

And the First One Now Will Later Be Last: Time-Reversal in Cormack–Jolly–Seber Models

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Abstract. The models of Cormack, Jolly and Seber (CJS) are remarkable in providing a rich set of inferences about population survival, recruitment, abundance and even sampling probabilities from a seemingly limited data source: a matrix of 1's and 0's reflecting animal captures and recaptures at multiple sampling occasions. Survival and sampling probabilities are estimated directly in CJS models, whereas estimators for recruitment and abundance were initially obtained as derived quantities. Various investigators have noted that just as standard modeling provides direct inferences about survival, reversing the time order of capture history data permits direct modeling and inference about recruitment. Here we review the development of reverse-time modeling efforts, emphasizing the kinds of inferences and questions to which they seem well suited.

Key words and phrases: Capture–recapture models, contributions to population growth, Cormack–Jolly–Seber models, metapopulations, reverse-time.

“The present now will later be past,
The order is rapidly fading,
And the first one now will later be last,
For the times they are a-changin.”
(Dylan, 1964)

“But I was so much older then,
I’m younger than that now.”
(Dylan, 1965)

“Time is running backwards,
And so is the bride.”
(Dylan, 1989)

1. INTRODUCTION

The 2014 film “The Theory of Everything” ends with a sequence of clips from the life of physicist Stephen Hawking, beginning at age 72 and moving sequentially backward through time to his scientific beginning as a

young Ph.D. student at Cambridge. The sequence mirrored Hawking’s idea that a theory about the beginning of the universe might be deduced by considering its current expansion and then reversing time to consider increasing compactness and the eventual origin. Thus, clever individuals (e.g., Dylan, Hawking) in various disciplines have used time reversal as a mental device to gain insights and inferences about origins.

Cormack–Jolly–Seber (CJS) models (Cormack, 1964, Jolly, 1965, Seber, 1965) consider data that begin with individuals that are marked at a certain sampling occasion and released back into the population. Recaptures of these marked animals in successive sampling occasions provide the raw data for inference about survival rates and probabilities of recapture (Cormack, 1964). Additional modeling of captures of previously unmarked animals permits inference about population size and recruitment of new individuals into the population (Jolly, 1965, Seber, 1965), referred to as Jolly–Seber (JS) modeling. These seminal papers thus demonstrated that it is possible to use capture history data to obtain inferences about not only population size, but also associated rates of gain and loss. These inferences are available by viewing capture history data in the standard temporal sequence, moving from older

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sampling occasions to more recent ones. However, it has been recognized at various times that certain inferences about population dynamics (e.g., recruitment) are more easily and directly obtained by reversing the temporal ordering of capture–recapture data, beginning with final recaptures and moving backward to end with initial captures. In this paper, I will attempt to motivate reverse-time and temporal symmetry versions of CJS models and discuss applications.

2. A BRIEF HISTORY

In his studies of tsetse flies in Tanganyika Territory, C. H. N. Jackson (Jackson, 1936, 1939), with acknowledged statistical assistance from R. A. Fisher, recognized the temporal symmetry of capture–recapture data and developed “positive” and “negative” methods for estimating animal abundance, extending basic ideas presented by Lincoln (1930). The positive method entailed recording the number of animals marked on a certain sampling occasion and following their declining rates of recapture through time. The negative method, in contrast, focused on recaptures of previously marked animals occurring on a particular occasion and on the proportions of these that were originally marked in successively older sampling occasions. Jackson (1936, 1939) emphasized the conceptual similarity of the two approaches and noted that they should give similar abundance estimates. He also considered rates of loss from, and gain to, the population, noting that inferences about these could be based on statistics computed during implementation of his positive and negative abundance estimation methods, respectively.

The seminal papers of Cormack, Jolly and Seber were naturally followed by various extensions and new developments by biostatisticians and quantitative ecologists. D. S. Robson was among those statisticians who developed an important research program in capture–recapture modeling, producing an impressive list of graduate students who became leaders in this field of endeavor. The master’s degree work of one of those students, K. H. Pollock, involved development of formal tests for mortality and recruitment using capture–recapture data. The test for recruitment was developed by reversing the temporal order of capture–recapture data and using an approach equivalent to that for testing for mortality in standard time-ordered data. Specifically, Pollock, Solomon and Robson (1974) noted that this time reversal of data “produces the backward dual of definitions and results given for the forward process” and that “a backward process with recruitment and no

mortality is statistically equivalent to a forward process with mortality and no recruitment.”

Following the observations of Pollock, Solomon and Robson (1974), the first applications for open-population models with time-reversed data used the conditional approach of Cormack (1964) to estimate a “seniority” parameter associated with recruitment of animals to the population (e.g., Pradel, 1996, Pradel et al., 1997). This same approach was even used with data on fossil detections to estimate the periods of origination for invertebrate taxa over geologic time frames (Nichols et al., 1986). Consistent with the original model of Cormack (1964), the description and applications of Nichols et al. (1986) and Pradel (1996) were based on models that assumed a single group of organisms (or taxa) subject to the same probabilities of detection and recruitment. Pradel et al. (1997) used the same approach to model data from cohorts of flamingoes, *Phoenicopterus ruber roseus*, ringed initially as chicks (hence of known age when recaptured), and estimate probabilities of age-specific recruitment. Nichols et al. (2000) introduced the use of multistate models (Arnason, 1972, 1973, Hestbeck, Nichols and Malecki, 1991, Brownie et al., 1993, Schwarz, Schweigert and Arnason, 1993) with reverse-time data in order to draw inferences about contributions to population growth rate by individuals of different ages or from different locations. Pradel (1996) recognized that simultaneous forward- and reverse-time modeling of a single data set made use of all of the information about population dynamics found in capture history data. This synthesis moved beyond the original approaches of Jolly (1965) and Seber (1965) in which survival and capture probabilities were model parameters that were estimated directly, whereas population size and recruitment were treated as random variables that could be obtained as derived estimates.

3. SINGLE STATE MODELING: OPEN POPULATION DATA

3.1 Basic Modeling

Both the CJS model and its reverse-time analog are based on capture–recapture data for individually marked animals. Animals are captured at discrete sampling occasions, typically short in duration. The time periods separating consecutive sampling occasions are typically long, relative to population dynamics, such that gains and losses are likely to occur between occasions. Such sampling with the expectation of population change between successive sampling occasions

will be referred to as “open population sampling,” meaning open to change between occasions. Newly captured animals are given an individually identifiable mark (e.g., leg band, ear tag) and released back into the sampled population. Previously captured animals are recorded as recaptures for that period. Resulting capture history data are represented as vectors of 1’s, denoting captures, and 0’s, denoting no capture, with an entry for each of K total sampling periods of the study. For example, capture history (0 1 1 0 1) indicates an animal that was first caught and marked at sampling period 2 of a 5-period study ($K = 5$). It was recaptured at periods 3 and 5 and not captured at period 4.

