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Modeling Individual Animal Histories with Multistate Capture–Recapture Models

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SUMMARY

Many fields of science begin with a phase of exploration and description, followed by investigations of the processes that account for observed patterns. The science of ecology is no exception, and recent decades have seen a focus on understanding key processes underlying the dynamics of ecological systems. In population ecology, emphasis has shifted from the state variable of population size to the demographic processes responsible for changes in this state variable: birth, death, immigration, and emigration. In evolutionary ecology, some of these same demographic processes, rates of birth and death, are also the determinants of fitness. In animal population ecology, the estimation of state variables and their associated vital rates is especially problematic because of the difficulties in sampling such populations and detecting individual animals. Indeed, early capture–recapture models were developed for the purpose of estimating population size, given the reality that all animals are not caught or detected at any sampling occasion. More recently, capture–recapture models for open populations were developed to draw inferences about survival in the face of these same sampling problems. The focus of this paper is on multi-state mark–recapture models (MSMR), which first appeared in the 1970s but have undergone substantial development in the last 15 years. These models were developed to deal explicitly with biological variation, in that animals in different “states” (classes defined by location, physiology, behavior, reproductive status, etc.) may have different probabilities of survival and detection. Animal transitions between states are also stochastic and themselves of interest. These general models have proven to be extremely useful and provide a way of thinking about a remarkably wide range of important ecological processes. These methods are now at a stage of refinement and sophistication where they can readily be used by biologists to tackle a wide range of important issues in ecology. In this paper, we draw together information on the state of the art in multistate mark–recapture methods, explaining the models and illustrating their use. We provide a modeling philosophy and a series of general principles on how to conduct analyses. We cover key issues and features, and we anticipate the ways in which we expect the models to develop in the years ahead. In particular:

- MSMR can now be used in a straightforward fashion by population biologists, thanks to the development of sound goodness-of-fit procedures, reliable parameter identifiability diagnostics, and robust user-friendly computer software. Constrained models and model selection procedures can be used in the ANOVA-like philosophy commonly used over the last 15 years for survival models, to answer a variety of biological questions. We develop as an example a treatment of meadow vole *Microtus pennsylvanicus* data.

- As in survival models, random effects should be an integral part of this philosophy. Some simple approaches to random effects are illustrated.
- States can be defined in a very general way, for example, by combining several criteria, such as sites and reproductive states, and can include nonobservable states. We develop as an example a multisite recruitment model of roseate terns *Sterna dougallii*.
- MSMR models appear as a natural framework for combining different sources of information, viewed as different events that can be organized into mutually exclusive alternatives.
- With the available developments, MSMR models are becoming a standard tool in population biology, as shown by a rapid growth of their use in the literature. In particular, given the ease with which a variety of constrained models can now be developed, MSMR models appear as less data hungry than was often feared.
- MSMR models make it also possible to unify a large array of methodology, and, as such, are both a step towards further unification in a “mother of all” model, and a sound basis for further generalizations.
- Future developments concern a variety of generalizations such as the reverse time approach and population size estimation. “Multievent” models, accounting for uncertainty in state determination, and integrated state–space models are key generalizations already in full development.

I. INTRODUCTION

Studies of animal and plant population dynamics aim at improving our understanding of changes in numbers in populations, whether for fundamental studies of population ecology and regulation (Murdoch 1994; Newton 1998; Turchin 1995) or for applied purposes such as the management and conservation of populations (Beissinger and McCullough, 2002; Lande *et al.*, 2003; Williams *et al.*, 2002). While changes in numbers can be directly addressed using successive surveys, at least in principle, it is the mechanisms behind these changes that are of interest. Over the last century, demographic modeling (Caswell, 2001; Leslie, 1945; Sharpe and Lotka, 1911) has focused attention on demographic flows of individuals (i.e., on the numbers of individuals entering the population by birth and immigration and leaving the population by death and emigration). This focus on flows is the basis of birth–immigration–death–emigration (*bide*) models (Bartlett, 1960; Bailey, 1964; Pulliam, 1988) and of similar stratified models with animals grouped by age (Caswell, 2001; Goodman, 1967; Leslie, 1945) and then more generally by stage (Caswell, 2001; Lebreton, 1996; Lefkovich, 1965). Even in the

context of functional ecology, as already stressed decades ago by Goodall (1972), a large part of ecosystem flows are realized through the birth and death of individuals in populations. The interest in flows, rather than just in their result, changes in population size, is the counterpart in population dynamics of a general move in ecology from pattern to process (Mackenzie *et al.*, 2006; Swihart *et al.*, 2002). Indeed, similar changes in numbers can result from very different flows of individuals, and only a study of flows can lead to a deep understanding of population mechanisms and provide some predictive ability. As a consequence, this interest in demographic flows is now central to population ecology and to applied studies induced by the growing concerns on the impact of human activities on the biosphere. Examples of human impact on animal populations requiring an assessment of demographic flows are the mortality in seabird populations induced by longline fisheries, as a consequence of the ingestion of hooks by birds attracted by the baits (Weimerskirch *et al.*, 1997), and the sport harvest of waterfowl populations (Anderson, 1975; Anderson and Burnham, 1976; Williams *et al.*, 2002).

In evolutionary ecology, interest shifts from rates and flows to the corresponding probabilities (e.g., of surviving, reproducing) for individual animals, or to rates and flows for animals of the same genotype (Fisher, 1930). This shift of focus raises a number of questions about individual quality, plasticity of traits and demographic performance, and trade-offs between demographic processes. Studies of individual quality include efforts to identify measurable covariates associated with quality, where quality reflects fitness. Variation among individuals in quality is an important determinant of such demographic performance measures as extinction probability (e.g., Conner and White, 1999). To the extent that such variation is heritable, it is a determinant of the rate of natural selection (Fisher, 1930). Questions about plasticity include the degree to which its selection depends on the perturbation regime to which individuals are subjected. The study of trade-offs includes such topics as the existence of a cost of reproduction (Roff, 1992; Stearns, 1989, 1992). For example, will reproduction early in life induce a cost in survival or future reproduction? If so, how is an evolutionary balance between different “strategies” achieved? The central point is that the same underlying probabilities or latent parameters govern the processes of survival and reproduction regardless of whether interest is in evolution or population dynamics. This correspondence between fitness components and demographic rate parameters is intimately linked to the *per-capita* assumption that arises in population biology from the basic biological fact that organisms come only from other organisms. Thus, approaches to estimation of survival, reproduction and, in some cases, movement are of interest to a variety of disciplines, ranging from evolutionary ecology, to population ecology and management, to community ecology.

This increasing interest in demographic flows has induced the development of empirical approaches to measure them, initially for the purpose of providing parameter estimates for demographic models. It appeared very early (Fisher and Ford, 1947; Jackson, 1933, 1939; Lincoln, 1930) that using marked individuals was a key approach, providing insight into population mechanisms in the same way as the tracer method does in chemical kinetics (Welch *et al.*, 1972). Severe limits appeared in the application of methods derived from human demography, such as life tables (Chiang, 1984; Dublin and Lotka, 1936; Pearl, 1940), to populations in the wild (Anderson *et al.*, 1985; Burnham and Anderson, 1979). Statistical methods for analyzing sampling of marked individuals have to account in a statistically sound way for the practical impossibility of following individuals exhaustively through time and space in animal populations, a rule with few exceptions (e.g., Bérubé *et al.*, 1999, Bighorn sheep *Ovis canadensis*; Coulson, 1968, Kittiwake gull *Rissa tridactyla*). This rule often applies also to plant populations, not only in the case of dormancy (the absence of an aboveground part), but also when individuals are aboveground (Alexander *et al.*, 1997; Kéry, 2004; Kéry and Gregg, 2004). As a consequence of a sustained pace of development since the 1960s (Lebreton, 1995), such statistical methods to estimate demographic rates and flows when not all marked individuals are detected now constitute a wide and diverse framework, broadly called capture–mark–recapture methods, or, in a more general fashion, mark–reencounter methods. These methods are reviewed by Schwarz and Seber (2000) and Seber and Schwarz (2002).

