $K - 2$ capture probabilities, $K - 2$ seniority parameters and two product parameters with components not separately identifiable, yielding a total of $3(K - 2) + 2 = 3K - 4$ parameters. Under the time-specific model with λ-parameterization $(\varphi_t, p_t, \gamma_t)$ the parameters

$$\varphi_1, \varphi_2, \ldots, \varphi_{K-2}; p_2, p_3, \ldots, p_{K-1}; \lambda_2, \lambda_3, \ldots, \lambda_{K-2}; \lambda_1 / p_1; \varphi_{K-1} p_k; \lambda_{K-1} p_k$$

can be estimated. This parameter list includes $K - 2$ survival parameters, $K - 2$ capture probabilities, $K - 3$ population growth rates, and three product parameters, yielding a total of $2(K - 2) + (K - 3) + 3 = 3K - 4$ parameters.

Various types of alternative modelling should be possible using the basic parameterizations of Pradel (1996), and the potential for addressing interesting biological questions is discussed in Section 4. One methodological topic meriting consideration in reduced-parameter models that utilize these parameterizations involves the manner in which the λ_i and f_i parameters are defined as functions of φ_i, parameters that also appear in the model (e.g., see equations (13) and (14)). Thus, modelling one set of parameters as temporally constant (e.g. $\varphi_i = \varphi$) may impose unintended constraints on the parameters λ_i or f_i. Because of the lack of work on this topic, we simply recommend caution at this time. In cases where interest is focused on a parameter such as λ_i, a conservative approach might be to allow full time-specificity in capture and especially survival probabilities when evaluating alternative models for the λ_i. However, whether this approach performs better than others is yet to be determined.

Another consequence of placing constraints on the different parameters of Pradel's (1996) models involves the identifiability of other parameters. Consider the following reduced-parameter models, model $(\varphi_t, p_t, \gamma.)$ and model $(\varphi_t, p_t, \lambda.)$. Under model $(\varphi_t, p_t, \gamma.)$, the constant γ permits the estimation of p_1, but not of the separate components of the product parameter $\varphi_{K-1} p_K$. This model thus contains $K - 2$ survival rates, $K - 1$ capture probabilities, the single γ, and the product parameter $\varphi_{K-1} p_k$ for a total of $2K - 1$ parameters to be estimated. However, under model $(\varphi_t, p_t, \lambda.)$, the constraint on λ permits estimation of p_1, p_K and φ_{K-1}, for a total of $2K$ estimable parameters. This example simply illustrates that the selected parameterization has consequences for issues such as identifiability. Once again the approach of Catchpole *et al.* (1998) for investigating issues of identifiability should be especially useful in considering reduced-parameter models.

2.3.4 Temporal symmetry models: use with resighting data.   It is possible to use the approach of Pradel (1996) to estimate λ_i based only on resightings of marked birds (Dreitz *et al.*, this issue). The general sampling situation basically involves resightings of adult birds banded in previous years, often as young. It is well-known that survival estimates (e.g. Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton *et al.*, 1992) are based on marked animals only. Similarly, it is possible to estimate abundance using resighting data with additional data on the number of unmarked (e.g. animals sighted at each sampling period, u_i, e.g. Hestbeck & Malecki, 1989). These unmarked animals are not released with marks back into the population and are thus essentially treated as losses on capture when using common computing software. In order to estimate population size, the capture probabilities are estimated based on the marked animals only (m_i denotes the number of marked animals caught in sampling period i) and then applied to the unmarked animals as well:

$$\hat{N}_i = \frac{u_i + m_i}{\hat{p}_i}. \tag{15}$$

It is clear that resighting data from such a sampling design can be used to estimate λ_i. For example, the estimator in equation (15) can be used in conjunction with the estimator in equation (1).

Data from this type of resighting design can also be used to estimate λ_i using the temporal symmetry approach of Pradel (1996). The unmarked data are again treated as losses on capture, such that the usual parameter denoting the probability that a captured bird survives the capture process, η_i, now denotes the probability that a randomly selected bird from all those sighted at time i is a marked bird. Stated differently, $\hat{\eta}_i$ estimates the proportion of marked birds among the entire sample of sighted birds. The usual estimator of λ_i from equation (7) now estimates nothing of interest, whereas the estimator (equation (8)) developed to deal with losses on capture (denoted as λ_i') estimates the growth rate for the population. Because the η_i are likely to be relatively small in such resighting studies, we recommend the use of software that explicitly incorporates losses on capture in the implementation of the Pradel (1996) models (also see Hines & Nichols, this issue).

2.3.5 Assumptions underlying temporal symmetry models.   As Pradel's (1996) temporal symmetry models simply represent different ways to parameterize the original Jolly-Seber model, the basic assumptions are the same as for the Jolly-Seber and superpopulation approaches (see Sections 2.1 and 2.2). The general assumption of homogeneity of rate parameters now applies to Pradel's γ_i as well as to the usual p_i and φ_i. Cormack-Jolly-Seber (CJS) survival estimates are known to be robust to deviations in model assumptions such as heterogeneous capture probabilities (e.g. Carothers, 1973, 1979) and permanent trap response (Nichols *et al.*, 1984b). Because of the similarity of standard-time CJS modelling to estimate φ_i, and reverse-time modelling to estimate γ_i, it might be assumed that $\hat{\gamma}_i$ and $\hat{\lambda}_i$ would be robust as well. However, this is not true. One important difference between CJS estimation of survival and reverse-time estimation of γ_i is that the former process is based entirely on marked animals, so that assumptions about the homogeneity of capture probabilities apply to marked animals only. Reverse-time modelling, however, requires the assumption of homogeneous capture probabilities for both marked and unmarked animals, and this assumption is more restrictive and more difficult to meet. Robustness of estimates based on the temporal symmetry modelling approach has been investigated by Hines & Nichols (this issue).

3 Estimating contributions of demographic components to λ

3.1 *Conceptual framework*

The ecological literature reflects a recent interest in the relative contributions of different demographic components and their associated vital rates to population growth (e.g. Heppel *et al.*, 2000). Here, we describe a probabilistic approach to viewing such contributions and then consider different ways of estimating the resulting probabilities. As in the previous discussion of λ and its estimation, assume interest in a single, open animal population with no age-specificity. In this simplest case, we would like to estimate the relative contributions to population growth between i and $i+1$ (λ_i) of two demographic components: (1) surviving animals from the population at time i (denote these as S_i), and (2) new recruits (denote these as B_i). The recruits result from reproduction and/or immigration, enter the population between times i and $i+1$, and are present at $i+1$. We view population size, N_{i+1}, number of survivors, S_i, and number of new recruits, B_i, as random variables (Nichols *et al.*, 2000b). Population size at time $i+1$ can be written as the sum of these two demographic components:

$$N_{i+1} = S_i + B_i. \tag{16}$$

We can view these two components (S_i and B_i) of N_{i+1} as following a binomial distribution conditional on N_{i+1} and governed by a parameter, γ_{i+1}, denoting the probability that a member of N_{i+1} is a survivor from the previous period (i.e. a member of S_i). The probability distribution of S_i, conditional on N_{i+1}, is thus written as:

$$Pr(S_i|N_{i+1}) = \frac{(N_{i+1})!}{(S_i)!(N_{i+1}-S_i)!}\gamma_{i+1}^{S_i}(1-\gamma_{i+1})^{N_{i+1}-S_i} \tag{17}$$

where $B_i = N_{i+1} - S_i$.

Based on equations (16) and (17), the expectation for population growth rate can be decomposed as follows:

$$\lambda_i \approx \frac{E(S_i)+E(B_i)}{E(N_i)} = \frac{\gamma_{i+1}N_{i+1}+(1-\gamma_{i+1})N_{i+1}}{E(N_i)}.$$

The γ_{i+1} parameters reflect the relative contributions of the two components, S_i and B_i, to population growth. As a specific example, if $\gamma_{i+1} = 0.75$, then a member of N_{i+1} is three times more likely to be a survivor from time i than to be a new recruit, and survival within the population can be viewed as three times more important to population growth over the interval i to $i+1$.

These parameters, γ_{i+1}, can be used to draw inferences about the relative effect of hypothetical changes in the two demographic components on the population growth between i and $i+1$. For example, assume that recruitment had been reduced by proportion α between i and $i+1$, such that recruitment during this interval was really $(1-\alpha)B_i$. The proportional change in λ_i resulting from proportional change α in recruitment is given by $\alpha(1-\gamma_{i+1})$. The population growth rate that would have resulted from a proportional reduction in recruitment of magnitude α would thus be given by $\lambda_i[1-\alpha(1-\gamma_{i+1})]$.