The basic CJS model conditions on the initial capture and models the subsequent capture history with two kinds of parameters, one of which describes the ecological survival process and the other the sampling process. Survival (ϕ_t) denotes the probability that an animal alive and in the sampled population at time (sampling period) t is still alive and in the population (i.e., has not died or permanently emigrated) at time $t + 1$. Capture probability (p_t) denotes the probability that a marked animal alive and in the sampled population at time t is captured then. The CJS probability associated with the example capture history (0 1 1 0 1), conditional on initial capture in period 2, is given by

$$\begin{aligned} \text{Pr}_{\text{CJS}}(0\ 1\ 1\ 0\ 1|\text{release in period 2}) \\ = \phi_2 p_3 \phi_3 (1 - p_4) \phi_4 p_5. \end{aligned}$$

The CJS likelihood is then proportional to the product of these conditional probabilities for all animals released during the study.

The reverse-time (RT) analog of the CJS model conditions on the final capture of each animal and models the capture history as a function of capture probabilities and seniority parameters (Pradel, 1996). Capture probabilities are defined as for the CJS model, with the exception that for most RT applications they now apply not only to marked animals but also to new unmarked animals (as in the Jolly–Seber [JS] model, Jolly, 1965, Seber, 1965). The seniority parameter, γ_t , is defined as the probability that an animal alive and in the population at time t was also alive and in the population at time $t - 1$. This parameter thus deals with “survival” into the past, distinguishing new (not a member of the sampled population on a previous sampling occasion) animals from animals that were members of the population at the previous sampling period also. The probability associated with the above capture history under

the RT model can be written as

$$\begin{aligned} \text{Pr}_{\text{RT}}(0\ 1\ 1\ 0\ 1|\text{last capture in period 5}) \\ = \gamma_5 (1 - p_4) \gamma_4 p_3 \gamma_3 p_2 (1 - \gamma_2 p_1). \end{aligned}$$

As for the CJS model, the RT likelihood is proportional to the product of the probabilities for all observed capture histories.

Estimation under the RT model can be accomplished using software developed for the CJS model by simply reversing the capture histories. So for a reverse-time analysis, the above standard-time capture history (0 1 1 0 1) could be entered into CJS software as capture history (1 0 1 1 0). Output labeled as $\hat{\phi}_1$ would be reinterpreted as $\hat{\gamma}_5$, $\hat{\phi}_2$ as $\hat{\gamma}_4$, etc. Program MARK (White and Burnham, 1999) performs RT analyses directly with no need to alter data or to relabel estimators. The estimated capture probabilities for the CJS and RT analyses are identical in sampling situations where no animals are lost on capture (e.g., caught but died or for some other reason were not released) and are otherwise different (with slightly different meanings). Under the full CJS model with all parameters time-specific (ϕ_t, p_t), p_1 cannot be estimated, and only the product $\phi_{K-1} p_K$ (not the separate parameters) can be estimated. Similarly, under RT analyses p_K cannot be estimated, and only the product $\gamma_2 p_1$ is estimable.

3.2 Recruitment

An important reason for the interest in the seniority parameter of an RT analysis is the interpretation of its complement as a measure of recruitment. Thus, $1 - \hat{\gamma}_t$ estimates the probability that an animal in the population at time t is a new recruit, in the sense that it was not in the population at time $t - 1$ (or any time prior to t). Pradel et al. (1997) used RT modeling to estimate age-specific probabilities of first breeding in flamingoes. They conditioned on cohorts of birds ringed as young at breeding colonies and recorded subsequent recaptures when these birds nested at the same breeding colonies. Initial captures as young were removed from the data set (i.e., for each marked individual, the initial “1” of the capture history was changed to “0”) in order to focus the analysis on breeding birds. Times of recapture corresponded to both calendar year and age within each cohort, and the analysis focused on age of first breeding. In this application, $1 - \hat{\gamma}_t$ estimated the probability that a bird recaptured as nesting at age t was nesting for the first time. Cooch et al. (1999) conducted a similar analysis with lesser snow geese (*Anser caerulescens caerulescens*), noting that

this approach does not assume that once recruited, each bird breeds every year thereafter. Instead, if recruited birds are viewed as having some probability of breeding each year, then the capture probability parameter from open population RT models now estimates the product of this post-recruitment breeding probability and probability of capture, conditional on having been recruited as a (potential) breeder (Cooch et al., 1999). The robust design sampling approach (see Section 3.5) permits separate inference about probabilities of capture and breeding.

3.3 Population Growth

Cormack (1964), Jolly (1965) and Seber (1965) provided estimators for survival (ϕ_t) and capture (p_t) probabilities. With the additional assumption that capture probabilities apply to unmarked as well as previously marked animals, Jolly (1965) and Seber (1965) noted that abundance or population size could be estimated as

$$(1) \quad \hat{N}_t = \frac{n_t}{\hat{p}_t},$$

where n_t denotes the number of animals (marked + unmarked) captured at time t . They also noted that new recruits to the population at time $t + 1$ could be estimated as

$$\hat{B}_t = \hat{N}_{t+1} - \hat{\phi}_t \hat{N}_t.$$

So it has long been clear that all of the components of population growth could be estimated from a capture–recapture data set. Pradel (1996) recognized that a combination of forward-time and reverse-time views could be used to estimate population growth rate and recruitment rate directly. Briefly, he proposed modeling a capture–recapture data set simultaneously with probabilities of capture (p_t), survival (ϕ_t) and seniority (γ_t). Pradel (1996) further noted that by equating two different ways of writing the expected number of animals alive and in the population at successive times, it is possible to write the expectation of realized population growth rate directly as the ratio of seniority and survival parameters. Specifically, consider the set of animals alive and in the focal population in two successive time periods, t and $t + 1$. The expected value of the number of animals in this set can be written either as the expected number of animals at time t that survived until period $t + 1$ ($\phi_t N_t$) or as the expected number of animals at time $t + 1$ that were also in the population at time t ($\gamma_{t+1} N_{t+1}$). Equating these two

expectations and rearranging leads to the following estimator for realized population growth rate, λ_t :

$$E(\lambda_t) = E\left[\frac{N_{t+1}}{N_t}\right] = \frac{\phi_t}{\gamma_{t+1}}.$$

The above reference to *realized* population growth rate is intended to draw a distinction between the ratio of actual population sizes in two successive periods (the above estimator) and the asymptotic growth rate (e.g., Caswell, 2001) defined by any set of survival and reproductive rates (more generally, rates of loss and gain) assumed to remain constant over time. The notation λ_t indicates time-specificity (t), thus distinguishing this realized population growth rate from a time-invariant, asymptotic rate.