In parallel to the development of mark–reencounter methodology, many long-term field programs, notably on vertebrates, were developed and produced high quality data sets based on marked individuals (see e.g., Clutton-Brock, 1988; Newton, 1989; Perrins *et al.*, 1991). The initial questions addressed with these data sets involved survival and reproductive rates for static groups of animals in particular locations. Subsequent biological questions, however, involved variation in survival and reproduction over time as animals moved from one location to another (e.g., Clobert *et al.*, 2001; Hanski, 1999) or as they changed from one physiological or behavioral state to another (e.g., McNamara and Houston, 1996). Such questions required focus not only on state-specific survival and reproduction, but also on transition probabilities between different states.

For example, Spendelov and his collaborators (Lebreton *et al.*, 2003; Spendelov, 1991; Spendelov and Nichols, 1989; Spendelov *et al.*, 1995), in the course of a long term study of roseate terns *S. dougalli*, gathered data on individuals in three breeding sites over 11 years. A typical individual history over these 11 years is “00000a00A0C”, indicating that this particular individual was marked as a chick in year 6 at colony A, later seen as a breeder in year 9 in colony A and in year 11 in colony C (lower case being for

nonbreeders, capitals for breeders). How can one estimate dispersal rates and rates of accession to reproduction from such data? Do these rates vary among years relative to environmental factors? In such empirical approaches, an individual is not only alive or not, but can be in one of several states (nonbreeder, breeder in locations A, B, or C). At the same time, an individual still alive can be missed in a given year (in years 7, 8, and 10 in the individual history above). The key biological questions require us to be able to account simultaneously for the several states and for the incomplete detection. It is thus particularly fortunate, as recalled in a historical account below, that the development of capture–reencounter methods presently culminates in multistate models (Brownie *et al.*, 1993; Hestbeck *et al.*, 1991; Lebreton and Pradel, 2002; Schwarz *et al.*, 1993), in which transition of individuals between sites or states is considered in a capture–reencounter context.

However, despite their strong biological relevance, MultiState Mark–Recapture (MSMR, Kendall *et al.*, 2006) models are difficult to use, and indeed not yet widely used. This is particularly unfortunate, as a multistate point of view is critical for the development of demographic models (Caswell, 2001 Chapter 3) and MSMR models are a natural tool for estimating the parameters of demographic models (Lebreton, 1996; Nichols *et al.*, 1992, p. 310, Caswell and Fujiwara, 2002). Pradel (2009) noted that, in the years 2003–2006, hardly more than 5% of papers dealing with capture–recapture used, or were devoted to, multistate models. The two main reasons are that no synthesis is available despite, or perhaps because of, rapid advances (Lebreton and Pradel, 2002), and MSMR models have often been considered as data hungry (Seber and Schwarz, 2002, p. 8; Anderson *et al.*, 1993, p. 378) although reduced parameter models were proposed early in the development of these models (Hestbeck *et al.*, 1991). Given this strong potential (Nichols and Kendall, 1995) and the diverse and recent developments dispersed in the literature, a new synthesis is clearly needed to organize these developments, to propose some further ones, and to stimulate the use of multistate models by population biologists to address a variety of biological questions related to individual variability in the broad sense.

Thus, the purpose of this paper is to provide a unified theory for multistate models, including illustrative case studies, with the hope of opening the way to broader use and further developments, in the spirit of Lebreton *et al.* (1992), who provided a unified view of single-state survival models. For the sake of clarity, we will rely heavily on the material in Lebreton *et al.* (1992) and restrict our attention to models conditional on first release, or, for short, conditional models, with the following steps:

- Recall briefly the history of capture–recapture methodology, in particular the progressive move to an emphasis on rates and the early development of multistate models (II);

- Present the structure of conditional models (parameterizations, likelihood, Maximum Likelihood estimation, goodness-of-fit) based on a simple two-site example and show how “single state” survival models can be viewed as special cases of these (III);
- Develop constrained models and address model selection, using fixed (IV) and random (V) effects;
- Show how complex situations can be addressed by combining states, with models and examples for dispersal and recruitment (VI) first, and then with mixtures of information (VII);
- Discuss the state of the art and perspectives, including speculations about future developments (VIII).

II. A HISTORICAL ACCOUNT

Following the standard historical path from pattern to process, capture–recapture methods were first developed to estimate population size (e.g., [Lincoln, 1930](#)). Flows of individuals, such as mortality and recruitment were later introduced as nuisance parameters to permit estimation of the size of a population changing over time (e.g., [Darroch, 1959](#)). Mortality and recruitment were considered in a comprehensive probabilistic approach by [Jolly \(1965\) and Seber \(1965\)](#). [Cormack \(1964\)](#) anticipated the survival part of their model, that considers only marked individuals, that is, conditional on releases. The resulting Cormack–Jolly–Seber (CJS) models consider time-dependent survival and recapture probabilities. When population size estimation is considered (i.e., in the Jolly–Seber approach in the strict sense), survival probabilities, recruitment and population size can be estimated over time from successive samples of individually marked animals (for a modern technical presentation, see [Burnham, 1991](#)). The rapid development of interest in flows of individuals, described in the introduction, and the potential of the Jolly–Seber framework led to a progressive shift of emphasis in the use of the Jolly–Seber and related models, from the estimation of population size to the estimation of survival and recruitment ([Brownie, 1987; Burnham *et al.*, 1987; Clobert and Lebreton, 1987](#)). This shift induced a move to models conditional on the numbers of marked individuals released, the CJS models. In parallel, it was realized that time-dependence in the parameters was restrictive, “the Jolly–Seber model being accused of being either too restrictive” or “too general” ([Cormack, 1979](#)). Generalizations of various kinds, such as age-dependent models ([Pollock, 1975, 1981](#)) appeared. Several authors independently developed constant parameter models ([Brownie *et al.*, 1986; Clobert *et al.*, 1985; Jolly, 1982](#)). These developments and their associated parameterizations required iterative calculations to obtain

estimates, for which specialized software has been available for more than 15 years (Brownie *et al.*, 1986; Choquet *et al.*, 2004; Clobert and Lebreton, 1987; Hines, 1994; Pradel and Lebreton, 1991; White, 1983; White and Burnham, 1999).

Authors began to model the time-dependence in survival probability, conveniently transformed, as a linear relationship with an environmental covariate, built into the model (Clobert and Lebreton, 1985; North and Morgan, 1979; for a recent and comprehensive review, see Grosbois *et al.*, 2008). Indeed, the development of generalized linear models (McCullagh and Nelder, 1989; Nelder and Wedderburn, 1972) during the 1970s had provided a framework for a systematic development of such constraints on parameters. Generalized linear model ideas rapidly influenced the development of capture–recapture models in the 1980s (Clobert *et al.*, 1987; Cormack, 1989). Simultaneously, sound goodness-of-fit tests of basic models became available (Burnham *et al.*, 1987; Pollock *et al.*, 1985). A comprehensive framework was developed with models considering several groups of individuals, variation over age and time in probabilities of survival and recapture, and many different types of constraints in parameters based on quantitative and/or categorical covariates, that is, covering regression and analysis of variance ideas. Key papers include those by Buckland (1980), Pollock (1981), Sandland and Kirkwood (1981), Brownie and Robson (1983), Clobert *et al.* (1987) and Pradel *et al.* (1990). The comprehensive framework resulting from this progress is reviewed by Lebreton *et al.* (1992). The examples in Lebreton *et al.* (1992) show that, as in contingency table analysis by log-linear models (Fienberg, 1977; Morgan, 1992) or dose–response models by logit or probit analysis (Morgan, 1992), the user is often faced with a wide array of biologically reasonable models. Model selection procedures (Akaike, 1973; Burnham and Anderson, 1992, 1998, 2002) appeared then as a more reliable approach than a series of hypothesis tests, as the latter are unavoidably plagued by difficulties in controlling the level and power of the tests. The overall approach proposed by Lebreton *et al.* (1992) consisted of the following steps:

- Start from a general “umbrella” model, for which the fit to the data could be tested.
- Proceed in a step-down approach among competing models with various combinations of effects covering the key questions in relation to the biology and the design of the study (e.g., is probability of capture best considered as related to a measure of field effort, is survival related to rainfall, does survival differ between sexes?).
- Obtain parameter estimates from a final model based on general model selection procedures. The Akaike information criterion (AIC; Akaike, 1973) appeared as a simple overall criterion with many practical and

theoretical advantages (Burnham and Anderson, 1998, 2002), although its blind and exclusive use has been duly criticized (Guthery *et al.*, 2005; Stephens *et al.*, 2005), and alternative model selection criteria are being considered (Link and Barker, 2006; Taper, 2004).