In the material that follows we consider the estimation of these parameters, γ_{i+1}, reflecting proportional contributions of demographic components to λ_i, We consider the same three modelling approaches as in Section 2 for the estimation of

λ_i, again focusing on the temporal symmetry approach because it permits more direct estimation and is easily implemented in MARK (White & Burnham, 1999).

3.2 Jolly-Seber and robust design approaches

As was the case with λ_i, it is possible to estimate γ_i, using the original estimates presented by Jolly (1965) and Seber (1965). Recall that the Jolly-Seber estimator for the number of new recruits (assuming no losses on capture) is given by:

$$\hat{B}_i = \hat{N}_{i+1} - \hat{N}_i \hat{\varphi}_i, \quad i = 2, \dots, K-2$$

the estimated difference between abundance at $i+1$ and survivors from i. Estimation of γ_i can be accomplished either by:

$$\hat{\gamma}_{i+1} = \frac{\hat{N}_i \hat{\varphi}_i}{\hat{N}_{i+1}} \qquad (18)$$

or as

$$1 - \hat{\gamma}_{i+1} = \frac{\hat{B}_i}{\hat{N}_{i+1}} \qquad (19)$$

Estimator (18) is simply the ratio of estimated survivors from period i still present at $i+1$ to the estimated abundance at $i+1$. Estimator (19) shows the complement of γ_{i+1} (the probability that a member of N_{i+1} is 'new' in the sense that it was not present at i) as the ratio of estimated new animals at $i+1$ to estimated abundance at $i+1$. Under the Jolly-Seber model, the above estimators (18, 19) for γ_i are defined for sample periods $i = 3, \dots, K-1$. Under the robust design (Pollock, 1982; Pollock *et al.*, 1990), the estimators of equations (18) and (19) are still used, and the $\hat{\gamma}_i$ are available for all periods for which they are defined, $i = 2, \dots, K$.

3.3 Superpopulation approach

The demographic contribution parameters, γ_i, can also be estimated under the superpopulation approach (Crosbie & Manly, 1985; Schwarz & Arnason, 1996). Specifically, they are estimated as the following function of the survival and entry probabilities (Schwarz, in press):

$$1 - \hat{\gamma}_{i+1} = \frac{\hat{\beta}_i}{\hat{\beta}_i + \sum_{j=0}^{i-1} \left[\hat{\beta}_j \prod_{l=j+1}^{i-1} \hat{\varphi}_l \right]}. \qquad (20)$$

The numerator of equation (20) is the probability that a member of the super-population (N) entered between periods i and $i+1$. The denominator of expression (20) is the probability that a member of N is alive in the population at $i+1$. Equation (20) is thus a natural estimator for the probability that a member of N_{i+1} is a new recruit.

As was the case with estimation of λ_i using the superpopulation approach, the φ_i and β_i are estimated numerically using maximum likelihood (Schwarz & Arnason, 1996; Arnason & Schwarz, 1999), and the γ_i are then estimated by substituting the $\hat{\beta}_i$ and $\hat{\varphi}_i$ into equation (20). Constraints such as $p_1 = p_K = 1$, or perhaps

$p_1 = p_2, p_{K-1} = p_K$, must be imposed to permit estimation of the needed parameters under the full time-specific model (φ_t, p_t, β_t) (see Schwarz & Arnason, 1996).

3.4 Pradel's temporal symmetry approach

In Section 2.3, γ_i was defined as the probability that an animal present just before sampling occasion i was present in the sampled population just after sampling at occasion $i-1$. This 'seniority' parameter of Pradel (1996) is thus the parameter reflecting the relative contribution of survivors from the previous period to population growth rate (see Nichols *et al.*, 2000b). γ_i can be directly estimated using either reverse-time modelling or the temporal symmetry models of Pradel (1996). Program MARK provides estimates under a 'recruitment-only' model, which conditions on the final recapture and then estimates the γ_i and p_i' described in Section 2.3. MARK provides approximately unbiased estimates under this reverse-time model regardless of whether or not some captured animals are not released following capture. Thus, in the case of losses on capture, MARK appropriately yields different estimates of capture probability depending on the time order of the analysis. Reverse-time modelling with the robust design can also be used to obtain estimates of γ_i (Nichols *et al.*, 2000b), and this approach may be especially useful in the case of substantial heterogeneity of capture probabilities.

Under the full temporal symmetry likelihood, MARK provides approximately unbiased estimates of γ_i for the case of all animals released following capture. In the case of losses on capture, MARK provides approximately unbiased estimates of p_i (as opposed to p_i') and biased estimates of γ_i (see Hines & Nichols, this issue). The GAUSS program written by Hines and described by Pradel (1996) does provide approximately unbiased estimates of γ_i for the full temporal symmetry model even when there are losses on capture.

In Section 2.3.4, it was noted that λ_i could be estimated using only resighting data. If a recruitment-only model (reverse-time modelling conditional on final capture) is used with resighting data only, then γ_i will be estimated as 1 for all periods that include no releases of previously unmarked animals. This corresponds to intuition, as all marked animals seen at period i were necessarily present in the previous sampling period. Estimates of γ_i obtained using the full temporal symmetry model of Pradel (1996) with unmarked animals, u_i, recorded and included as not released on capture (Section 2.3.4) will also be positively biased, but can be modified to estimate the quantity of interest properly. Specifically, if $\hat{\gamma}_i$ is the estimate obtained using the temporal symmetry model of Pradel (1996) with unmarked animals recorded but not released, then the following modified estimator properly estimates the probability that an animal sighted at i is an 'old' animal (present at $i-1$):

$$\hat{\gamma}_i' = \frac{\hat{\gamma}_i}{1 - (\hat{p}_{i-1})(1 - \hat{\eta}_{i-1})}. \tag{21}$$

Recall that $(1-\eta_i)$ denotes the probability that a randomly selected animal from all those sighted at time i is an unmarked animal. The denominator of equation (21) thus estimates the probability that an animal present at $i-1$ is not detected as an unmarked animal at that period. This 'adjustment' to the standard estimator, $\hat{\gamma}_i$, is needed because unmarked animals detected at $i-i$ have no opportunity to be detected as old animals at time i.

4 Discussion

4.1 Population growth rate, λ_i

4.1.1 Observation-based estimation methods.   Capture-recapture modelling is not the only way to estimate population growth rate, λ_i. For animals that are easily observed, such methods as line transects (Buckland *et al.*, 1993) and aerial surveys with double-sampling (e.g. Smith, 1995) can be used to estimate population size and, hence, growth rate. If there is special interest in modelling λ_i within the framework of an estimation model (as opposed to modelling the estimates themselves, $\hat{\lambda}_i$), then it should be possible to construct joint likelihoods that contain the observation data for multiple sampling periods. The data for each sampling period would contain the information needed to estimate the corresponding abundance, N_i. If interest is in direct estimation of λ_i, then it should be possible to specify a single abundance, e.g. N_1, and then to write all other abundances in terms of this single abundance and subsequent population growth rates, λ_i. For example, abundance for period i would be rewritten as:

$$N_i = N_1 \prod_{j=1}^{i-1} \lambda_j. \tag{22}$$

Joint likelihoods for virtually any formal abundance estimation method (e.g. Seber, 1982; Lancia *et al.*, 1994; Williams *et al.*, in press) can be developed for use with data from multiple sampling periods and reparameterized using equation (22) for direct estimation and modelling of population growth. If the natural parameterization of the abundance estimation method uses density (D_i), rather than abundance (N_i), then D_i and D_1 can be substituted for N_i and N_1, respectively, in equation (22). The main point is that capture-recapture need not be used for readily-observed animals. Instead, it should be possible to estimate directly and model population growth using whatever estimation methods are most appropriate for the kind of data collected.

4.1.2 Projection matrix approaches to estimation of λ_i.   In studies directed at count data for readily-observed species, it is most common to estimate abundance and population growth rate directly. However, in studies of marked animals, it is not so common to estimate λ_i directly using any of the methods described in Section 2. Instead, it is common to estimate survival and reproductive rates, and to then use these estimates to construct population projection matrices (Caswell, 1989a, 2001). Specifically, time-specific estimates of survival and reproductive rates are obtained, and averages of these time-specific estimates are then used to construct projection matrices. Analytic or simulation methods can then be used to compute the asymptotic growth rate defined by the average vital rates. Such an asymptotic growth rate is frequently thought to be descriptive in some way of the average rate of population growth over the period of analysis. Several reasons exist for viewing such asymptotic λs with caution, and we present a few of these here.