A natural way to define reproductive or recruitment rate, f_t , is the number of new recruits at time $t + 1$ per animal in the population at time t , such that

$$\lambda_t = \phi_t + f_t.$$

The original Pradel (1996) model (ϕ_t, γ_t, p_t) can thus be reparameterized in multiple ways, including (ϕ_t, λ_t, p_t) and (ϕ_t, f_t, p_t), permitting direct modeling of realized population growth rate and/or recruitment rate as functions of covariates, for example. The combination of forward- and reverse-time modeling has thus led to a number of models that focus on different parameters relevant to population dynamics (Pradel, 1996; also see Williams, Nichols and Conroy, 2002, pages 511–518). The ability to estimate the realized population growth rate as a derived parameter using the formulation of Jolly (1965) and Seber (1965) was noted above. The superpopulation approach of Crosbie and Manly (1985) and Schwarz and Arnason (1996) provides yet another approach to inference about recruitment and realized population growth, and relationships among all three approaches are discussed by Nichols and Hines (2002) and Barker, Cooch and Schwarz (2002).

Population ecologists often profess interest in the relative contributions of different population processes or components to population growth. For example, both the retrospective approach of life table response experiments and the prospective concepts of sensitivity and elasticity of asymptotic population growth rate to elements of population projection matrices reflect this interest (Caswell, 2001). The seniority parameter of single-age capture–recapture can be viewed as a binomial parameter separating members of a population at any time, $t + 1$, into contributions associated with

survivors from the previous period (S_t) and new animals (B_t) (see Nichols et al., 2000):

$$\begin{aligned} E[\lambda_t] &\approx \frac{E(N_{t+1})}{E(N_t)} = \frac{E(S_t) + E(B_t)}{E(N_t)} \\ &= \frac{\gamma_{t+1}\bar{N}_{t+1} + (1 - \gamma_{t+1})\bar{N}_{t+1}}{\bar{N}_t}, \end{aligned}$$

where \bar{N}_t denotes $E(N_t)$.

Thus, for example, the proportional contribution of survivors (“old animals”) to λ_t is given by γ_{t+1} and that of new recruits by $(1 - \gamma_{t+1})$. These RT parameters (e.g., γ_{t+1}) provide a nonasymptotic approach to questions similar to those for which the asymptotic approaches of sensitivity and elasticity (for prospective analyses) and life table response experiments (for retrospective analyses) were developed (see Caswell, 2001). For example, the contribution parameters can be used to address questions such as the following: if survival had been reduced by factor α , by how much would the realized population growth rate have been reduced? RT analysis yields the answer: $\alpha\gamma_{t+1}$.

At the beginning of this section it was noted that both Jolly (1965) and Seber (1965) showed how to estimate all of the parameters associated with population change from capture–recapture data. Similarly, we do not have to resort to RT modeling to estimate the proportional contribution parameters, γ_t . For example, under the original Jolly–Seber parameterization, γ_t can be estimated as a derived parameter as follows:

$$\hat{\gamma}_t = \frac{\hat{\phi}_{t-1}\hat{N}_{t-1}}{\hat{N}_t}.$$

The Pradel (1996) model (ϕ_t, f_t, p_t) essentially decomposes λ_t into additive survival and recruitment components such that γ_t can be estimated as (Williams, Nichols and Conroy, 2002, page 514)

$$\hat{\gamma}_t = \frac{\hat{\phi}_{t-1}}{\hat{\phi}_{t-1} + \hat{f}_{t-1}}.$$

Thus, RT modeling is not the only way to draw inferences about proportional contributions of demographic parameters to realized population growth. Instead RT modeling simply provides a natural way to draw such inferences and permits the direct modeling of the contribution parameters as functions of covariates, for example.

3.4 Other Applications: Paleobiology

Paleobiologists interested in rates of taxonomic origination and extinction face the same basic problem as

that faced by ecologists studying free-ranging animal populations. For example, just as the population ecologist who sets traps to catch small mammals in a field can never hope to catch every animal in the field, paleobiologists who sample rock or sediment from different geologic ages cannot hope to find fossil remains of every taxon that was extant during the period represented by the sample. Capture–recapture methods such as CJS models that explicitly deal with detection probabilities <1 are well suited to inference in paleobiology (Nichols and Pollock, 1983). In paleobiological applications, detection histories correspond to specific identifiable fossil taxa rather than individual animals. For each taxon within some taxonomic group of interest, records of detections (denoted as 1) or nondetections (denoted as 0) at different points in geologic time provide data that can be analyzed using CJS models, with ϕ_t representing the complement of extinction or the probability that a taxon extant in geologic period t is still extant at period $t + \Delta t$, where Δt is the time separating two consecutive geologic periods. Detection probability, p_t , is interpreted as the probability that at least one fossil representative of the focal taxon is detected, given that the taxon was extant at that geologic period. The complement of the RT seniority parameter, $1 - \gamma_t$, estimates the probability that a taxon extant at period t is new in the sense that it originated during the interval between period $t - \Delta t$ and t (Nichols et al., 1986, Connolly and Miller, 2001a, Connolly and Miller, 2001b). Similarly, it is possible to focus on f_t as a per taxon origination rate (Connolly and Miller, 2001b). These CJS and JS methods have not been widely adopted in paleobiology but should provide much stronger inferences than the common analyses assuming that the duration of a taxon is directly given by geologic periods of first and last detection.

4. SINGLE STATE MODELING: ROBUST DESIGN

4.1 Basic Modeling

All of the above applications of RT modeling have been based on so-called “open” population data, in which consecutive sampling occasions are separated by enough time that gains and losses to the population are likely to occur. In contrast, “closed” population data are based on sampling occasions that are sufficiently close together in time that neither gains nor losses are expected (e.g., Otis et al., 1978, Chao and Huggins, 2005). The “robust design” of Pollock (1982) combines sampling at these two different temporal scales, and includes multiple “secondary” sampling periods

that occur close together in time within “primary” periods, defined as the periods between which the population is assumed to be open to gains and losses. The original motivation for the robust design was based on the biases associated with abundance estimates based on open population models such as JS, when certain assumptions were violated. Closed models had been developed to relax these assumptions, permitting more robust inference about abundance.

The robust design and the associated ability to estimate abundance and capture probability using closed population models provide several advantages for RT modeling. One advantage is the ability to relax the critical assumption for RT modeling that capture probabilities are the same for animals that have and have not been captured before. Capture–recapture data within primary periods can be grouped by previous capture status (caught before or not), and tests of equal capture probabilities for these two groups can be conducted. If evidence of differences is found, the 2-group structure can be retained for RT modeling. Another advantage of the robust design is the ability to estimate parameters that cannot be estimated under standard JS or RT models. For example, multi-age CJS models that use open population data (e.g., Pollock, 1981) do not permit inference about the capture probability for the youngest age class. However, multi-age RT modeling requires the ability to estimate capture probability of young animals, and this is possible under the robust design.