This modern framework to estimate and model survival has been widely used (Schwarz and Seber, 2000) for at least two reasons:

- It shifted the biologist's attention from specific models and technical statistical questions to model structure and biological questions.
- It provided tools (including user-friendly software, Choquet *et al.*, 2004; Pradel and Lebreton, 1991; White and Burnham, 1999) to efficiently exploit the huge amount of high quality data produced by many long term field programs directed at obtaining repeated observations through time on marked individuals.

A number of interesting biological inferences have resulted from the application of these methods. For bird populations, Clobert and Lebreton (1991) provided strong evidence that annual survival rates were generally higher than indicated by previous studies that did not adequately deal with detection probabilities. Studies provided evidence for age specificity in survival (Loery *et al.*, 1987; Pollock, 1981), including inferences about senescence (Pugesek *et al.*, 1995; Nichols *et al.*, 1997). Covariate modeling has provided evidence for the importance of various environmental variables (e.g., Barbraud and Weimerskirch, 2001, 2003; Loison *et al.*, 2002; Sillert *et al.*, 2000) to avian survival rates. Departure of birds from migration stopover sites is analogous to mortality, and capture–recapture analyses thus have been used to understand departure patterns and to investigate avian ecology at stopover sites. Stopover duration has been estimated (Kaiser, 1995; Schaub *et al.*, 2001), and strong evidence of the influence of environmental factors on departure probabilities has been provided (Schaub *et al.*, 2004a). The relationship between breeding probability and detection probability at a breeding colony has permitted inferences about breeding probabilities (Pugesek *et al.*, 1995), including costs of early reproduction (Viallefont *et al.*, 1995). Reverse-time modeling introduced robust inference methods to the study of accession to reproduction (Pradel *et al.*, 1997b).

Mark-recapture studies of mammals have provided strong evidence of both sex-specificity and senescent decline in ungulate survival probabilities (Loison *et al.*, 1999). Covariate modeling has provided inferences about the relative effects of density-dependent and independent factors on survival of small mammals (Julliard *et al.*, 1999; Leirs *et al.*, 1997; Lima *et al.*, 1999) and ungulates (Gaillard *et al.*, 1997). The typical high elasticity (Caswell, 2001; Caswell *et al.*, 1984) of adult survival relative to that of young survival in

large mammals led to the prediction that temporal variation in adult survival should be small relative to that of young survival. Indeed, reviews of mammalian studies employing mark–recapture methods provided evidence in favor of this prediction, providing evidence of canalization of the fitness components that have the largest effects on fitness (Gaillard and Yoccoz, 2003). CJS modeling has also led to inferences about declining survival rates in endangered cetacean species (Caswell *et al.*, 1999; Fujiwara and Caswell, 2001).

The CJS models evolved in many other different directions that cannot be fully reviewed here (but see general reviews in Seber, 1982; Williams *et al.*, 2002), notably to handle heterogeneity in parameters among individuals, recognized long ago as a key problem (Carothers 1973, 1979) for which design (Kendall *et al.*, 1995; Pollock, 1982) and modeling approaches (Brownie and Robson, 1983; Pradel, 1993; Sandland and Kirkwood, 1981) have been proposed. Fortunately, this is still an active field of research (Clark *et al.*, 2005; Link, 2003; Pledger and Efford, 1998; Pledger and Schwarz, 2002; Pledger *et al.*, 2003; Pradel, 2005).

In the same fashion, generalized linear models have been developed to include not just fixed effects but also random effects, so too in the field of capture–reencounter, models have been developed in which effects are assumed to be drawn randomly from a distribution (Burnham *et al.*, 1987). In a random effect, the categories of the effect are viewed as having been obtained by random sampling from a population of categories (Searle *et al.*, 1992). This can be the case with variation over time if each year is supposed to result from a random environmental process. The variation in, for instance, the survival probability, is then measured by a variance over time rather than by a collection of time-dependent estimates (Burnham *et al.*, 1987, 260 ff). Random effects in linear constraints are very appealing for a variety of questions, from modeling individual heterogeneity in survival (Pledger and Schwarz, 2002) and detection probabilities (Clark *et al.*, 2005; Link, 2003), to detecting density-dependence (Barker *et al.*, 2002) and modeling treatment effects on survival (Clark *et al.*, 2005). Surprisingly, they have been little used to investigate consequences of environment variability on population growth, although adequate dynamical models exist (Tuljapurkar, 1990). Capture–reencounter models with random effects present specific technical difficulties, in particular computational ones (Brooks *et al.*, 2000, 2002; Burnham and White, 2002). For this reason they have been moderately used in practice. This state of affairs may change rapidly with the spread of Bayesian algorithms (Brooks *et al.*, 2000, 2002; Clark *et al.*, 2005; Link and Barker, 2005).

The basic modeling approach outlined above, based on constrained CJS-type models, is implicitly strongly reductionist, as it focuses nearly exclusively on survival, and reduces the information at the time of capture–recapture

to just the record of presence, with at most the categorization of individuals in groups according to permanent attributes. However, in parallel to these developments and their transfer to population biologists, a wide diversification of capture–recapture models was initiated in several different directions:

- Arnason and Schwarz (Arnason, 1972, 1973; Schwarz *et al.*, 1993) considered multisite models in which individuals could be captured over several sites. There were a few forerunners of multisite models for closed populations (Chapman and Junge, 1956; Darroch, 1961).
- Several authors considered models in which the local survival from birth to first reproduction (recruitment) (Nichols *et al.*, 1990; Rothery, 1983) and the rate of recruitment (Clobert *et al.*, 1994) could be estimated. The latter authors based their approach on the transfer of individuals from a group of individuals not yet detected as recruited, to known as recruited at the time of first observation as a reproducer.
- Burnham (1993), Barker (1997), and Catchpole *et al.* (1998) considered models for mixtures of information, namely recaptures of live individuals and both records of dead individuals (“recoveries”) and live resightings reported by members of the public.
- Skalski *et al.* (1993) and Hoffman and Skalski (1995) developed models in which survival is related to continuous covariates defined at the individual level. These covariates are assumed to be constant over time. Bonner and Schwarz (2005) extended these models to cover continuous individual covariates changing over time.
- Burnham (1993) considered the problem of temporary emigration (movement to an unobservable state) in open capture–recapture models, and Kendall and Nichols (1995) and Kendall *et al.* (1997) showed how to estimate the probability of temporary emigration by sampling at two different temporal scales (using Pollock’s (1982) robust design).
- Pollock *et al.* (1974) considered the possibility of time-reversal in capture–recapture models, and Nichols *et al.* (1986) and Pradel (1996) used reverse-time CJS models to estimate seniority parameters that reflected the probability that a randomly selected individual captured at a specific sampling occasion was an “old” individual, in the sense of having been alive in the sampled population the previous sampling occasion. Pradel (1996) extended this thinking to simultaneous forward and reverse time modeling of a single data set in order to directly estimate the realized population growth rate.