Perhaps the most obvious caution involves the asymptotic nature of projection matrix λs. While they might be expected to perform well in the absence of temporal variation in vital rates, it is not clear what projection matrix λs should estimate in the case of substantial temporal variation in vital rates.

Another caution involves the importance of movement to abundance and population growth. The λ_i estimated directly using either capture-recapture or observa-

tion-based methods should reflect changes in numbers on the sampled area(s), and should thus integrate rates of survival, reproduction and movement. In contrast, single-location population projection matrices typically reflect an asymmetry with respect to movement. The complements of survival rate estimates computed using capture-recapture and various other methods include both mortality and permanent emigration from the study area. Such survival estimates are often combined in projection matrices with fecundity estimates that are based solely on components of reproductive rate (e.g., litter size, clutch size, fledglings per nest). Matrices constructed using such estimates thus include movement in the complements of survival rates (the components of loss), but not in the fecundity parameters (the components of gain). One consequence of this movement asymmetry is that the asymptotic rates of population increase that are computed from such matrices are frequently too small.

Cooch *et al.* (2001) developed an innovative approach to dealing with the movement asymmetry common to many projection matrix investigations. Their approach involves specifying projection matrix off-diagonal elements as functions of both survival and immigration rate parameters. For situations in which the number of immigrants is determined primarily by the number of animals in the destination population, rather than in the source population(s), this approach seems very reasonable.

Questions involving asymptotic rate of increase could also be addressed using multistratum projection models (e.g. Rogers, 1966; Schoen, 1988; Lebreton, 1996) that explicitly incorporate movement. However, use of this approach to deal with movement requires that at least one of the modelled strata represents 'the rest of the world' or all potential sources of immigrants other than the locations under study. However, the modelling of the dynamics of such 'catch-all' strata is likely to be very difficult because of lack of information, yet very important to asymptotic characteristics of the metapopulation system.

Still another caution involves the importance of probability of breeding in estimating the fecundity rates to be included in projection matrices. The components of reproductive rate used to estimate fecundity (clutch size, nest success, postfledging survival) are typically conditioned on animals that reproduce, whereas projection matrix fecundity values should also reflect the probability of breeding. In general, projection matrices are typically constructed using some vital rates that are estimated reasonably well and some that are estimated poorly or not at all. The existence of such 'weak links' makes inference problematic.

Projection matrices were developed to project the population-dynamic consequences of repeated application of specific sets of vital rates. λ and related asymptotics specify these consequences and are extremely useful for such prospective analyses. In contrast, λs computed from average values of vital rates should not necessarily be expected to reflect average population growth for the period over which the vital rate estimates were obtained. Instead, we believe that direct focus on either time-specific abundance, or on time-specific parameters that integrate the various components of vital rates and movement (e.g. φ_i and γ_i), should usually provide a more reasonable means of estimating λ_i. These estimates, $\hat{\lambda}_i$, will not necessarily be useful in prospective analyses, but should be useful in reflecting changes in abundance on specified study areas over specified study periods.

4.1.3 Testing and using count statistics as indices.   The ability to model and directly estimate λ_i provides interesting opportunities for evaluating indices and, if they

population size, and equation (24) might provide a reasonable estimator for λ_i. For the tern data, the ratio of count statistics ranged from 0.56 to 1.85 (Table 1).

We included in the model set a model with the same structure as $(\varphi_t, p_t, \lambda_t)$, except that we modelled λ_i as:

$$\lambda_i = \beta \left(\frac{n_{i+1}}{n_i} \right). \tag{25}$$

Under the hypothesis that the count statistic is a good index, β should be close to 1, and the AIC for the new model $(\varphi_t, p_t, \lambda_n)$, should be low. The resulting estimates were $\hat{\beta} = 0.89$, $\hat{SE}(\hat{\beta}) = 0.044$, and the model had the smallest AIC value in the model set, $\Delta AIC = 0.0$. We do not view the ultrastructural model of equation (25) as a perfect description of the data, but prefer to view it as a random effects model (see Link, 1999; White & Burnham, 1999) with residual variation about the relationship of equation (25). We thus computed a variance inflation factor, $\hat{c}$, as the likelihood ratio statistic for the test of model $(\varphi_t, p_t, \lambda_n)$ versus the general model $(\varphi_t, p_t, \lambda_t)$, divided by the corresponding degrees of freedom: $\hat{c} = 5.78/4 = 1.45$. This $\hat{c}$ was then applied to the model-based variance estimates to obtain more appropriate variance estimates (Burnham *et al.*, 1987; Lebreton *et al.*, 1992 Link, 1999). The annual estimates of population growth rate resulting from the ultrastructural modelling ranged from 0.50 to 1.65 and had substantially smaller standard errors than the $\hat{\lambda}_i$ based on the full, time-specific model (Table 1). We tried some ultrastructural models in addition to that of equation (25), although this model performed the best of those that were tried and was preferred *a priori*, based on the expected relationship under the assumption of a good index (equations (23) and (24)).

The point of this example is to suggest that direct estimation of λ_i may provide opportunities for testing the critical, yet seldom tested, assumption underlying index statistics. If it does appear that the count statistic provides a reasonable index, then the extra information provided by the counts can aid in the estimation of λ_i. In our example, the gains in precision were substantial. Large-scale surveys such as MAPS (e.g. DeSante *et al.*, 1995) that incorporate both capture-recapture and point counts, offer the potential to test the utility of the point counts as indices to avian abundance using the type of analysis presented here.

4.1.4 Combining capture-recapture and abundance data using joint likelihoods. In Section 4.1.1, we suggested that observation-based data collected for use with formal estimation methods could be used to model λ_i. Specifically, we suggested that equation (22) could be used to provide the link between abundance and population growth rate. In some studies, investigators collect both capture-recapture and observation-based data for use in estimation. In the case of passerine studies, for example, one might collect capture-recapture data with mist-netting, in addition to point count data obtained under either distance sampling (Buckland *et al.*, 1993) or double-observer (Nichols *et al.*, 2000a) protocols. In such studies, joint likelihoods could be developed incorporating both types of data with their respective models of the sampling process. The separate components of the likelihood dealing with the different data types would be linked by the shared parameters, λ_i. The modelling strategy might include a general model in which the λ_i for the different data types were modelled with separate parameters and a reduced-parameter model in which the λ_i were shared by both components of the

likelihood. Use of likelihood ratio testing and AIC would first provide an indication of the reasonableness of the assumption that the modelled λ_i indeed represented the same parameter. If this was concluded to be true, then the estimates of λ_i resulting from the joint modelling should be more precise than estimates resulting from the use of either approach separately.

We note that combining data types for use with joint likelihoods is not new and has been profitably used in other estimation problems involving capture-recapture and ring-recovery modelling (see Williams *et al.*, in press). The robust design can be viewed as a combination of data from capture-recapture studies of closed and open populations (Pollock, 1982; Pollock *et al.*, 1990). Nichols *et al.* (1992) and Nichols & Hines (1993) dealt with tag loss by considering joint likelihoods with separate components for recapture and resighting data. The joint model of Burnham (1993) combines capture-recapture and ring recovery data, and the models of Barker (1997) combine capture-recapture data with ancillary observations. Freeman *et al.* (1992) combined ring recovery data with observations of radio-marked individuals, and Powell *et al.* (2000) used both capture-recapture and radio-telemetry data. In an application very similar to the ideas presented above on estimating λ_i, Besbeas *et al.* (in review) recently combined Common Bird Census data with ring recovery data in a joint likelihood in which the two components shared survival parameters. The addition of the census data permitted inference about recruitment rate (a parameter not directly studied) and about the role of recruitment in bringing about changes in population growth.

It seems most reasonable to us to address questions about density-dependence by investigating the relationship between abundance or density and the vital rates themselves (e.g. Nichols *et al.*, 1984a; Leirs *et al.*, 1997). However, many ecologists prefer to focus on the relationship between λ_i and N_i. Such investigations are inevitably based on estimates, and the negative covariance between $\hat{\lambda}_i = \hat{N}_{i+1}/\hat{N}_i$ and $\hat{N}_i$ induced by sampling variation renders the suite of proposed tests for density-dependence virtually useless (see Shenk *et al.*, 1998). Perhaps, observation-based data could be parameterized with time-specific abundance, N_i, and capture-recapture data could be parameterized with λ_i. The link between the two components of the likelihood would then occur via specification of a functional relationship, e.g. $\lambda_i = f(N_i)$. Sampling variation would still exist in the estimates, but the independent data sets should not produce the negative sampling covariance that exists between $\hat{\lambda}_i$ and $\hat{N}_i$ when both sets of parameters are estimated from the same data. It would seem that such modelling would produce valid tests for density-dependence of population growth. ARMA and related models parameterized in this manner would be expected to yield more reasonable results than those based on single data sets.