Yet another advantage of the robust design for RT modeling concerns the phenomenon of temporary emigration. In the modeling of open populations, “exterior 0’s” occurring at the beginning (before the first “1”) or end (after the final “1”) of a capture history are ambiguous, in the sense that the animal could have been present but gone undetected or it could have been absent from the population. This ambiguity can be resolved with the help of “interior 0’s” that occur at some sample period after the first detection and before the final detection. For example, the illustrative capture history from above (0 1 1 0 1) contains an exterior 0 (period 1) and an interior 0 (period 4). The animal could have been present in period 1 and simply not caught, or it may not have yet entered the sampled population. But the 0 for period 4 occurred for an animal that was present in the population; we know this because we caught it before and after period 4, and we thus know to model this 0 with $(1 - p_4)$.

One consequence of this type of CJS modeling is that it requires the assumption that temporary emigration (an animal is still in the overall population but simply

absent from the area exposed to sampling efforts) is either absent or occurs at random [probability of temporary emigration is the same for all animals in the overall population (Burnham, 1993, Kendall, Nichols and Hines, 1997)], in which case temporary emigration is simply a component of nondetection. The two most widely used approaches for relaxing the assumption of no (or random) temporary emigration are to impose constraints (typically constraining parameters to be constant over time) on the CJS model (e.g., Kendall and Nichols, 2002, Schaub et al., 2004) or to use the “robust design” (Pollock, 1982) for sampling. If the population is assumed to be closed (no gains or losses occur) over the secondary samples, then these samples permit estimation of detection probability (e.g., Otis et al., 1978, Chao and Huggins, 2005) for animals that have not temporarily emigrated, hence providing a way to separate probabilities of detection and temporary emigration.

Indeed, both approaches to dealing with temporary emigration permit an interior 0 to reflect either of two possible events: the animal is present in the sampled area and not detected, or the animal is temporarily absent from the area exposed to sampling and thus has 0 probability of being detected. Both of these approaches are available for use with RT modeling of capture–recapture data. The robust design is the more flexible of the two approaches and is hence the focus of this section. It should be noted that the original robust design approach to dealing with temporary emigration (Kendall, Nichols and Hines, 1997) was based on the CJS framework and viewed as a single state problem. However, later treatments (e.g., Kendall and Nichols, 2002) viewed temporary emigration as a multistate problem (see Section 5), with two observation states, temporary emigrants with detection probability $p = 0$ and nonemigrants with $p > 0$.

There are many potential reasons for wanting to disentangle capture probability and the probability of temporary emigration in both standard and RT modeling. One example was noted in Section 3.2 on inferences about recruitment. Cooch et al. (1999) used RT modeling to estimate age-specific probabilities of recruiting to the adult breeding population for lesser snow geese. They noted that all adults that had been recruited to the breeding population did not necessarily breed each year, instead foregoing breeding in some years (exhibiting temporary emigration) and being unavailable for sampling at breeding colonies. In the case of random temporary emigration with open population data, the estimated capture probability from a RT analysis

estimates the product of the probability of capture and the probability of nonbreeding or temporary emigration, and other parameters are estimated without bias. RT modeling with data collected under the robust design permits direct estimation of the probability of nonbreeding for recruited adults. If the probability of nonbreeding in a year is not random, but instead dependent on breeding status in the previous year (i.e., Markovian), then analysis using RT analogs of CJS models will yield biased estimates of all model parameters (Kendall, Nichols and Hines, 1997). However, RT models using robust design data permit reasonable inferences even in the case of Markovian temporary emigration (Kendall, Nichols and Hines, 1997). In addition to standard inferences about animal population dynamics, the use of the robust design as a means of separating nondetection and temporary absence is very important in two specific applications of capture–recapture modeling: community modeling and occupancy modeling.

4.2 Other Applications: Community Modeling

Modeling of animal or plant communities is often based on lists of species detected in a sampled area at various sampling occasions under the robust design. During the spring of each year, for example, biologists might compile a list of birds detected for perhaps three consecutive weeks. Species identities are substituted for individual marked animal identities, such that detection histories contain information on the sampling periods in which each species was and was not detected. For example, a detection history of (1 1 0 0 0 0) would indicate a species that was detected during the first two secondary sampling periods of primary period 1 and was not detected at any of the three secondary sampling periods of primary period 2. Closed population models are then used with secondary period data within each primary period to estimate detection probabilities and the total number of species present for that primary period, recognizing that some species were likely present but undetected in some or even all of the secondary sampling periods. Sampling in multiple primary periods (e.g., years in this example) permits inference about the probability that a species present in primary period t is absent (locally extinct, ε_t) in period $t + 1$. Local extinction of this sort is typically viewed as a form of temporary emigration, in the sense that the species is still in the species pool associated with the local site, but simply not present at the site in a particular year. In community

studies, local extinction is thus equated with the parameter reflecting temporary emigration in population-dynamic modeling. Permanent extinction (elimination from the species pool) is viewed as rare and thus typically not considered in such models, but can be readily incorporated under a CJS framework as $1 - \phi_t$.

Reverse-time modeling is carried out by conditioning on species detected at primary period $t + 1$ and estimating (again using closed models) how many of these species were locally present the previous period (γ_{t+1}). The complement of the RT seniority parameter ($1 - \gamma_{t+1}$) can be viewed as species turnover, as it estimates the fraction of species present at $t + 1$ that was not present the previous period, t , and thus immigrated and colonized the local site (Nichols et al., 1998). The distinction between this application and the fossil analyses described above is that the fossil analyses dealt with long-term taxonomic origination and extinction, usually either globally or over large areas. Analyses are based on a geologic time scale, and extinction in this paleobiological case is permanent. In contrast, the community modeling application of RT modeling is based on a potential pool of species, each of which may or may not be locally present in the area exposed to sampling efforts. Extinction, immigration and turnover are thus viewed as local phenomena because origination of new species and permanent extinction are extremely rare events on an ecological time scale. So RT modeling is useful for inference about community dynamics but requires sampling that corresponds to the robust design. Original uses of this RT approach were based on a two-step, *ad hoc* approach to inference, primarily because the expected substantial heterogeneity in species detection probabilities dictated use of jackknife estimators for abundance that permitted heterogeneous detection probabilities (Otis et al., 1978).