The Arnason–Schwarz model opened the way for subsequent work on multistate models in the same way that the CJS model did for survival models. Constancy constraints analogous to those used in survival models (i.e., the CJS family reviewed above) were incorporated in the multisite

models by [Hestbeck *et al.* \(1991\)](#), who studied annual survival and movement of Canada Geese *Branta canadensis* among three large wintering zones on the Eastern coast of North America. [Hestbeck *et al.* \(1991\)](#), using software MS-SURVIV developed specifically for multistate models (see also [Brownie *et al.*, 1993](#); [Hines, 1994](#)), were able to consider a variety of models with different constraints on survival, movement, and capture parameters. [Nichols *et al.* \(1992, 1994\)](#) considered these multisite models as *multistate models*, that is, considered that individuals could move within a finite set of states potentially much more general than just geographical states and including dynamic individual state variables such as reproductive status (reproductive and nonreproductive individuals), body mass (large and small individuals), and even mortality status (dead and alive). This point of view had three key advantages:

- On the biological side, it coincided with the development of ideas and questions about individual variability, individual quality, fitness components, and life history strategies in evolutionary biology;
- On the statistical side, it opened the way to a systematic use of multistate models as a comprehensive framework for the analysis of individual data ([Lebreton and Pradel, 2002](#)), including the recruitment ([Pradel and Lebreton, 1999](#)) and information mixture ([Lebreton *et al.*, 1999](#)) models mentioned above.
- On the modeling side, it also corresponded closely to that underlying stage-classified matrix population models and provided a natural approach to inference for the parameters of these models ([Fujiwara and Caswell, 2002a](#); [Leirs *et al.*, 1997](#); [Nichols *et al.*, 1992](#)).

With comprehensive software now available (MARK, [White and Burnham, 1999](#); M-SURGE, [Choquet *et al.*, 2004](#)), multistate models can now be used as “canonical models for analyzing individual covariates that change over time” ([Lebreton and Pradel, 2002](#)). The most straightforward models can be viewed as Markov chains (e.g., [Iosifescu and Tautu, 1973](#)) with nonexhaustive detection of individuals. The insertion of a dead “state” among the states clearly shows the Markov chain structure by making the stochastic matrix of the chain explicit ([Caswell, 2001](#), Section 6.1.2; [Lebreton *et al.*, 1999](#)). From this point of view multistate models are closely related to models with continuous individual covariates changing over time ([Bonner and Schwarz, 2005](#)) in which the change in the covariate has to be modeled as a Markovian process. The relationship between multistate models and hidden Markov chains was emphasized by [Dupuis \(1995\)](#) and became perfectly clear with recent generalizations ([Newman *et al.*, 2006](#); [Pradel, 2005](#)). The terms “states” and “multistate” ([Nichols and Kendall, 1995](#)) implicitly

emphasize that the individuals' state can change over time. They appear, as a consequence, preferable (Pollock, personal communication reported in [Lebreton and Pradel, 2002](#)) to the terms “strata” ([Brownie *et al.*, 1993](#)) and “multistrata” ([Lebreton *et al.*, 1999](#)), which are commonly viewed as referring to permanent groups, as in “stratified sampling”.

We tend to view state variables very generally as key characteristics associated with, and used to distinguish among, individuals. One way of classifying state variables is to focus on whether they are *static* or *dynamic*. For example, in many vertebrates, sex is a state variable that is static in the sense that it characterizes an animal throughout its lifespan. Static state variables are easily modeled by focusing on groups of animals categorized by the variable of interest (e.g., [Lebreton *et al.*, 1992](#)). Age and body mass are two state variables that change over time and can be characterized as dynamic. Dynamic state variables can be further characterized as resulting from *deterministic* or *stochastic* processes. Age is a deterministic state variable, in that changes in age are entirely predictable. Consider a species sampled once each year, in which a captured animal is categorized as either young or adult, and in which young become adults within 1 year. If an animal is young at the sample period in year i , then it will be an adult at the sample period for year $i + 1$, if it happens to survive until then. Such dynamic state variables can be handled via models that specifically incorporate the deterministic transitions that characterize the process (e.g., the age-specific models of [Brownie *et al.*, 1986](#); [Pollock, 1981](#); [Lebreton *et al.*, 1992](#)). Body mass, however, is a stochastic state variable, in that knowledge of an animal's body mass this spring does not permit unambiguous inference about an animal's mass the next spring. In this case, transitions are stochastic, and must be modeled using general multistate models (e.g., [Arnason, 1972](#); [Brownie *et al.*, 1993](#); [Schwarz *et al.*, 1993](#)). This classification system for state variables emphasizes the point that multistate models are generalizations of earlier models that were developed to deal with specific classes of state variables with constrained transitions. Multistate models can be particularized to models that deal with static variables (e.g., sex groups) or deterministic, dynamic state variables (e.g., age), via appropriate constraints on the general multistate structure.

In the material that follows, we develop the idea of multistate models as providing a canonical framework for a large class of capture–recapture models. We describe general models and then develop specific structures to address specific classes of biological questions. We assume a basic knowledge of single state models and of general statistical concepts such as parametric models, likelihood and associated techniques (Maximum Likelihood Estimation, Likelihood Ratio Tests, etc.; see for example, [Mood *et al.*, 1974](#)), and model selection ideas as popularized by AIC ([Burnham and Anderson, 1998, 2002](#)).

III. CONDITIONAL MULTISTATE MODELS AS A GENERALIZATION OF SURVIVAL MODELS

A. Multistate Models and Data: Meadow Vole Example

In multistate capture–recapture models, individuals move among a finite number of states, s , or die, according to a finite Markov chain, between discrete time occasions. Survivors are detected (“recaptured”) in each state, not exhaustively at each occasion. The individuals are sampled over K occasions. When they are detected (“captured”), their state at this occasion is known. The individuals are considered as released with a mark at the time of their first capture, and in what follows, everything is considered conditional on this release. When the individuals are not detected, even if alive, their state is unknown.

We take here as a first example of application of MSMR an experimental study of meadow voles, *M. pennsylvanicus*, at Patuxent Wildlife Research Center, Laurel, Maryland (Coffman *et al.*, 2001). The capture–recapture data were collected on two grids, A and B, from September, 1991, through May, 1993. Each grid consisted of a 7×15 rectangle of trapping stations 7.6 m apart. We considered each rectangular grid to be comprised of two square grids representing the two location states (Figure 1). State 1 was defined by trapping rows 1–7, and state 2 by trapping rows 9–15. Both location states were squares with 7×7 trapping stations. Grid A received a “fragmentation” treatment. During primary sampling periods 1–4, the grid was continuous, and between periods 4 and 5 it was plowed and disced (Figure 1, see also Coffman *et al.*, 2001). This fragmentation treatment was imposed by plowing a 7.6 m strip of bare ground between the two grid halves and around the periphery of the grids. Sampling periods 5–12 were thus viewed as post-treatment. The other grid (B) served as a paired control grid. It was never plowed and remained continuous for the duration of the study (Figure 2).

Within each grid, the two grid halves or location states were the patches of interest, and movement occurred when an animal present on one half in one sampling period was present on the other half in the next sampling period. Sampling was conducted at two temporal scales following the robust design of Pollock (1982). The example reported here uses only information at the scale of the primary sampling periods, every 8 weeks, with $K = 11$ occasions. Animal movements were expected to be symmetric between the two halves of each grid. With respect to this remark, an unusual feature of this example is that the numbering of states is arbitrary, in the sense that state 1 in grid A bears no more relationship to state 1 in grid B than to state 2 in grid B.