4.1.5 Joint likelihood robust design. The robust design of Pollock (1982) was mentioned in Sections 2.1 and 3.2, in conjunction with the Jolly-Seber model, as an alternative source of estimates of abundance, N_i, and new recruits, B_i. Kendall *et al.* (1995) showed how to develop joint likelihoods for capture-recapture data obtained at two different temporal scales. The closed-population and open-population portions of the likelihoods are linked because they share capture probability parameters. The robust design models of Kendall *et al.* (1995, 1997) can be termed 'conditional' in the sense that capture probabilities for the closed portions of the likelihoods are written as conditional on the total number of animals caught at least once. An alternative parameterization that may prove useful in estimating λ_i

includes abundances, N_i, as parameters of the closed portions of the likelihood and can thus be termed 'unconditional'. For example, the models of Otis *et al.* (1978) implemented in CAPTURE (Rexstad & Burnham, 1991) include abundance as a parameter in the likelihood.

We envisage a parameterization for the K-sample closed-population portions of the joint likelihood that is based on the parameterization of equation (22). The likelihood could include the parameter for population size for the initial primary period, N_1, but all abundances for subsequent primary periods would be written as products of N_1, and the appropriate λ_i (see equation (22)). These λ_i parameters would be shared by the open portion of the likelihood, modelled using Pradel's (1996) temporal symmetry approach. As when count data are combined with open-model capture-recapture data (Section 4.1.4), the addition of closed-population data should result in increased precision of the parameter estimates. In addition, as in Section 4.1.4, it should be possible to model density-dependence directly using N_i from one portion of the likelihood and λ_i from the other portion.

4.1.6 Combining capture-recapture and other vital rate data using joint likelihoods. Some studies might combine capture-recapture sampling with other sampling directed at vital rates or their components (Green, 1999). For example, in avian studies it is fairly common to locate nests and estimate nest success, one component of reproductive rate, using a Mayfield-type estimator (Mayfield, 1961; Johnson, 1979; Hensler & Nichols, 1981). It is also becoming more common to combine radio-telemetry on a subsample of birds with traditional capture-recapture (e.g. Powell *et al.*, 2000). Such designs sometimes permit separate estimation of true survival and permanent emigration, the two primary components of loss.

Joint analyses of such data sets offer the ability to address questions about the temporal covariation of parameters. Such covariation is relevant to one of the approaches to defining 'importance' of demographic components and vital rates (see Section 4.2.1). For example, Caswell's (2000) definition of retrospective perturbation analysis focuses on historical patterns of temporal covariation between vital rates and population growth rate. 'Key factor analysis' (e.g. Morris, 1959; Varley & Gradwell, 1960) and related approaches (e.g. Reynolds & Sauer, 1991; Johnson *et al.*, 1992) are based on time series of estimates of vital rates and population size or growth rate. Morris (1959, p. 580) defined key factors as those 'that cause a variable ... mortality and appear to be largely responsible for the observed changes in population size'. Correlation and regression analyses are used to investigate the relative correspondence between temporal variation in the different vital rates and in population size or growth. Key factor analysis and related approaches have seen only limited success in animal population ecology, primarily because of the failure to properly incorporate sampling variation and covariation in applications of the key factor approach (Kuno, 1971; Manly, 1977, 1979).

Joint analyses of different data sets permitting estimation of abundance and λ_i, as well as components of population gain and loss, offer the possibility of conducting retrospective analyses focused on temporal covariation in a manner that properly accounts for sampling variation. For example, λ_i could be modelled as a function of such factors as nest success (e.g. using nest visitation data), proportion of adults that breeds (e.g. using data on presence-absence of brood patch or other indicators of breeding among captured birds, possibly using multistate modelling to account for differences in capture probabilities of birds in the two states, Nichols *et al.*,

1994), and survival or emigration rates (e.g. using telemetry data). Ultrastructural modelling of λ_i using such quantities estimated in another portion of the likelihood should provide a robust means of addressing questions about temporal covariation of λ_i and specific vital rates. A similar approach could be used to decompose total rates of loss $(1 - \varphi_i)$ or gain (e.g. using per capita recruitment rate first defined in Section 2.2, f_i). For example, $(1 - \varphi_i)$ could be based on capture-recapture data and modelled as a function of rate of emigration based on telemetry data. In summary, we believe that this joint likelihood approach using different data sets provides a reasonable way to investigate temporal covariation between component rates and integrated rate parameters that are functions of these components.

4.1.7 Capture-recapture estimation of λ_i using more complicated models.   Pradel's (1996) temporal symmetry approach to the estimation of λ_i is relatively new, and there has been little work on extension of this approach to more complicated models. An exception to this is very recent work on estimation of λ_i using multistate models (Lebreton, personal communication). This approach has potential utility in estimating population growth of single-site populations composed of individuals in multiple physiological or behavioural states, as well as of animals sampled at multiple locations in a metapopulation system. Because of the generality of the multistate framework, Lebreton's generalization of λ_i estimation should be widely applicable.

4.1.8 Additional uses of $\hat{\lambda}_i$.   Here, we simply list some additional uses of Pradel's (1996) approach. In addition to the modelling of λ_i suggested in previous sections, we note the possibility of modelling λ_i as functions of environmental covariates. Certainly, the modelling of the vital rates that produce λ_i (e.g. φ_i, f_i) as functions of environmental covariates is a useful approach to understanding environmental influences on population dynamics (e.g. North & Morgan, 1979; Lebreton *et al.*, 1992). In some cases, however (e.g. when an environmental covariate influences multiple vital rates), it will be useful to investigate overall environmental influences by directly modelling a parameter such as λ_i that integrates the effects on different vital rates and reflects changes in the state variable of interest, N_i.

Population growth rate itself is a parameter that can be used to judge the health of a population over a period of study. If a capture-recapture time series is reasonably long, then a variance components approach (Burnham *et al.*, 1987; Skalski & Robson, 1992; Link & Nichols, 1994; Gould & Nichols, 1998) can be used to estimate the true temporal variance of λ_i using a random effects perspective (White & Burnham, 1999). This variance is very relevant to extinction probability (e.g. Lewontin & Cohen, 1969; Leigh, 1981; Goodman, 1987) and emphasizes the potential utility of the direct estimation and modelling of λ_i for population viability analyses (also see White, 2000).

4.2 Contributions of demographic components to λ

4.2.1 Relative 'importance' of components to λ: temporal covariation.   Much has been written in recent years about ways of assessing 'importance' of vital rates or demographic components to population growth rate, and recent discussions (Heppel *et al.*, 2000) obviate the need for a review here. Instead, we will focus primarily on the manner in which direct capture-recapture estimation can contribute to these concepts. As noted in Section 4.1.5, one approach to identifying important vital rates or demographic components focuses on historical patterns of

temporal covariation between vital rates and population growth rate (Morris, 1959; Varley & Gradwell, 1960; Caswell, 2000). We believe that use of multiple data sources from the same study location in joint likelihoods that include parameters for population growth and vital rates (or associated components) provides a means of addressing temporal covariation through the use of ultrastructural modelling (see Section 4.1.6). This approach should be superior to the numerous applications of key factor analysis that are based on repeated counts.

Life table response experiments (LTREs) provide another approach to assessing covariation of λ and vital rates (Levin *et al.*, 1987; Caswell, 1989b, 1996, 2000; Cooch *et al.*, 2001). The objective of the LTRE approach differs from that of the approach described in Section 4.1.6 in the nature of the λ that is selected for investigation. The approach using joint likelihoods and ultrastructural modelling focuses on the expected time-specific rates of population change ($\lambda_i = E(N_{i+1}/N_i)$), whereas the LTRE approach focuses on asymptotic growth rates (denoted as $\lambda_i^\star$) that are defined by the time-specific vital rates. The methodological decision should thus be based on the objectives of the effort, as both approaches provide reasonable ways to meet their respective objectives.