4.3 Other Applications: Occupancy Modeling

Multiseason occupancy modeling requires detection–nondetection sampling of multiple sites or sample units over time for a single focal species (MacKenzie et al., 2003, MacKenzie et al., 2006). Within each primary period, multiple visits provide a detection history for each site. These histories have the same basic appearance as the capture histories for individual animals, vectors of 1's and 0's indicating detection, or not, at each secondary period within each primary period. Occupancy dynamics at a particular site are modeled as a first order Markov process, with probability of occupancy in primary period $t + 1$ being different for sites that were (complement of local extinction probability)

and were not (local probability of colonization) occupied in primary period t . As with community dynamics, local extinction is viewed as temporary, not permanent, and is thus equivalent to temporary emigration in population models (Barbraud et al., 2003, MacKenzie et al., 2003).

RT modeling permits direct inferences about parameters relevant to occupancy dynamics. Simply reversing the time order of data and using a standard multiseason occupancy model (MacKenzie et al., 2003, MacKenzie et al., 2006) yields RT estimators corresponding to the local colonization and extinction parameters of forward-time analyses. The “colonization” probability of RT analysis now estimates the probability that a site not occupied at time t was occupied at time $t - 1$. Restated, it estimates the expected fraction of all unoccupied sites at t that were occupied at $t - 1$, but went locally extinct. The “local extinction” probability of RT analysis now estimates the probability that a site occupied at time t was not occupied at $t - 1$. This parameter can thus be viewed as a “turnover” metric, reflecting the expected fraction of sites occupied at time t that are newly occupied (were not occupied in primary period $t - 1$). Applications of the turnover estimator might include predictions of higher turnover for areas experiencing species invasions or for edges of focal species ranges that are becoming more favorable because of climate change.

5. MULTISTATE MODELING

5.1 Basic Modeling

Arnason (1972, 1973) generalized the CJS model to multiple geographic strata, permitting time- and location-specific capture probabilities, p_t^r , and probabilities of individuals in stratum r at time t both surviving and being in a specific location s at time $t + 1$, $\phi_t^{r,s}$. Multistate CJS modeling (denoted as MS) saw virtually no use for two decades following the papers by Arnason (1972, 1973), but was resurrected and further developed in the early 1990s (Hestbeck, Nichols and Malecki, 1991, Schwarz, Schweigert and Arnason, 1993, Brownie et al., 1993) and is now widely used in animal population ecology (Lebreton et al., 2009). It was recognized early on that the concept of “state” could apply not only to an animal’s current location but also to characteristics of the animal itself, such as body mass (Nichols et al., 1992) or reproductive condition (Nichols et al., 1994). RT multistate modeling can be useful when state is defined as location, animal age and other individual characteristics.

Sampling for MS models is similar to that for which CJS models were developed, with the addition that animal state is recorded at each detection. For example, MS capture history (1 0 2) denotes an animal caught in state 1 at sampling occasion 1, released, not caught at sampling occasion 2, but caught at sampling occasion 3 and determined to be in state 2. The associated probability can be written as

$$\begin{aligned} \Pr_{\text{MS}}(1\ 0\ 2|\text{release at period 1 in state 1}) \\ = [\phi_1^{11}(1 - p_2^1)(\phi_2^{12}) + \phi_1^{12}(1 - p_2^2)(\phi_2^{22})]p_3^2. \end{aligned}$$

The additive terms in brackets reflect the uncertainty associated with the animal’s state at occasion 2, when it was not detected. As with the CJS model, the MS likelihood is proportional to the product of probabilities associated with the capture histories of all animals released during the study.

The time-reversed analog of the MS model conditions on the final capture of each animal and models the capture history as a function of state-specific capture probabilities and seniority parameters (Nichols et al., 2000). Capture probabilities are defined as for the MS model, with the exception that for most RT applications they now apply not only to marked animals but also to new unmarked animals. The seniority parameter, $\gamma_t^{r,s}$, is defined as the probability that an animal of state r that is alive and in the population at time t was alive in the population in state s at time $t - 1$. This parameter thus deals with “survival” into the past and with state transitions. The probability associated with the above capture history under the multistate reverse-time (MRT) model can be written as

$$\begin{aligned} \Pr_{\text{MRT}}(1\ 0\ 2|\text{last capture at period 3 in state 2}) \\ = [\gamma_3^{22}(1 - p_2^2)\gamma_2^{21} + \gamma_3^{21}(1 - p_2^1)\gamma_2^{11}]p_1^1. \end{aligned}$$

Additive terms again reflect state uncertainty in occasion 2 when the animal is not caught, and the likelihood is again proportional to the product of probabilities associated with all of the captured animals.

When all captured animals are released back into the population (e.g., no removals or deaths on capture), the p_t^r from both forward and reverse-time modeling are the same. State-specific abundance can be estimated using these capture probability estimates by simply adding state-specific superscripts to equation (1):

$$(2) \quad \hat{N}_t^r = \frac{n_t^r}{\hat{p}_t^r}.$$

5.2 Geographic Strata

Animal populations are seldom isolated to the extent that population growth depends only on local rates of survival and reproduction. It is much more common for animals to move among locations (Clobert et al., 2001), with animals from one location contributing recruits to other local populations. This reality has led to the concept of metapopulations (e.g., Hanski, 1998) and to ideas about sources, sinks and, more generally, contributions of specific locations to population growth in other locations and in entire movement-linked systems (e.g., Holt, 1984, Pulliam, 1988, Runge, Runge and Nichols, 2006). MRT modeling provides relevant inferences about the proportional contributions of animals from multiple locations to other specific locations or to a system of locations.

Consider two study areas, denoted 1 and 2, in which animals are marked, released and recaptured over time. Sampling occasions are temporally separated such that we expect changes to occur to the populations between successive occasions. The sampling situation is thus that for which CJS models were developed, except that sampling is carried out on two, rather than single, populations. Define S_t^{rs} as the number of animals in location s at time $t + 1$ that were in location r at time t , and B_t^s as the number of recruits to location s at $t + 1$ from outside the 2-population study system. We can write the abundance at location 1 as the sum of three components:

$$(3) \quad N_{t+1}^1 = S_t^{11} + S_t^{21} + B_t^1.$$

The three terms in the sum represent the survivors from time t that remain in location 1, the animals from location 2 that moved into location 1 and the immigrants to location 1 from outside the study system. Each of these three terms can be viewed as a multinomial random variable conditional on N_{t+1}^1 and parameters γ_{t+1}^{1s} , representing the probability that a member of N_{t+1}^1 was in location s at time t . Thus, γ_{t+1}^{11} is associated with S_t^{11} , γ_{t+1}^{12} with S_t^{21} , and $1 - \gamma_{t+1}^{11} - \gamma_{t+1}^{12}$ with B_t^1 .