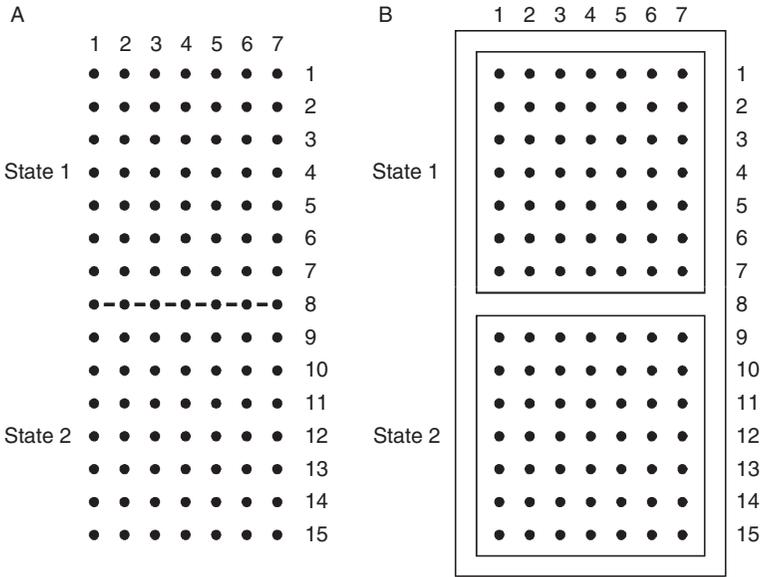


Figure 1 (A) Configuration of grid A during sampling periods 1–4 and grid B for the entire study. Dots represent trap stations. The 7 columns and 15 rows yield 105 trap stations on each grid. The 2 “location states” of each grid are identified as the 2 squares defined by rows 1–7 and rows 9–15. An animal was identified as having moved if it was caught in 1 location state in 1 period and in a different state in another period. The habitat on each grid during the specified periods was continuous (no fragmentation) and similar for the 2 location states. (B) Configuration of grid A during sampling periods 5–12 following fragmentation. Plowing yielded a strip of bare ground 7.6 m in width around the periphery of the entire grid and between the 2 location states (grid halves). The bare ground strips were maintained for all periods following their creation (5–12).

Further questions and predictions, related in particular to the treatment in grid A after occasion 4 will be examined later.

The data were organized in four groups, based on sex (males and females) and grid (A and B). In each of these four groups, an individual that is alive and on the grid is in either state 1 or 2, the two halves of the concerned grid. The two states are thus geographical sites, as in the earliest examples of MSMR models. A few typical capture–recapture histories are given in Table 1. When an animal is seen before and after an occasion at which it remained undetected, it is known to be alive, as in a single state survival model. However, it may have been in either of the two sites (e.g., individual #1 sampling occasion 7 in Table 1). The calculation of the probabilities of the capture histories has to account for this uncertainty, which is a key feature of MSMR models.

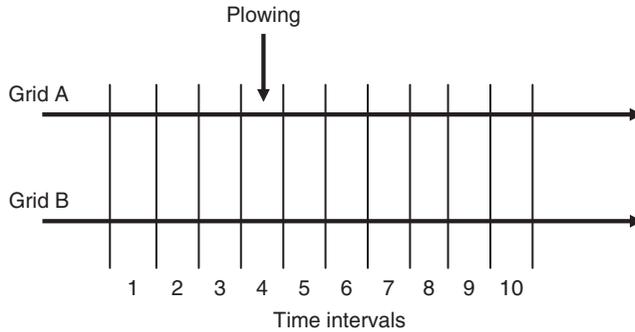


Figure 2 Temporal sampling design of the vole *M. pennsylvanicus* experiment. Each grid, A and B, consists of 2 states (grid “halves”) between which individuals can move. Grid A was submitted to a fragmentation treatment by plowing during interval 4, that is, between capture occasions 4 and 5.

Table 1 Example individual capture histories of voles *M. pennsylvanicus*, over 11 occasions and 2 sites

Individual	Occasion											Comments
	1	2	3	4	5	6	7	8	9	10	11	
1	0	0	0	0	2	2	0	2	2	0	0	Seen in 2 only, in 1 or 2 at occ.7
2	0	0	0	0	2	2	2	2	2	2	0	Seen in 2 only, in 1, 2 or dead at occ.11
3	0	0	0	1	0	0	0	0	0	0	0	Seen in 1, never seen again
4	0	0	0	1	0	1	1	1	1	1	1	Seen in 1 only, in 1 or 2 at occasion 5
5	0	0	0	1	1	1	1	1	1	0	0	Seen only in 1, in 1, 2 or dead at occ.10, 11
6	2	1	0	1	0	0	0	0	0	0	0	Seen in 2 and 1, in 1 or 2 at occ. 3
7	2	2	1	1	0	0	0	0	0	0	0	Seen in 1 and 2, in 1, 2 or dead after occ.4
8	1	1	2	0	1	1	1	1	1	0	0	Seen in 1 and 2, in 1 or 2 at occ.4
9	2	0	0	0	0	0	0	0	0	0	0	Seen in 2, never seen again

The data in this example can be summarized as a multistate m -array, M , (Brownie *et al.*, 1993) in which the capture histories are split into several segments, and the segments arranged by rows according to the occasion of release and by columns according to the occasion of next recapture (with a

“never recaptured column”). The m -array M for female voles on grid B is presented in Table 2. Since each release and recapture took place in a particular state, each cell of the multistate m -array contains an $s \times s$ matrix m_{ij} , where i is the occasion of release and j the occasion of next recapture. The off-diagonal numbers in these matrices are relatively small, because movement tended to be the exception rather than the rule.

The individuals released in a given state at a given occasion are distributed according to their occasion and state of next recapture, or in the category never recaptured, in a mutually exclusive fashion. Assuming independence among individuals, conditional on the number released on this occasion in this state, the terms in each row of the m -array (including the never seen again) follow a multinomial distribution. The multinomial distribution is the natural generalization of the binomial to more than two outcomes (e.g., Mood *et al.*, 1974, p. 137). A MSMR model will thus be based on a set of parameters and a set of assumptions making it possible to calculate the cell probabilities of these multinomial probabilities. MSMR models thus represent attempts to approximate the dynamical process that gave rise to the data, using parameters that correspond to quantities of biological interest, as well as parameters needed to model the underlying sampling process.

B. The Conditional Arnason–Schwarz (CAS) Model

The first MSMR model for open populations was a time-dependent model proposed by Arnason (1972, 1973) and developed by Schwarz *et al.* (1993). Since it is considered here as conditional on first releases, we will refer to it as the CAS model.

The equivalent of the time-dependent survival probabilities of the CJS model are time dependent $s \times s$ transition matrices ϕ_k ($k = 1, \dots, K-1$). The capture probabilities are considered as dependent on the state at the time/occasion of sampling and on time. They are grouped in $s \times 1$ matrices (“vectors”) of recapture probabilities p_k ($k = 2, \dots, K$). The diagonal matrices built from these vectors are denoted as $D(p_k)$. The probabilities of not recapturing an individual, defined as the vector $q_k = 1_s - p_k$, where 1_s is a $s \times 1$ matrix of ones, are grouped in the diagonal matrices $D(q_k)$. Indices for states will be noted in parentheses, for example, as $\phi_3(1, 2)$ for the probability of transition from state 1 at time 3 to state 2 at time 4. Generic indices i, j , and k will be used for occasions, u and v for states. There are $(K-1)s^2 + (K-1)s$ parameters $\phi_k(u, v)$ and $p_k(u)$. We denote as θ the vector of these parameters.

The probability corresponding to a piece of a capture history such as “102” must account for the fact that the individual could have been either in state 1 or in state 2 at occasion 2, when missed at time 2. Thus, the probabilities consist of sums of products, in the example above, $(\phi_1(1, 1)$

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Table 2 An example of a multistate m -array, an efficient summary of multistate capture–recapture data for time-dependent models: female voles *M. pennsylvanicus*, grid B (see text)

Released			Recaptured																					
Occasion	State	Number	Occasion.	2		3		4		5		6		7		8		9		10		11		Never
i	u	R_{iu}	State	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
1	1	7		4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
1	2	11		1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
2	1	8				2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
2	2	11				0	8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
3	1	10						7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
3	2	19						0	11	0	2	0	0	0	0	0	0	0	0	0	0	0	0	6
4	1	23								11	1	0	0	1	0	0	0	0	0	0	0	0	0	10
4	2	23								1	1	0	0	0	0	0	0	0	0	0	0	0	0	11
5	1	33										20	0	3	1	0	1	0	0	0	0	0	0	8
5	2	42										3	16	1	5	0	2	0	0	0	0	0	0	15
6	1	29												20	0	1	0	0	0	0	0	0	0	8
6	2	28												1	19	0	1	0	1	0	0	0	0	6
7	1	31														17	0	0	0	0	0	0	0	14
7	2	38														1	11	0	0	0	0	1	0	25
8	1	34																15	0	0	0	0	0	19
8	2	28																0	13	1	1	0	0	13
9	1	21																		130	0	2	0	6
9	2	19																		0	9	2	1	7
10	1	19																				6	0	13
10	2	13																				0	1	12

$q_2(1)\phi_2(1,2) + \phi_1(1,2)q_2(2)\phi_2(2,2))p_2(2)$. This is a key feature by which multistate CR models differ from single state models, in which the corresponding probabilities are simply products.