4.2.2 Relative 'importance' of components to λ: proportional contributions. As is the case for the methods for investigating temporal covariation (Section 4.2.1), the methods for estimating γ_i presented in Section 3 are retrospective, in the sense that they pertain to a specific historical period. However, the approach involving γ_i does not share the focus on temporal covariation of population change and demographic components or vital rates. Instead, we present a direct decomposition of population growth rate into demographic components. The γ_i parameters are not based on temporal covariation with population growth, but instead reflect the magnitudes of contributions to growth.

Our focus on proportional contributions to λ_i can be viewed as a retrospective analogue of elasticity analyses (Caswell *et al.*, 1984; de Kroon *et al.*, 1986; van Groenendael *et al.*, 1988; Caswell, 1989a, 2001). Elasticity (e_{ij}) of projection matrix element a_{ij} is defined as:

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{\partial \lambda}{\partial a_{ij}} \quad \frac{a_{ij}}{\lambda}. \tag{26}$$

Elasticity is the proportional change in the asymptotic λ resulting from an infinitesimal proportional change in matrix element a_{ij} (Caswell *et al.*, 1984; de Kroon *et al.*, 1986). Elasticities based on projection matrices sum to 1 (e.g. de Kroon *et al.*, 1986; Messerton-Gibbons, 1993) and can thus be interpreted as relative contributions to population growth rate. This interpretation leads naturally to the view that elasticity reflects the relative importance of the associated vital rate, in the sense that proportional changes in vital rates with large elasticities bring about larger changes in λ than do the same proportional changes in vital rates with smaller elasticities.

As noted above, the γ_{i+1} parameters estimated using our approach are closely related to the concept of elasticity of λ_i with respect to demographic components and their associated vital rates. In Section 3 we decomposed expected population growth rate, λ_i, into components associated with survivors from the previous period, $E(S_i)$, and new recruits, $E(B_i)$. We can compute a time-specific analogue of elasticity for the survivor component as:

$$\frac{\partial \log \lambda_i}{\partial \log E(S_i)} = \gamma_{i+1}.$$

If we focus on vital rates associated with demographic components rather than the components themselves, then we can express the numbers of survivors and recruits as functions of the population at time i and again compute an analogue of elasticity. If we denote survival rate from time i to $i+1$ as $E(S_i/N_i) = \varphi_i$, then the analogue of elasticity of λ_i with respect to φ_i is again given by:

$$\frac{\partial \log \lambda_i}{\partial \log \varphi_i} = \gamma_{i+1}.$$

Despite the analogy between these proportional contribution parameters (γ_i) and elasticities derived from population projection matrices, these quantities differ in several respects. Perhaps the most obvious difference involves the asymptotic nature of elasticity measures derived from projection matrices, contrasted with the applicability of the $\hat{\gamma}_i$ to the specific time interval ($i-1$ to i). We cannot necessarily use a specific $\hat{\gamma}_i$ to characterize a population over a long period of time (although a mean of $\hat{\gamma}_i$ might be useful for such a purpose), and neither can we expect an asymptotic elasticity value to necessarily be a useful descriptor for population change over a specific interval. The asymptotic nature of elasticity analyses leads to uncertainty about their relevance to situations involving either transient dynamics that precede asymptotic behaviour, or simple temporal variation in vital rates and population growth. We might expect elasticity analyses to provide reasonable approximations for situations involving relatively small temporal variation, but perhaps not for populations inhabiting highly variable environments. Generally, we would expect the γ_i parameters to be more useful in retrospective analyses (where 'retrospective' refers simply to estimation over a specific historical period, and not to temporal covariation), and matrix-based elasticities to be more useful for prospective analyses.

Another difference between elasticities and γ_i involves geographic closure and the incorporation of movement into inferences about population change. Projection matrix approaches are typically parameterized with birth and death rates (see Section 4.1.2) and are ideal for populations that are geographically closed. If our attention is focused on changes in numbers of animals on a particular area of interest, however, movement is frequently an important contributor to population dynamics. We can estimate γ_i parameters corresponding to contributions from other sampled locations and, in some cases, from all non-sampled areas (see Section 4.2.3 and Nichols *et al.*, 2000b). Even if we estimate γ_i using data from single-age, single-location studies as described in Section 3, the inference about relative contributions of losses and gains to γ_i includes movement and is not restricted to an abstract system governed by birth and death rates in the absence of movement.

4.2.3 Capture-recapture estimation of γ_i using more complicated models.   In Section 3, we focused on the contributions of old survivors and new recruits to population growth rate, but the approach can be readily extended to deal with multiple ages and strata (e.g. locations, physiological states, etc). For example, Nichols *et al.* (2000b) considered a 2-age model in order to compute γ_i associated with (1) surviving adults from the previous period; (2) surviving young from the previous period; and (3) immigrants. This analysis permits separation of the relative contributions of *in situ* reproduction and immigration to population growth (e.g. Connor *et al.*, 1983; Nichols & Pollock, 1990), a topic that seems very relevant to questions

about source-sink (Pulliam, 1988) and open-recruitment (Roughgarden *et al.*, 1985, 1988) systems. Nichols *et al.* (2000b) also considered a single-age, multiple-location model. The resulting $\hat{\gamma}_i$ decomposed population growth rate at one location into components associated with immigration from each sampled location as well as from outside the study system of sampled locations. These estimates should be relevant to defining source-sink systems (Pulliam, 1988) and to modelling metapopulation dynamics (e.g. Hanski & Gilpin, 1997).

4.2.4 Additional uses of $\hat{\gamma}_i$.   Temporal variation in the relative contributions of different demographic components is a topic of recent interest in population dynamics (Gaillard *et al.*, 1998). Estimates of γ_i and associated sampling variances and covariances over a period of time can be used to estimate true temporal variance in the relative contribution of a component of interest using a variance components approach (see Burnham *et al.*, 1987; Skalski & Robson, 1992; Link & Nichols, 1994; Gould & Nichols, 1998; White, 2000). The relative variability versus stability of contributions of different demographic components to population growth is an interesting characteristic that may be relevant to predictions and projections of future population dynamics.

   Reduced-parameter models can be developed to incorporate restrictive assumptions about temporal variation in the proportional contribution parameters. In particular, evaluation of the assumption that $\gamma_i = \gamma$ should be relevant to the question of whether use of asymptotic elasticities derived from projection matrices is reasonable. In some instances, it may be useful to model the γ_i using an ultrastructural modelling approach (e.g. Lebreton *et al.*, 1992). For example, we might consider modelling the γ_i as a function of environmental covariates or information about neighbouring populations.

4.2.5 On the relevance of elasticity and γ_i to conservation and management.   The recent literature contains disagreement about the relevance of various measures of 'importance' of vital rates to population growth rate (e.g. see Heppel *et al.*, 2000). Here we consider two general objectives of conservation/management efforts and consider the relevance of elasticity and γ_i to these objectives. The first objective is often loosely said to involve identification of the 'cause' of a change in population growth rate and the subsequent reversal of λ_i by management directed at the 'causal factor'. The idea of a 'cause' of a change in λ_i appears to be a logically conditional statement, conditioned on two points in time. The λ_i for the two times must differ, and the differences in associated vital rates can be viewed as the 'cause' of the change. In some cases, we may be able to associate a specific environmental factor with the vital rate that differs between the two times, and if this factor can be influenced by management actions, then such actions might be recommended. An example of such a situation might involve the reduced reproductive rates and, hence λ_i, of raptor populations in North America associated with application of organochloride pesticides (e.g. Newton, 1986, 1998). Restrictions on pesticide use were implemented and affected populations exhibited increased reproductive rates and λ_i (e.g. Newton, 1986, 1998). Although capture-recapture estimates of λ_i and associated vital rates (e.g. φ_i, f_i) can be very useful in the identification of 'cause', as defined here, estimated proportional contributions of vital rates to λ_i do not appear to be especially relevant to this sort of objective.

   The other general objective of conservation/management might be simply to bring about a change in λ_i. Either abundance or λ_i is judged to be unacceptable,

and the task is to bring about a desired change via management action. In this case, demographic differences between the present and some specified past time are not necessarily relevant, as the decision to bring about change is based on the present state of the system. This approach is typical of many management programs (e.g. Nichols *et al.*, 1995). In some cases, only one type of management action is possible (e.g. hunting regulations), and information about relative contributions of different vital rates to λ_i will not be especially relevant to management decisions. However, if multiple management actions affecting different vital rates are possible, then consideration of elasticities and γ_i can be an important part of the decision process. Even in this situation, though, we believe that blind focus on parameters with the highest values of elasticity and γ_i is not wise (see Heppel *et al.*, 2000 for similar views).