Based on equations (2) and (3), the expectation of realized population growth rate for location 1 can be written as

$$\begin{aligned} E[\lambda_t^1] &\approx \frac{E(S_t^{11}) + E(S_t^{21}) + E(B_t^1)}{E(N_t^1)} \\ &= \frac{\gamma_{t+1}^{11} \bar{N}_{t+1}^1 + \gamma_{t+1}^{12} \bar{N}_{t+1}^1 + (1 - \gamma_{t+1}^{11} - \gamma_{t+1}^{12}) \bar{N}_{t+1}^1}{\bar{N}_{t+1}^1}, \end{aligned}$$

where \bar{N}_t^1 also denotes $E(N_t^1)$.

Thus, the γ_t^{rs} reflect the proportional contributions of each study system location to realized population growth at location r . As with single-state RT modeling, these contribution parameters can be used to address questions about realized population growth rate similar to those addressed about asymptotic λ using approaches such as sensitivity, elasticity and life table response experiments (Caswell, 2001). As an example, the proportional reduction in population growth rate for location 1 (λ_t^1) expected to have resulted from a proportional reduction α in the contribution from location 2 (a reduction in either movement from 2 to 1 or survival of animals from state 2) would be given by $\alpha \gamma_{t+1}^{12}$.

In many cases interest will be focused on the population size and growth of the entire system rather than on one of its components. The MRT framework can be useful for system-wide inferences as well. Population growth rate for a 2-patch system can be written as

$$(4) \quad \lambda_t = \frac{N_{t+1}^1 + N_{t+1}^2}{N_t^1 + N_t^2},$$

where the absence of a superscript denotes the entire system rather than a specific location within it. As for a single location, decomposition of system-wide λ_t can be accomplished via

$$\begin{aligned} E[\lambda_t] &\approx (E(S_t^{11}) + E(S_t^{21}) + E(B_t^1) + E(S_t^{22}) \\ &\quad + E(S_t^{12}) + E(B_t^2)) / (E(N_t^1) + E(N_t^2)) \\ &= (\gamma_{t+1}^{11} \bar{N}_{t+1}^1 + \gamma_{t+1}^{12} \bar{N}_{t+1}^1 + (1 - \gamma_{t+1}^{11} - \gamma_{t+1}^{12}) \\ &\quad \cdot \bar{N}_{t+1}^1 + \gamma_{t+1}^{22} \bar{N}_{t+1}^2 + \gamma_{t+1}^{21} \bar{N}_{t+1}^2 \\ &\quad + (1 - \gamma_{t+1}^{22} - \gamma_{t+1}^{21}) \bar{N}_{t+1}^2) / (\bar{N}_t^1 + \bar{N}_t^2), \end{aligned}$$

where \bar{N}_t^r denotes $E(N_t^r)$. In the above expression, members of each state of the system-wide population at time $t + 1$ are classified into their respective components from the previous time (t) using the γ_{t+1}^{rs} .

As when focusing on the population of a specific location, the γ_{t+1}^{rs} parameters can be used to assess the relative effects on system-wide λ_t of proportional reductions of component vital rates. For example, consider the relative effect on λ_t of a reduction α in the survival rate of animals in location 1 between times t and $t + 1$. This reduction influences animals in location 1 at time t that remained in location 1 as well as animals that moved from locations 1 to 2, and the relative effect on system-wide λ_t can be estimated as

$$\frac{\alpha(\hat{\gamma}_{t+1}^{11} \hat{N}_{t+1}^1 + \hat{\gamma}_{t+1}^{21} \hat{N}_{t+1}^2)}{\hat{N}_{t+1}^1 + \hat{N}_{t+1}^2}.$$

This expression weights the parameter estimates of $\gamma_{t+1}^{r,s}$ by the estimated proportional compositions of the local populations to which they pertain.

5.3 Age Strata

Age is often associated with variation in vital rates and is thus frequently incorporated in capture–recapture modeling. Pollock (1981) developed the first age-specific extension of CJS models for sampling situations in which age of newly captured individuals can be determined without error. Age determination in many species is limited to first year (young) and after first year (adult) designations. In the Pollock (1981) model, age transitions are naturally viewed as deterministic; that is, a young animal caught in year t will always be an adult in year $t + 1$. Adults actually include many different annual age classes (2 year olds, 3 year olds, etc.), but vital rates are often assumed to be the same for members of this age category. RT models that incorporate age-specificity and that include a multi-age “adult” class differ from standard time models in that transitions from the adult to the young age class, for example, cannot be viewed as deterministic. Because a year 2 adult cannot be distinguished from a year 3 or 4 adult, we are forced to view age transitions in RT as stochastic, so MRT models provide the appropriate structure.

In addition to stochastic age transitions, another aspect of RT modeling that differs from standard time CJS modeling is the inability to estimate capture probability for young animals under a standard design for open capture–recapture models. Pollock’s (1981) age-specific modeling of survival and capture probabilities conditions on the initial capture and release of an animal, so the capture probability of young animals never appears in the modeling and is simply not relevant to inference about survival. MRT modeling conditions on final capture and prior capture probabilities are required in the modeling. However, if young animals are only available as initial captures and can only be recaptured when they become adults, standard open model designs do not permit inference about capture probability for young. The robust design (Section 4) solves this problem by permitting inference about capture probabilities of young based on captures and recaptures occurring within a season.

The relevance of age-specific RT models to ecology concerns the source of new adults in a local population. Although definitions of ecological sources and sinks (Pulliam, 1988) appearing in the literature are varied, many draw a distinction between local populations that

maintain a realized population growth rate $\lambda_t \geq 1$ via in situ reproduction versus those that require immigrants from elsewhere to maintain population growth. Age-specific RT models can be used to decompose the realized growth rate of the adult population into components associated with adult survivors, young survivors (in situ reproduction) and immigrants, thus permitting assessments about the relative importance of immigration to the local population.

Using parenthetical superscripts to denote young (age 0) and adults (age 1), we can write the realized population growth rate for adults as

$$\lambda_t^{(1)} = \left[\frac{N_{t+1}^{(1)}}{N_t^{(1)}} \right].$$

Define $\gamma_{t+1}^{(a)}$ as the probability that an adult animal at time $t + 1$ was a surviving animal of age a in the local population at time t . The parameters $\gamma_{t+1}^{(0)}$ and $\gamma_{t+1}^{(1)}$ can then be viewed as multinomial probabilities and used to decompose the adult abundance at time $t + 1$, and thus the realized population growth rate, into 3 components:

$$(5) \quad N_{t+1}^{(1)} = S_t^{(01)} + S_t^{(11)} + B_t^{(1)}.$$

Thus, an adult at time $t + 1$ may be a surviving young animal, $S_t^{(01)}$, with probability $\gamma_{t+1}^{(0)}$, a surviving adult, $S_t^{(11)}$, with probability $\gamma_{t+1}^{(1)}$, or an immigrant, $B_t^{(1)}$, with probability $1 - \gamma_{t+1}^{(0)} - \gamma_{t+1}^{(1)}$.