We denote as $\pi_{ij}^{uv}(\theta)$ the cell probability corresponding to $m_{i,j}(u, v)$, that is, the number seen again for the first time at occasion j in state v among the $R_i(u)$ released at occasion i in state u . The s^2 cell probabilities, $\pi_{ij}^{uv}(\theta)$, for $u = 1, \dots, s$ and $v = 1, \dots, s$, can be obtained simultaneously, as the $s \times s$ matrix $\pi_{i,j}(\theta)$, using matrix formulas (Brownie *et al.*, 1993). These formulas are given for $K = 4$ occasions of capture in Table 3 (after Choquet *et al.*, 2002). For the last interval, ϕ_{K-1} and $D(p_K)$ appear only as the matrix product $\beta_K = \phi_{K-1} D(p_K)$, with s^2 scalar parameters instead of s^2+s in ϕ_{K-1} and $D(p_K)$. As a consequence, in the CAS model, only $(K - 1) s^2 + (K-2)$ parameters at most are separately identifiable (Brownie *et al.*, 1993). The identifiability problem here is intrinsic to the model. The actual number of estimable parameters for a particular data set can be much lower because of further “confounding” between parameters caused by sparse data. For instance, if the estimates of the probabilities of recapture in $D(p_k)$ are 0 because there are no recaptures at occasion k ($k < K-1$), only the elements of the matrix $\phi_{k-1}\phi_k$ will be estimable. Such instances are common with real data, and, because they will vary from one data set to another, they are usually referred to as extrinsic identifiability problems.

The likelihood, expressing the information in the data relative to the parameters, can be written as the product of the multinomial probabilities, conditional on the number released $R_k(i)$. Like most CR models, MSMR models belong thus to the wide class of product-multinomial models. The product of conditional probabilities is a partial likelihood (Cox, 1975), for which the properties of usual likelihoods hold. The logarithm of the partial likelihood for the CAS model is then (writing $\pi_{ij}^{uv}(\theta)$ as π_{ij}^{uv} for the sake of brevity):

Table 3 Matrix formula for the multinomial probabilities of the Conditional Arnason–Schwarz model, for $K = 4$ occasions of capture

Occasion of release	Occasion of recapture		
	2	3	4
1	$\phi_1 D(p_2)$	$\phi_1 D(q_2)\phi_2 D(p_3)$	$\phi_1 D(q_2)\phi_2 D(q_3)\phi_3 D(p_4)$
2		$\phi_2 D(p_3)$	$\phi_2 D(q_3)\phi_3 D(p_4)$
3			$\phi_3 D(p_4)$

$$\log(L(\theta)) = C + \sum_{i,j,v} m_{i,j}(u, v) \log(\pi_{i,j}^{v,y}) + \sum_{i,v} (R_i(u) - r_i(u)) \log(1 - \sum_{j,v} \pi_{i,j}^{v,y}) \quad (1)$$

C is formed of log factorial terms and does not depend on θ , $r_i(u)$ is the number of the $R_i(u)$ ever recaptured ($r_i(u) = \sum m_{i,j}$), and the last term thus accounts for the individuals never seen again.

If there is a single site or state, the matrices ϕ_{K-1} and $D(p_K)$ are 1×1 matrices, that is, scalar and the indices u and v disappear: the CAS model then reduces to the CJS model. As usual, Maximum Likelihood Estimates (MLEs) $\hat{\theta}$ are obtained by maximizing the (partial) likelihood or log-likelihood above. In contrast to the CJS model for which explicit formulas exist for all K , this is the case for the CAS model only for $K = 2$ or 3 (Pradel *et al.*, 2003). The MLEs have to be obtained by numerical iterative maximization of the likelihood, or, equivalently, minimization of the deviance defined as $-2 \log(L(\theta))$, for $K > 3$. They benefit from the usual asymptotic properties: absence of bias, minimum variance (among asymptotically unbiased estimators), and normal distribution. The deviance $-2 \log(L(\hat{\theta}))$ or more commonly, the relative deviance $dev = -2 \log(L(\hat{\theta})) + 2C$ will be used in model comparison and selection.

Alternatively, the likelihood can be obtained by calculating the probabilities of all observed capture histories using the Markov chain formulation (Caswell, 2001, Section 6.1.2), and, based again on the independence of individuals, acknowledging the fact that the distribution of the numbers of individuals in the various capture histories is multinomial. Even if the probabilities of unobserved capture histories are not needed, this approach will be computationally cumbersome and slow for large data sets and complex models.

Several alternative parameterizations exist. The MLEs will be in one-to-one correspondence with those above, and the deviance will be the same. For an easier biological interpretation, the transition matrices are frequently decomposed as the product of a column-stochastic movement matrix ψ_k and a diagonal survival matrix ϕ_k : $\phi_k = \psi_k \phi_k$ (Hestbeck *et al.*, 1991). Grosbois and Tavecchia (2003) propose another parameterization of the survival-transition probabilities in probabilities of fidelity and probabilities of relative movement. These decompositions assume that survival probability depends only on the state at the beginning of the interval of interest (on state at occasion k) and not also on the transition (state at occasion $k + 1$). If this assumption is not reasonable, then biased estimates can result (Hestbeck, 1995). Joe and Pollock (2002) and Ergon *et al.* (2009) have developed models that permit survival during an interval to depend on the states at occasions k and $k + 1$ (states u and v), by assuming different distributions of transition times during an interval.

Results of the CAS model by grid for the vole data, males only for the sake of clarity, are presented in Figure 3. The adequacy of this general model can be questioned in two different ways:

- First, as is well known for single state survival models (Begon, 1983), a time-dependent model such as the CAS model brings few direct answers to biological questions, here for instance about the symmetry of dispersal or the effect of the fragmentation treatment. Exactly as for the CJS model for survival, the CAS model can be either too restrictive (e.g., no age dependence) or too general (e.g., time variation included even though not needed). The CAS model will thus be viewed as a starting point for more general or particular models. A model that is adequately generalized will remove bias, both in the point estimates of parameters and in the estimates of the standard errors of these estimates. A model with as few parameters as possible will help the investigator focus on the biological questions and also tends to increase precision.

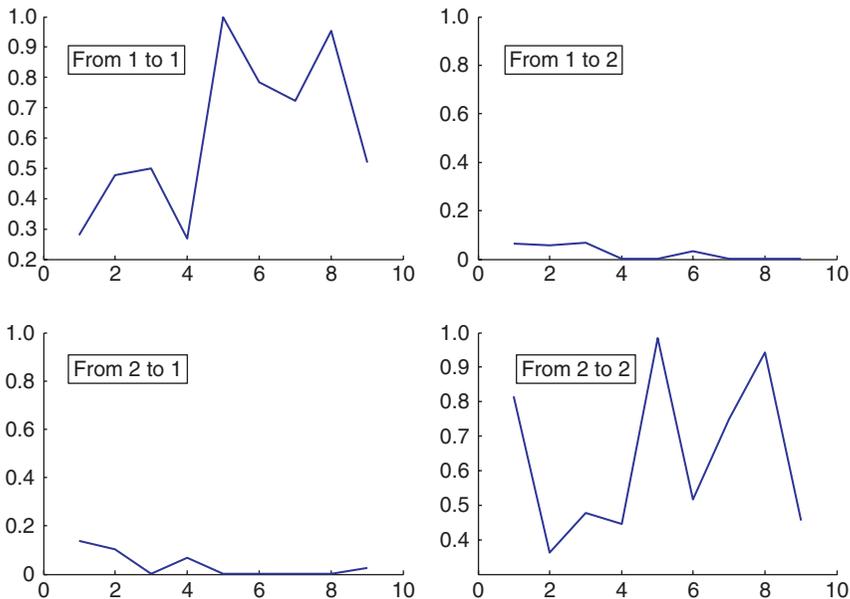


Figure 3 Estimated transition probabilities for the male vole *M. pennsylvanicus* data, based on the Conditional Arnason–Schwarz (CAS) model. The transition probabilities are given for intervals 1–9, and are not separately estimable from probabilities of recapture for the last interval, 10. Movements between the two states (grid halves) are low (from 1 to 2 and from 2 to 1), and, as expected from the design, fairly symmetrical. However, as explained in the text, biological inferences from such a general model are limited and constrained models derived from this starting point are more useful.