Instead, we propose the following metric as a conceptual guide to thinking about elasticity and management actions:

$$m_{k,ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} \quad \frac{\partial \log a_{ij}}{\partial x_k} \quad \frac{\partial x_k}{\partial y_k} \tag{27}$$

where x_k denotes management action of type k, which can be viewed as a continuous variable (e.g. proportion of nests artificially protected from predation), y_k denotes the unit costs (e.g. in some common currency such as dollars) of management actions of type x_k, and $m_{k,ij}$ thus represents the proportional change in λ resulting from the influence of a small change in management action of type x_k on vital rate a_{ij}, per unit cost associated with the action. The first term of equation (27) represents elasticity, e_{ij}, or its real-time analogue γ_i, and reflects our belief that this quantity is indeed relevant to management decisions. The second term of equation (27) represents the proportional change in vital rate a_{ij} associated with small changes in some continuous action x_k, and the final term reflects the cost of implementing the change in management action x_k. Although we apologize for the sloppy mathematical notation, we believe that expression (27) makes the relevant point that management decisions should be based not only on elasticity and related concepts, but also on the existence and knowledge of management actions that influence the different vital rates and on the true costs of these management actions.

Equation (27) pertains to effects on λ_i of changes in vital rate a_{ij} brought about by changes in management action x_k. If interest is focused not on a single vital rate, but on all vital rates influenced by changes in action x_k, then we might consider the following expression:

$$m_{k.} = \sum_{ij} \frac{\partial \log \lambda}{\partial \log a_{ij}} \quad \frac{\partial \log a_{ij}}{\partial x_k} \quad \frac{\partial x_k}{\partial y_k}. \tag{28}$$

Much of the science of animal conservation and management is associated with the second term of equations (27) and (28), which involves changes in vital rates associated with different management actions. Sometimes, managers admit the existence of structural uncertainty characterized by different competing models of how vital rates respond to specific management actions. In such cases, adaptive management represents a reasonable way to proceed (Walters, 1986; Williams, 1996). In the case of North American waterfowl management, for example, four models are used to characterize our uncertainty about the manner in which changes in hunting regulations are translated into changes in the vital rates (specifically,

reproductive rates (via density-dependence) and age-specific survival rates; e.g. Nichols *et al.*, 1995; Johnson *et al.*, 1997; Williams *et al.*, in press). Estimates of population growth and survival are very relevant to the adaptive management process, as comparisons of these estimates to the predictions of the competing models are used each year to formally update the measures of faith in the different models (Williams, 1996; Williams *et al.*, in press).

Thinking in terms of expressions (27) and (28) is also relevant to conservation problems for which objectives have not yet been formally specified. For example, adult survival will nearly always exhibit the largest elasticity for long-lived bird species. However, it may be virtually impossible to influence adult survival via any sort of management, whereas it may be possible to influence at least some components of reproductive rate, such as nest success. Despite the far greater elasticities associated with adult survival (e.g. the first term of expressions (27) and (28)), sometimes it may be wise to focus management efforts on reproductive rate, as reproduction may be much more responsive to cost-effective management actions (the second two terms in expressions (27) and (28)).

Expressions (27) and (28), and indeed our entire discussion in this section, are abbreviated and greatly simplified. Issues such as covariances among vital rates and density-dependence can potentially complicate matters but go beyond the scope of this paper. Our intention is to make two central points. The first is simply that quantities such as elasticity and γ_i that reflect the relative contributions of different vital rates to population growth are not relevant to some conservation questions (e.g. searches for 'the cause' of a specified demographic change). Our second point is that e_{ij} and γ_i are relevant to more general questions about management and conservation, but even then need to be considered in conjunction with other information about the effects of specific management actions on the different vital rates and the relative costs of these actions.

In addition to these central points of the above discussion, we offer the observation that many management and conservation efforts appear to be characterized by fuzzy thinking. Many efforts include a focus on metrics (such as elasticity) that are indeed relevant to management and conservation, but we see little indication of clear thinking about exactly how such metrics fit into a decision-theoretic approach to meeting management or conservation objectives. Dynamic optimization approaches that yield state-specific management strategies have been used sporadically in natural resource management for some time (e.g. Anderson, 1975; Williams, 1982, 1989; Johnson *et al.*, 1997; Williams *et al.*, in press), but still do not seem to be widely appreciated as the most reasonable approach to difficult management and conservation problems. We strongly recommend consideration of such decision-theoretic approaches for those seriously interested in management and conservation problems.

4.3 Informed estimation of λ_i and γ_i: some cautions

In this final section we simply warn the reader against uncritical estimation and use of estimates, $\hat{\lambda}_i$ and $\hat{\gamma}_i$. With respect to estimation methods themselves, it is important to treat losses on capture properly when dealing with actual losses and when treating sightings of unmarked animals as losses on capture when using resighting data to estimate λ_i and γ_i. It is also important to recognize that either of two population growth rates can be estimated for studies with losses on capture; growth rates associated only with natural processes or growth rates that include

the sampling losses. Of course selection of the appropriate parameter for any particular study depends entirely on the question(s) being addressed.

Survival rate estimates resulting from conditional CJS modelling are known to be fairly robust to many kinds of assumption violations, and it is tempting to assume that this robustness also characterizes other rate parameters such as λ_i and γ_i. As noted above, however, reverse-time and temporal symmetry modelling require equal capture probabilities for marked and unmarked animals, and failures of this assumption can have serious consequences for estimates of λ_i and γ_i, producing substantial bias in many cases (Hines & Nichols, this issue). The assumption of equal capture probabilities for marked and unmarked animals is difficult to test without the robust design (Nichols *et al.*, 1984b) and thus requires special vigilance.

A final point not yet discussed involves changes in the size of the study area and resultant consequences for the interpretation of parameters such as λ_i and γ_i. For example, consider an increase in the size of the study area that occurs during sampling period $i + 1$. Because λ_i is defined as the expected ratio of abundances at periods i and $i + 1$, an increase in study area would be expected to produce an increase in λ_i even in the absence of any increase in survival or recruitment rate (see Hines & Nichols, this issue, for an expression for the magnitude of the bias). Similarly, the relative contribution of survivors to population growth between i and $i + 1 (\gamma_{i+1})$ will be reduced because of the increased number of 'new' animals associated with the new portion of the study area. The recommendation is simply to consider such changes in study area when interpreting estimates of λ_i and γ_i and to identify properly the parameter needed to address the question(s) of interest.

5 Conclusions

We believe that direct estimation of λ_i and γ_i using capture-recapture data presents interesting opportunities that should be exploited. In Section 4, we discussed several ideas for joint analyses using capture-recapture and other data to better estimate quantities of interest (e.g. λ_i) and to address questions that remain resistant to other approaches. We speculate that the direct estimation approaches described in this review should provide better *estimates* than the multi-step approach of computing average vital rates and computing λ_i and e_{ij} using projection matrix asymptotics. This conjecture could be tested via computer simulation, and this might be an interesting exercise. Such an exercise would also provide some idea of how much faith to place in such asymptotics when direct estimation approaches are not possible. We emphasize that this speculation concerns only the use of projection matrix asymptotics as estimates corresponding to specific places and times. Projection matrix asymptotics are clearly useful for prospective analyses and are the tool of choice for such work.

We view the direct estimation methods reviewed here simply as contributions to the animal ecologist's toolbox. This toolbox already includes standard capture-recapture methods for estimation of abundance and vital rates, and projection matrix methods for investigating asymptotic characteristics of populations governed by specified sets of vital rates. We also view these methods as providing a step towards the unification of distinct approaches to the study of animal population dynamics. Demographic estimation and projection are closely related endeavours, and it is useful to recognize their similarities as well as their differences. A final recommendation is simply to specify analytic objectives clearly in order to facilitate selection of the appropriate tool for accomplishing them.

Acknowledgements

REFERENCES

ANDERSON, D. R. (1975) Optimal exploitation strategies for an animal population in a Markovian environment: A theory and an example, *Ecology*, 56, pp. 1281-1297.

ARNASON, A. N. & SCHWARZ, C. J. (1999) Using POPAN-5 to analyse banding data, *Bird Study*, 46 (suppl.), pp. S157-S168.

BARKER, R. J. (1997) Joint modeling of live-recapture, tag-resight, and tag-recovery data, *Biometrics*, 53, pp. 666-677.

BESBEAS, P. T., FREEMAN, S. N., MORGAN, B. J. T. & CATCHPOLE, E. A. (2001) Stochastical model for animal abundance and demographic data. Institute of Mathematics and Statistics, Univ. Kent at Canterbury, Report UKC/IMS/01/16.

BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P. & LAAKE, J. L. (1993) *Distance Sampling: Estimation of Biological Populations* (London, Chapman & Hall).

BURNHAM, K. P. (1993) A theory for combined analysis of ring recovery and recapture data. *In:* J. D. LEBRETON & P. M. NORTH (Eds) *The Study of Bird Population Dynamics Using Marked Individuals*, pp. 199-213 (Berlin, Birkhauser Verlag).

BURNHAM, K. P. & ANDERSON, D. R. (1998) *Model Selection and Inference* (New York, NY, Springer).

BURNHAM, K. P., ANDERSON, D. R., WHITE, G. C., BROWNIE, C. & POLLOCK, K. P. (1987) *Design and Analysis of Methods for Fish Survival Experiments Based on Release-recapture* (Am. Fish. Soc. Monogr. 5. 437 pp.)

CAROTHERS, A. D. (1973) The effects of unequal catchability on Jolly-Seber estimates, *Biometrics*, 29, pp. 79-100.

CAROTHERS, A. D. (1979) Quantifying unequal catchability and its effect on survival estimates in an actual population, *J. Anim. Ecol.*, 48, pp. 863-869.

CASWELL, H. (1989a) *Matrix Population Models. Construction, Analysis, and Interpretation* (Sunderland, MA, Sinauer Assoc. Inc.).

CASWELL, H. (1989b) The analysis of life table response experiments. I. Decomposition of treatment effects on population growth rate, *Ecological Modelling*, 46, pp. 221-237.

CASWELL, H. (1996) Analysis of life table response experiments. II. Alternative parameterizations for size- and stage-structured models, *Ecological Modelling*, 88, pp. 73-82.

CASWELL, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology, *Ecology*, 81, pp. 619-627.

CASWELL, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation* 2nd edn (Sunderland, MA., Sinauer Assoc.).

CASWELL, H., NAIMAN, R. J. & MORIN, R. (1984) Evaluating the consequences of reproduction in complex salmonid life cycles, *Aquaculture*, 43, pp. 123-134.

CATCHPOLE, E. A., MORGAN, B. J. T. & FREEMAN, S. N. (1998) Estimation in parameter-redundant models, *Biometrika*, 85, pp. 462-468.

CONNOR, E. F., FAETH, S. H. & SIMBERLOFF, D. (1983) Leafminers on oak: the role of immigration and in situ reproductive recruitment, *Ecology*, 64, pp. 191-204.

COOCH, E., ROCKWELL, R. F. & BRAULT, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example, *Ecol. Monogr*, 71, pp. 377-400.

CORMACK, R. M. (1964) Estimates of survival from the sighting of marked animals, *Biometrika*, 51, pp. 429-438.

CROSBIE, S. F. & MANLY, B. F. J. (1985) Parsimonious modelling of capture-mark-recapture studies, *Biometrics*, 41, pp. 385-398.

DE KROON, H., PLAISIER, A., GROENENDAEL, J. & CASWELL, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate, *Ecology*, 67, pp 1427-1431.

DESANTE, D. F., BURTON, K. M., SARACCO, J. F. & WALKER, B. L. (1995) Productivity indices and

survival rate estimates from MAPS, a continent-wide programme of constant-effort mist-netting in North America, *J. Appl. Stat.*, 22, pp. 935–947.

DREITZ, V. J., NICHOLS, J. D., HINES, J. E., BENNETTS, R. E., KITCHENS, W. M. & DEANGELIS, D. L. (2002) The use of resighting data to estimate the rate of population growth of the snail kite in Florida, *Journal of Applied Statistics*, this issue

FREEMAN, S. N., MORGAN, B. J. T. & CATCHPOLE, E. A. (1992) On the augmentation of ring recovery data with field information, *J Anim. Ecol.*, 61, pp. 649–657.

GAILLARD, J.-M., FESTA-BLANCHET, M. & YOCCOZ, N. G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival, *Trends in Ecology and Evolution*, 13, pp. 58–63.

GOODMAN, D. (1987) The demography of chance extinction. *In:* M. E. SOULE (Ed) *Viable Populations for Conservation*, pp. 11–34 (Cambridge, UK, Cambridge University Press).

GOULD, W. R. & NICHOLS, J. D. (1998) Estimation of temporal variability of survival in animal populations, *Ecology*, pp. 2531–2538.

GREEN, R. E. (1999) Applications of large-scale studies of demographic rates to bird conservation, *Bird Study*, 46, pp. S279–288.

HANSKI, I. & GILPIN, M. E. (Eds) (1997) *Metapopulation Biology* (San Diego, CA, Academic Press).

HENSLER, G. L. & NICHOLS, J. D. (1981) The Mayfield method of estimating nesting success: a model, estimators, and simulation results, *Wilson Bull.*, 93(1), pp. 42–53.

HEPPELL, S., PFISTER, C. & de KROON H. (Eds) (2000) Elasticity analysis in population biology: methods and applications, *Ecology*, 81, pp. 605–708.

HESTBECK, J. B. & MALECKI, R. A. (1989) Mark-resight estimate of Canada Goose midwinter number, *J. Wildl. Manage.*, 53, pp. 749–752.

HINES, J. E. & NICHOLS, J. D. (2002) Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data, *Journal of Applied Statistics*, this issue.

JOHNSON, D. H. (1979) Estimating nest success: the Mayfield method and an alternative, *Auk*, 96, pp. 651–661.

JOHNSON, D. H., NICHOLS, J. D. & SCHWARTZ, M. D. (1992) Population dynamics of breeding waterfowl. *In:* B. D. J. BATT, A. D. AFTON, M. G. ANDERSON, C. D. ANKNEY, D. H. JOHNSON, J. A. KADLEC & G. L. KRAPU (Eds), *Ecology and Management of Breeding Waterfowl*, pp. 446–485 (Minneapolis, MN, University of Minnesota Press).

JOHNSON, F. A., MOORE, C. T., KENDALL, W. L., DUBOSKY, J. A., CAITHAMER, D. F., KELLEY, JR., J. R. & WILLIAMS, B. K. (1997) Uncertainty and the management of mallard harvests, *Journal of Wildlife Management*, 61, pp. 202–216.

JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration— stochastic model, *Biometrika*, 52, pp. 225–247.

KENDALL, W. L., POLLOCK, K. H. & BROWNIE, C. (1995) A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design, *Biometrics*, 51, pp. 293–308.

KENDALL, W. L., NICHOLS, J. D. & HINES, J. E. (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design, *Ecology*, 78, pp. 563–578.

KUNO, E. (1971) Sampling error as a misleading artifact in 'key factor analysis', *Researches on Population Ecology*, 13, pp. 28–45.

LANCIA, R. A., NICHOLS, J. D. & POLLOCK, K. H. (1994) Estimating the number of animals in wildlife populations. *In:* T. BOOKHOUT (Ed), *Research and Management Techniques for Wildlife and Habitats*, pp. 215–253 (Bethesda, MD, The Wildlife Society).

LEBRETON, J.-D. (1996) Demographic models for subdivided populations: the renewal equation approach, *Theoretical Population Biology*, 49, pp. 291–313.

LEBRETON, J. D., BURNHAM, K. P., CLOBERT, J. & ANDERSON, D. R. (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies, *Ecol. Monogr.*, 62, pp. 67–118.

LEIGH, E. G. (1981) The average lifetime of a population in a varying environment, *J. Theor. Biol.*, 90, pp. 213–239.

LEIRS, H., STENSETH, N. C., NICHOLS, J. D., HINES, J. E., VERHAGEN, R. & VERHEYEN, W. (1997) Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent, *Nature*, 389, pp. 176–180.

LEVIN, L. A., CASWELL, H., DePATRA, K. D. & CREED, E. L. (1987) Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*, *Ecology*, 68, pp. 1877–1886.

LEWONTIN, R. C. & COHEN, D. (1969) On population growth in a randomly varying environment. *Proc. National Acad. Sci.*, 62, pp. 1057–1060.

LINK, W. A. (1999) Modeling pattern in collections of parameters, *J. Wildl. Manage.*, 63, pp. 1017- 1027.

LINK, W. A. & NICHOLS, J. D. (1994) On the importance of sampling variance to investigations of temporal variation in animal population size, *Oikos*, 69, pp. 539- 544.

MANLY, B. F. J. (1977) The determination of key factors from life table data, *Oecologia*, 31, pp. 111- 117.