As in the development of Section 5.2, the expected value of realized adult population growth rate can be written in terms of these components, and thus the reverse-time parameters:

$$\begin{aligned} E[\lambda_t^{(1)}] &\approx \frac{E(S_t^{(01)}) + E(S_t^{(11)}) + E(B_t^{(1)})}{E(N_t^{(1)})} \\ &= \frac{\gamma_{t+1}^{(0)} \bar{N}_{t+1}^{(1)} + \gamma_{t+1}^{(1)} \bar{N}_{t+1}^{(1)} + (1 - \gamma_{t+1}^{(0)} - \gamma_{t+1}^{(1)}) \bar{N}_{t+1}^{(1)}}{\bar{N}_t^{(1)}}. \end{aligned}$$

As in Section 5.2, the decomposition allows us to directly address questions about changes to realized population growth that would have occurred had specific components, or their associated vital rates, been increased or reduced. For example, we can compute the realized population growth rate that would have been expected if immigration had been eliminated (the growth rate claimed to be relevant to source-sink classification) as follows: $\lambda_t^{(1)} (\gamma_{t+1}^{(0)} + \gamma_{t+1}^{(1)})$. By focusing

on the probability that a member of $N_{t+1}^{(1)}$ is a member of a specific group of contributing components, the MRT $\gamma_{t+1}^{(a)}$ provide a natural parameterization for inferences about relative contributions.

This development of RT modeling inferences about age-specific contributions to population growth has been based on the simple case of 2 age classes, a young class, the duration of which is the same as the period between sampling occasions, and an adult class that includes all animals older than young (e.g., >1 year old in most applications). However, extensions of the forward time approach of Nichols and Pollock (1990) permit inference about age-specific contributions to an adult age class in the more general case of age-specific probabilities of entering this class (Cooch, Rockwell and Brault, 2001). For example, many seabirds and geese exhibit delayed reproduction, in the sense that they do not all return to the breeding colony to breed (and to be exposed to sampling efforts) at one year of age. Rather, some may return at age 1, others at age 2, etc., as governed by age-specific probabilities of recruiting to the adult breeding population. Although I am not aware of attempts to apply RT thinking to this problem, it may be possible to develop a RT model with seniority parameters indexed by hatch year that accounts for age-specific breeding and survival probabilities, as well as for detection probabilities of 0 for animals that are alive but have not yet been recruited to the adult, breeding population.

5.4 Example Application: Metapopulation Contributions

Concepts of source and sink populations were introduced by Holt (1984) and Pulliam (1988) and are widely used in ecological literature and thinking. Sinks are frequently defined as local populations that are maintained by immigration; that is, within-population survival and in situ reproduction do not produce a realized population growth rate $\lambda_t \geq 1$. However, this view does not consider emigration from the focal population to other local populations. The related concept of a metapopulation concerns multiple local populations of conspecifics linked by some movement of individuals (e.g., Hanski, 1998). Runge, Runge and Nichols (2006) recommended a shift from efforts to categorize local populations as sources or sinks, to efforts to estimate contributions of local populations to the entire metapopulation systems of which they are a part. This latter view acknowledges that such contributions include both internal focal population dynamics and export of emigrants to other local populations within the system.

Runge, Runge and Nichols (2006) defined the per capita contribution of focal population r at time t as the average number of individuals in the metapopulation system at time $t + 1$ contributed by each individual in the focal population r at time t . Sanderlin et al. (2012) extended this concept to that of relative contributions, c_t^r , the probability that a member of the metapopulation system at time $t + 1$ was contributed by local population r , or roughly the proportional contribution of local population r to realized metapopulation growth between t and $t + 1$. The conceptual and inferential framework for such metapopulation contributions is that presented above (Section 5.2) for multiple locations, with a focus on system-wide realized population growth, λ_t .

For a system comprised of m local populations, the realized population growth rate can be written as

$$(6) \quad \lambda_t = \frac{\sum_{r=1}^m N_{t+1}^r}{\sum_{r=1}^m N_t^r}.$$

Here we define N_t^r as the population of adults in focal population r , although the approach is easily generalized to include new young when estimating realized population growth rate. “State” can be defined by both age (young, first year, denote as state $a = 0$; adult, after first year, denote as state $a = 1$) and local population, leading to the following MRT seniority parameters, $\gamma_{t+1}^{rs(a)}$, defined as the probability that an adult present in local population r at time $t + 1$ was an animal of age $a = 1, 0$ in population s at time t (see Sanderlin et al., 2012). For example, the relative contribution of a particular location state to the realized metapopulation growth rate can be obtained as

$$c_t^s = \frac{\sum_{r=1}^m N_{t+1}^r (\gamma_{t+1}^{rs(1)} + \gamma_{t+1}^{rs(0)})}{\sum_{r=1}^m N_{t+1}^r}.$$

The numerator expresses the contributions of population s to each component of the metapopulation, N_{t+1}^r , and thus to system population growth. If the system is closed, in the sense of no immigration from outside the m local populations, then $\sum_{s=1}^m c_t^s = 1$. However, in the general case of immigration from outside the system, we can express this proportional contribution of immigration (denoted with superscript 0) to realized population growth between t and $t + 1$ as

$$c_t^0 = 1 - \sum_{s=1}^m c_t^s.$$

Sanderlin et al. (2012) conducted a robust design capture–recapture study of a metapopulation of banner-tailed kangaroo rats, *Dipodomys spectabilis*, distributed among 8 local populations in southeast Arizona, USA. The study covered 7 years of annual sampling (late July and early August each year), and they were able to designate captured individuals as adult or young (first year). They used reverse-time modeling to estimate relative contributions of each local population and to test a priori hypotheses about sources of variation in these contributions. More specifically, they computed a contribution matrix, providing model-averaged estimates of the relative contribution of every local population (plus outside immigration) to every other local population. For any pair of local populations, contributions of one local population to another were greater for young animals than adults, consistent with the tendency for greater dispersal of young animals (Skvarla et al., 2004). Contributions via dispersal were larger for nearby local populations than for distant ones, as expected. More central local populations received smaller contributions from extra-system immigration than more peripheral local populations. Model-averaged estimates of local population abundance and relative contributions of each local population to the entire metapopulation system are presented in Table 1 for two sets of years, selected a priori as appearing to have relatively high and low densities system-wide. Estimates of immigration from outside the study system were larger than expected, a finding common to the few cases where these contributions have been estimated (e.g., Connor, Faeth and Simberloff, 1983, Nichols and Pollock, 1990, Saracco, DeSante and Kaschube, 2008).