- Second, like for all product-multinomial models and, more generally, all models, goodness-of-fit is a key issue (McCullagh and Nelder, 1989, 24ff). The rationale of likelihood ratio tests between a first model M_1 and a second model M_2 nested in M_1 assumes that model M_1 fits the data, that is, the residual variability is compatible with that predicted from the multinomial distributions inherent in the model. If the more general model does not fit the data adequately, the difference in deviance will tend to be inflated, leading too often to significant tests, and thus to incorrect biological conclusions. For the same reasons, model selection based on the AIC will be biased if the set of models considered does not include a model that fits the data. A model is declared to fit the data simply if the data we have are indistinguishable from data simulated from that model, with the goodness-of-fit diagnostic tools we have. It does not imply it is a “true model”, first because there might be many different models fitting the data, and, second, because the processes that produced the data are reduced to simple probabilistic mechanisms just for the sake of analysis. Another important point is that the estimates of precision of the final estimates will also be biased if some lack-of-fit or overdispersion is ignored. The consequences of lack-of-fit are thus too deleterious to be ignored. At this stage, we cannot decide if the estimates of parameters in Figure 3 are valid or not.

C. The Jolly-Movement (JMV) Model

An alternative model, The JMV model, introduced by Brownie *et al.* (1993), is in this context a useful generalization of the CAS model since efficient Goodness-of-fit (GOF) procedures have recently been developed for this model (Pradel *et al.*, 2003, 2005). This more general multistate model is obtained by considering that the probabilities of recapture depend both on the state of arrival and the state of departure, still retaining time-dependence both for transition and recapture probabilities.

There seems at first glance to be little biological interest in considering a dependency of the recapture probability on the departure site. However, in the vole example, one could imagine that the probability of capture of a vole in half 2 of grid A can depend on whether it was in half 1 or 2 at the previous occasion in relation, for instance, with differences in behavior depending on whether the animal was a resident or recent immigrant.

In the JMV model (Brownie *et al.*, 1993), the survival-transition parameters are, as in the CAS model, grouped in time dependent $s \times s$ transition matrices ϕ_k ($k = 1, \dots, K-1$). The recapture probabilities, depending on the states at the beginning and end of the interval and on time, are grouped also in $s \times s$ matrices p_k ($k = 2, \dots, K$), while they were grouped in the diagonal

matrix $D(p_k)$ in the CAS model. For an individual having moved from state u to v between occasions $k - 1$ and k , terms such as $\phi_{k-1}(u, v)p_k(u, v)$ and $\phi_{k-1}(u, v)(1 - p_k(u, v))$ appear in the probability of the capture history. The capture history probabilities are obtained by the same formulas as for CAS (Table 3), with matrix p_k as defined above replacing the diagonal matrix $D(p_k)$, and element-wise matrix product, denoted as a dot, replacing the matrix product in matrix terms such as $\phi_{k-1} \cdot p_k$ and $\phi_{k-1} \cdot (I - p_k)$. For the last occasion only the s^2 products $\phi_{K-1}(u, v)p_K(u, v)$, that is, the element-wise matrix product $\phi_{K-1} \cdot p_K$ can be estimated. Thus, out of the $2(K - 1)s^2 = (2K - 2)s^2$ parameters of the JMV model, only $(2K - 3)s^2$ at most are separately identifiable, and often fewer, depending on the data. The parameter estimates can be obtained by the maximum likelihood method based on iterative algorithms, and suboptimal closed-form estimators exist as well (Brownie *et al.*, 1993). The formulas are strikingly similar to those of the CJS model, obtained for $s = 1$. We will see that the fit of the JMV model can be tested by generalizing in an appropriate fashion (Pradel *et al.*, 2003) the approach used for the GOF test of the CJS model proposed by (Pollock *et al.*, 1985). Indeed, the JMV model, even if it seems too complex and typically irrelevant biologically, appears as a more natural generalization of the CJS model than the CAS model (Brownie *et al.*, 1993; Pradel *et al.*, 2003).

D. Assumptions and Fit Assessment of the Jolly-Movement (JMV) Model

Difficulties with goodness-of-fit issues have been recurrent in the application of capture–recapture methodology (Begon, 1983). On the one hand, goodness of fit procedures are often obscurely technical, on the other hand, neglecting to check the fit of models to data can grossly bias model selection and lead to spurious results. In product-multinomial models, the deviance can in principle be used in a straightforward fashion to get an omnibus test of goodness-of-fit, since, under the assumptions of a given model, the deviance for that model asymptotically follows a χ^2 distribution. The rationale behind this approach is that the deviance can be viewed as a G-test statistic between the observed and expected numbers of individuals in the recapture histories, as it is the case for multinomial models in general (e.g., McCullagh and Nelder, 1989). Unfortunately, with multistate capture–recapture models, the sparseness of the data typically precludes, even more strongly than for single state models, the use of asymptotic χ^2 distributions for the deviance. For instance, with 5 states and 10 occasions there are nearly 10 million different capture histories (see however, for 3 states and 3 occasions, Hestbeck *et al.*, 1991). Although distributional results specific to asymptotic sparseness (number of cells tending to infinity with expected number in each

cell tending to 0) exist (e.g., [Zelterman, 1987](#)), their adaptation to the capture–recapture context has never been investigated. Moreover, the variety of departures from assumptions resulting from the larger complexity of the model causes an omnibus statistic like the deviance generally to be weak in power and poorly informative ([Burnham *et al.*, 1987](#); [Pollock *et al.*, 1985](#); [Pradel *et al.*, 2003, 2005](#)). Specific goodness-of-fit procedures are thus needed.

The basic assumptions inherent in both the JMV and CAS model are as follows:

- The rate parameters for individuals within a state are homogeneous;
- The capture sessions are instantaneous, or at least short compared to the time between sessions;
- The fate of an individual depends on its present state but not on its past;
- Fates and captures of individuals are independent.

The first and second assumptions imply that the same time dependent parameters apply to all individuals and the third assumption implies that this is the case whatever the previous history and the histories of other individuals. A straightforward consequence is that all the information in the data X for estimating the parameters θ is contained in the multistate m -array M , a statement summarized in:

$$\Pr(X|\theta) = \Pr(X|M)\Pr(M|\theta) \quad (2)$$

M is thus a set of sufficient statistics. Even for the JMV model, however, the number of sufficient statistics $m = (K - 1)^2 s^2$ is greater than the number of identifiable parameters $q = (K - 1) s^2 + (K - 2) s$ as soon as $K > 2$: the model is said to be nonsaturated. There is no set of sufficient statistics of lower dimensionality ([Pradel *et al.*, 2003](#)): the expected values in the m -array are quite involved and there is no obvious proportionality between rows as in the single state case.