MANLY, B. F. J. (1979) A note on key factor analysis, *Researches on Population Ecology*, 21, pp. 30- 39.

MAYFIELD, H. (1961) Nesting success calculated from exposure, *Wilson Bulletin*, 73, pp. 255- 261.

MESSERTON-GIBBONS, M. (1993) Why demographic elasticities sum to one: a postscript to de Kroon *et al.*, *Ecology*, 74, pp. 2467- 2468.

MORRIS, R. F. (1959) Single-factor analysis in population dynamics, *Ecology*, 40, pp. 580- 588.

NEWTON, I. (1986) *The Sparrowhawk* (Poyser, UK, Calton).

NEWTON, I. (1998) *Population Limitation in Birds* (San Diego, CA, Academic Press).

NICHOLS, J. D. & HINES, J. E. (1993) Survival rate estimation in the presence of tag loss using joint analysis of capture-recapture and resighting data. *In:* J. D. LEBRETON & P. M. NORTH (Eds) *The Study of Bird Population Dynamics Using Marked Individuals*, pp. 229- 243 (Berlin, Birkhauser Verlag).

NICHOLS, J. D., & POLLOCK, K. H. (1990) Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design, *Ecology*, 71, pp. 21- 26.

NICHOLS, J. D., POLLOCK, K. H. & HINES, J. E. (1984a) The use of a robust capture-recapture design in small mammal population studies: a field example with *Microtus pennsylvanicus*, *Acta Theriol.*, 29, pp. 357- 365.

NICHOLS, J. D. HINES, J. E. & POLLOCK, K. H. (1984b). Effects of permanent trap response in capture probability on Jolly-Seber capture-recapture model estimates, *J. Wildl. Manage.*, 48, pp. 289- 294.

NICHOLS, J. D., MORRIS, R. W., BROWNIE, C. & POLLOCK, K. H. (1986) Sources of variation in extinction rates, turnover and diversity of marine invertebrate families during the Paleozoic, *Paleobiology*, 12, pp. 421- 432.

NICHOLS, J. D., BART, J., LIMPERT, R. J., SLADEN, W. J. L. & HINES J. E. (1992) Annual survival rates of adult and immature eastern population tundra swans, *J. Wildl. Manage.* 56, 485- 494.

NICHOLS, J. D., HINES, J. E., POLLOCK, K. H., HINZ, R. L. & LINK, W. A. (1994) Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data, *Ecology*, 75, pp. 2052- 2065.

NICHOLS, J. D., JOHNSON, F. A. & WILLIAMS, B. K. (1995) Managing North American waterfowl in the face of uncertainty, *Annual Review of Ecology and Systematics*, 26, pp. 177- 199.

NICHOLS, J. D., HINES, J. E., SAUER, J. R., FALLON, F. W., FALLON, J. E. & HEGLUND, P. J. (2000a) A double-observer approach for estimating detection probability and abundance from point counts, *Auk*, 117, pp. 393- 408.

NICHOLS, J. D., HINES, J. E., LEBRETON, J.-D. & PRADEL, R. (2000b) The relative contributions of demographic components to population growth: a direct estimation approach based on reverse-time capture-recapture, *Ecology*, 81, in press.

NORTH, P. M. & MORGAN, B. J. T. (1979) Modeling heron survival using weather data, *Biometrics*, 35, pp. 666- 681.

OTIS, D. L., BURNHAM, K. P., WHITE, G. C. & ANDERSON, D. R. (1978) *Statistical Inference from Capture Data on Closed Animal Population*, pp. 1- 135. (Wildlife Monographs No. 62).

POLLOCK, K. H. (1982) A capture-recapture design robust to unequal probability of capture, *J. Wildl. Manage.*, 46, pp. 757- 760.

POLLOCK, K. H., SOLOMON, D. L. & ROBSON, D. S. (1974) Tests for mortality and recruitment in a *K*-sample tag-recapture experiment, *Biometrics*, 30, pp. 77- 87.

POLLOCK, K. H., NICHOLS, J. D., BROWNIE, C. & HINES, J. E. (1990) *Statistical Inference for Capture-recapture Experiments* (Wildlife Monographs, No. 107).

POWELL, L. A., CONROY, M. J., HINES, J. E., NICHOLS, J. D. & KREMENTZ, D. G. (2000) Simultaneous use of mark-recapture and radio telemetry to estimate survival, movement, and capture rates, *J Wildl. Manage.*, 64, pp. 302- 313.

PRADEL, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate, *Biometrics*, 52, pp. 703- 709.

PULLIAM, H. R. (1988) Sources, sinks, and population regulation, *American Naturalist*, 132, pp. 652- 661.

REXSTAD, E. & BURNHAM, K. P. (1991) User's guide for interactive program CAPTURE. *In*: *Abundance Estimation of Closed Animal Populations* (Fort Collins, CO, Colorado State University).

REYNOLDS, R. E. & SAUER, J. R. (1991) Changes in mallard breeding populations in relation to production and harvest rates, *Journal of Wildlife Management*, 55, pp. 483- 487.

ROGERS, A. (1966) The multiregional matrix growth operator and the stable interregional age structure, *Demography*, 3, pp. 537- 544.

ROUGHGARDEN, J., IWASA, Y. & BAXTER, C. (1985) Demographic theory for an open marine population with space-limited recruitment, *Ecology*, 66, pp. 54-67.

ROUGHGARDEN J., GAINES, S. & POSSINGHAM, H. (1988) Recruitment dynamics in complex life cycles, *Science*, 241, pp. 1460-1466.

SCHOEN, R. (1988) *Modeling Multigroup Populations* (New York, Plenum Press).

SCHWARZ, C. J. (2001) The Jolly-Seber model: more than just abundance, *J. Agric. Biol. Environ. Stat.*, 6, pp. 195-205.

SCHWARZ, C. J., & ARNASON, A. N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations, *Biometrics*, 52, pp. 860-873.

SEBER, G. A. F. (1965) A note on the multiple-recapture census, *Biometrika*, 52, pp. 249-259.

SEBER, G. A. F. (1982) *The Estimation of Animal Abundance and Related Parameters* (New York, Macmillan).

SHENK, T. M., WHITE, G. C. & BURNHAM, K. P. (1998) Sampling-variance effects on detecting density dependence from temporal trends in natural populations, *Ecol. Monogr.*, 68, pp. 445-463.

SKALSKI, J. R. & ROBSON, D. S. (1992) *Techniques for Wildlife Investigations: Design and Analysis of Capture Data* (San Diego, CA, Academic Press).

SMITH, G. W. (1995) A critical review of the aerial and ground surveys of breeding waterfowl in North America, *US Dept. Interior, Biological Science Report*, 5, pp.1-252.

SPENDELOW, J. A. (1982) An analysis of temporal variation in, and the effects of habitat modification on, the reproductive success of Roseate Terns, *Colinial Waterbirds*, 5, pp. 19-31.

SPENDELOW, J. A. & NICHOLS, J. D. (1989) Annual survival rates of breeding adult Roseate Terns (*Sterna dougallii*), *Auk*, 106, pp. 367-374.

VAN GROENENDAEL, J., DEKROON, H. & CASWELL, H. (1988) Projection matrices in population biology, *Trends in Ecology and Evolution*, 3, pp. 264-269.

VARLEY, G. C. & GRADWELL, G. R. (1960) Key factors in population studies, *Journal of Animal Ecology*, 29, pp. 399-401.

WALTERS, C. J. (1986) *Adaptive Management of Renewable Resources*, (New York, Macmillan).

WHITE, G. C. (2000) Population viability analysis: data requirements and essential analyses. *In*: L. BOITANI & T. K. FULLER (Eds) *Research Techniques in Animal Ecology*, pp. 288-331 (New York, Columbia University Press).

WHITE, G. C. & BURNHAM, K. P. (1999) Program MARK: survival rate estimation from both live and dead encounters, *Bird Study*, 46, pp. S120-139.

WILLIAMS, B. K. (1982) Optimal stochastic control in natural resource management: framework and examples, *Ecological Modelling*, 16, pp. 275-297.

WILLIAMS, B. K. (1989) Review of dynamic optimization methods in renewable natural resource management, *Natural Resources Modeling*, 3, pp. 137-216.

WILLIAMS, B. K. (1996) Adaptive optimization and the harvest of biological populations, *Mathematical Biosciences*, 136, pp. 1-20.

WILLIAMS, B. K., NICHOLS, J. D. & CONROY, M. J. (in press) *Analysis and Management of Animal Population* (San Diego, Academic Press).