Theory for metapopulation dynamics has outpaced empirical work (Kawecki and Ebert, 2004), and approaches based on MRT modeling seem well suited to testing theoretical ideas. Decomposition of metapopulation change into contributions of specific local populations should facilitate the testing of many mechanistic hypotheses about metapopulation dynamics. In addition to such testing, the described contribution metrics provide a currency that might be used to assign relative values to different local populations within a conservation setting. In the context of management decisions for metapopulation systems, MRT provides a convenient means of predicting both local and system-wide effects of actions that target specific local populations.

TABLE 1
Model-averaged estimates of abundance \hat{N}^r (SE) and relative contributions to the entire metapopulation \hat{c}^r (SE) from each local population for the reverse-time analysis of a kangaroo rat metapopulation structure in Cochise County, SE Arizona, USA, for high and low density years

Density	Local population (<i>r</i>)	\hat{N}^r (SE)	\hat{c}^r (SE)
High	1	23.45 (1.78)	0.152 (0.031)
	2	19.86 (1.32)	0.129 (0.031)
	3	29.02 (2.39)	0.178 (0.032)
	4	7.84 (0.59)	0.049 (0.031)
	5	14.56 (0.93)	0.089 (0.031)
	6	12.60 (0.99)	0.077 (0.031)
	7	2.37 (0.22)	0.018 (0.031)
	8	5.87 (0.43)	0.037 (0.031)
Low	1	16.48 (0.73)	0.189 (0.019)
	2	10.81 (0.52)	0.124 (0.019)
	3	12.25 (0.45)	0.126 (0.019)
	4	3.62 (0.28)	0.038 (0.019)
	5	14.44 (0.69)	0.149 (0.019)
	6	6.16 (0.34)	0.064 (0.019)
	7	4.12 (0.28)	0.047 (0.019)
	8	3.62 (0.28)	0.038 (0.019)

5.5 Multistate Miscellany

As described in Section 5.1, the original multistate models of Arnason (1972, 1973) assume that the state of an animal is correctly recorded at each capture. Thus, the state of an animal is unknown for each “0” in the capture history, but the state is known with certainty for all nonzero entries (captures). However, in some sampling situations, captures, or, more generally, detections, may be characterized by uncertainty. Such uncertainty usually arises not when the relevant state variable is location, but rather some characteristic of the individual animal, such as reproductive condition (e.g., breeding or not) or even sex, for some species. State uncertainty or multievent models have been developed for inference in these sampling situations (e.g., Kendall, Hines and Nichols, 2003, Pradel, 2005). Although multievent models have not been applied to RT analyses to my knowledge, if certain applications are characterized by state uncertainty, then use of these multievent models with time-reversed data should present no special problems.

Occupancy modeling (Section 4.3) was discussed under the robust design, but I noted that occupancy was a special case of temporary emigration modeling, and that the latter could be viewed as a case of

multiple observation states (available for detection or unavailable). The general issue of state uncertainty in capture–recapture models is equivalent to the issue of false positives in occupancy modeling. False positives occur when an animal or its sign is incorrectly identified as the focal species when it is actually some other species. As with state uncertainty and multievent modeling, approaches have been recently developed to deal with false positives (e.g., Miller et al., 2013, Chambert, Miller and Nichols, 2015), and their use with RT occupancy modeling should be straightforward.

The ability to directly estimate λ_t via a combination of standard time and RT parameters for the single state situation (Section 3.3) leads to a natural expectation that a similar approach should be available for the multistate case. Such direct estimation would be useful whether states are geographic locations, age classes or strata produced by any other means of structuring a population. However, extension of the approach of Pradel (1996) to multiple states is not so straightforward and has not yet been fully developed (although substantial progress has been made, J.-D. Lebreton pers. comm.) Until this development is completed, it should be recognized that realized population growth for a system of multiple states can be estimated only as a derived parameter by substituting estimates of N_t^r into equation (6). However, in many cases, such as those focusing on age-specificity, the ability to draw inferences about a specific class (e.g., adults) may be all that is required.

6. DISCUSSION

What makes the CJS model so remarkable in my opinion is that users can extract so much information about an animal population from a seemingly meager data source, a matrix of 0's and 1's, with the 0's characterized by substantial uncertainty. The fact that this matrix permits model-based inference about population size, recruitment, survival and sampling intensity is certainly impressive, with more recent extensions adding inference about temporary emigration, recruitment components, etc. RT modeling works with this same information source, and there is no claim that it permits inferences that cannot be obtained using the standard CJS formulation. Rather, the RT perspective permits direct modeling and inference about population growth rate and contributions to this rate, including various sources of new recruits.

The temporal symmetry models that combine reverse and standard time approaches to permit direct

inference about population growth rate (Pradel, 1996) have seen a fair amount of use in animal population ecology, including, for example, the demographic meta-analyses of the northern spotted owl data (*Strix occidentalis caurina*) from study areas across the Pacific northwestern United States (e.g., Anthony et al., 2006, Forsman et al., 2011).

Other uses of the RT approach have been limited, with application areas including animal population ecology, animal community ecology, paleobiology and occupancy dynamics. Use of RT modeling with capture history data from individuals of a single population permits direct modeling and inference about population growth rate (Pradel, 1996), relative contributions of different demographic components to this growth rate (Nichols et al., 2000) and age-specific recruitment to breeding populations (Pradel et al., 1997). Use of RT modeling with species-level detection-nondetection data permits direct inference about community turnover, the fraction of species in a local community that is "new" (not present the previous time period) (Nichols et al., 1998). For paleobiological data, RT modeling permits inference about rates of taxonomic origination (Nichols et al., 1986). And RT modeling applied to single-species detection-nondetection data across multiple sites permits direct inference about the fraction of occupied sites at any point in time that is newly occupied (MacKenzie et al., 2006).

Use of extensions to multiple states with MRT has been even more limited. However, the study of Sanderlin et al. (2012), with its full matrix of site-to-site contribution estimates, should motivate increased use of this approach for the study of metapopulation dynamics. The few MRT uses of which I am aware all focus on location or age or both of these state variables. However, use of MRT with other state variables characterizing individual animals holds promise as well. Cooch et al. (2012) suggested an epidemiological application in which MRT modeling is based on states defined by both location and individual disease state (e.g., susceptible, infected, recovered). They suggested that an MRT approach could provide direct inferences about the contributions of animals in different locations and disease states to population growth of local populations, and metapopulation systems of such populations (Cooch et al., 2012).

Ultimately the selection of modeling approaches and inference methods should be dictated by study objectives. The contention in this paper is that there is a set of ecological questions for which RT and MRT

modeling approaches should be the methods of choice. As suggested by Cooch et al. (2012), I suspect that there are a number of other potential application areas for which RT modeling would be especially useful as well. Finally, I emphasize that, regardless of how odd or nonstandard these RT approaches may appear at first glance, they remain firmly grounded in the conceptual framework provided to us a half-century ago by Richard Cormack, George Jolly and George Seber. These three scientists certainly deserve our appreciation and thanks.

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