In the single state case (CJS model), the assumptions could be tested in an efficient way in two main steps ([Pollock *et al.*, 1985](#)). The first step consists of checking that all animals captured on the same occasion do not differ whatever their past capture history, that is, there is no heterogeneity within a row of the m -array; the second step tests the assumption that the different rows of the m -array are homogeneous, that is, that the expected numbers are proportional. Both steps lead in practice to classical tests of homogeneity in appropriate contingency tables ([Everitt, 1977](#)). Their optimality relies on the fact that the model is saturated, because under the proportionality assumption inherent in the second component, the m -array is further collapsed in a set of minimal sufficient statistics S equal in number to the number of separately identifiable parameters.

Pradel *et al.* (2003) developed generalizations of this approach to the multistate case that take into account the difficulties mentioned above (see also Pradel *et al.*, 2005) and follow closely the logic of the single state tests. The account that follows is largely based on these papers. In the multistate case, the first step is retrieved essentially unchanged (there is just a greater variety of past capture histories); this is Test3G of Pradel *et al.* (2003). However, the second step—comparing the rows of the m -array—becomes more involved. The expected numbers in the different rows are no longer proportional but some are linear combinations of others (TestM of Pradel *et al.*, 2003). To exemplify, let us consider the part of the vole m -array corresponding to females in grid B released at occasions 2 and 3 and recaptured at occasions 4 and 5 (Table 4). A striking feature is that of the 11 individuals recaptured at occasion 4 and site 1, the 7 most recently released all come from site 1 itself (i.e., they did not move between occasions 3 and 4). However, of the 4 released two time steps earlier (occasion 2), 1 had been released at site 2. This individual must have moved. It may have moved to site 1 between occasions 2 and 3 (and remained there during the last interval just like the seven individuals that we know were at site 1 at this same occasion) or may have moved from site 2 to site 1 during the last interval in which case its behavior is atypical. Indeed, none of the 11 individuals captured in site 2 at the last occasion did move during the last interval. For individuals released more than one time step earlier, we must consider the possibility that they have moved in the interval. This is why, in probability terms, we must check whether any one of the first two rows of Table 4 is compatible with being a mixture of the last two rows of the same table, hence of individuals from the different sites (Pradel *et al.*, 2003).

Test3G and test M, taken together, constitute a near optimal goodness-of-fit test of the JMV model, although they do not fully benefit from the optimal properties of the single site goodness-of-fit procedure since the JMV model is not saturated. These tests can be further decomposed, using the classical

Table 4 Extract of the m -array corresponding to female voles *M. pennsylvanicus* on Grid B released at occasions 2 and 3 and recaptured at occasions 4 and 5

Released		Recaptured				
Occasion	State	Occasion	4		5	
i	j	State	1	2	1	2
2	1		3	0	0	0
2	2		1	0	0	0
3	1		7	0	1	0
3	2		0	11	0	2

techniques of partitioning of contingency tables, to highlight some specific alternatives. One partitioning is named with reference to spatial state, that is, sites, but seems relevant biologically in a general fashion. It looks at the role of memory of past locations as a determinant of movements (test WBWA of Pradel *et al.*, 2003). It compares the site of the previous (“Where Before” = WB) and of the next (“Where After” = WA) observations of the animals currently observed at the same site. For instance (Table 5), of 10 individuals from group 4 captured at site 2 on occasion 8 which had been captured at least once previously and were also later captured, 9 were last captured at this same site 2 and were again recaptured at site 2. However, the only individual from this group that was previously captured at site 1 was later recaptured at site 1. It could thus be that this last individual was making a scouting expedition to site 2 when it was captured there, but then returned to its site of residence, site 1. There are actually very few data available for this test with the voles. Overall, perhaps due to a lack of power, there is no evidence of a tradition or, stated differently, of relevance of previous locations to current survival and transition probabilities (test WBWA over all occasions and all groups: $\chi^2(9) = 8.27$, $P = 0.51$).

Overall, the fit of the JMV model to the vole data is excellent for all groups (Table 6), and the JMV model is thus an appropriate starting point without correction for the analysis, although one may suspect the particularly high P -level results from a shrinkage of the test statistic towards zero by sparseness ($\chi^2(204) = 164.92$, $P = 0.98$). With no specific suspicion of a dependence of capture probability on the state at the previous sampling occasion, the next step is to check the fit of the CAS model. We first compute a likelihood ratio statistic (Table 7) comparing the JMV and CAS models, according to which the CAS model is quite acceptable ($\chi^2(26) = 32.11$, $P = 0.22$). An overall goodness-of-fit test of the CAS model is obtained by summing the two

Table 5 An example of tradition (component of test WBWA relative to occasion 8, site 2)

1	0
0	9

Among the 28 voles *M. pennsylvanicus* observed at occasion 8 and site 2, only 15 had already been encountered and only 10 of them will be captured again. Of these 10, all but one had last been encountered on this same site 2 (row 2) and they will be captured again at site 2 (column 2). The only one to have last been encountered at site 1 (row 1) is also the only one that will next be captured at site 1 (column 1).

Table 6 Goodness-of-fit tests of the JMV models for the meadow vole *M. pennsylvanicus* data (see text)

Group	χ^2 value	<i>df</i>	<i>P</i> -value
1	16.939	42	1
2	43.018	40	0.34
3	51.139	66	0.91
4	53.826	56	0.56
Total	164.922	204	0.98

Table 7 Comparison between the CAS and the JMV model for the meadow vole *M. pennsylvanicus* data (*s* = 2 states, *K* = 11 occasions, *g* = 4 groups)

Model	Deviance	Number of parameters	Number of identifiable parameters		AIC
			Intrinsic	Numerical	
CAS	2925.1445	$g((K-1) + s^2) = 240$	$g((K-1) + s^2) = 232$	225	3375.1445
JMV	2889.0376	$2g(K-1) + s^2 = 320$	$g(2K-3) + s^2 = 304$	251	3391.0376
Difference	36.1069	80	72	26	

Under the assumption that both models are valid, 36.107 is asymptotically a realization of a χ^2 distribution with 26 *df*. The corresponding *P*-level is 0.0897.

χ^2 statistics above, which shows the CAS model is quite acceptable for the vole data ($\chi^2(230) = 197.03, P = 0.94$).

Even if these goodness-of-fit procedures are presented as formal statistical tests, they are better viewed as a set of goodness-of-fit diagnostics, as the components are interpretable and can suggest alternative models as starting points in cases where the JMV model is rejected.

IV. CONSTRAINED MODELS AND MODEL SELECTION

A. The Vole Case Study: Some Predictions

Regarding predictions and expectations, we expected no differences between grid halves (states) within either grid. Grids were placed in homogeneous grassland habitat and grid halves were of equal size, so we expected state, *s*, to be irrelevant in all of the modeling. The study was carried out over a 20-month period and thus included seasonal variation, but we did not make detailed

predictions about time-specific variation in parameters. The primary predictions about time involved possible changes in parameters following treatment on grid A. We predicted a decrease in movement probabilities (from one state [grid half] to the other) following the fragmentation treatment. We recognized that a decrease might occur by chance alone (seasonal effects and treatment effects were confounded in this test), so we also predicted that any reduction in movement following treatment on grid A would be larger than any possible seasonal reduction on grid B. Because the complement of our survival estimates includes both death and permanent emigration, we expect increases in local survival to follow the fragmentation treatment on grid A. As with movement, we expect the difference between survival in the pre- and post-treatment periods to be larger for the treatment grid, A.

Although the above predictions are the primary predictions involving temporal variation associated with the treatment effect, we also have some predictions about sex effects. The microtine literature contains abundant evidence that males tend to move more than females (e.g., Aars and Ims, 1999; Aars *et al.*, 1999; Ims and Andreassen, 1999; Krebs, 1966; La Polla and Barrett, 1993; Myers and Krebs, 1971; Wolff *et al.*, 1997), and we predicted higher rates of movement for males.

B. Constrained Conditional Multistate Models

All parameters in the JMV model and most of the parameters in the CAS model with s states appear in $s \times s$ matrices with s^2 elements. Moreover, these models in their basic versions are time-dependent. As a result the overall number of parameters increases rapidly with the number of states s and the number of occasions K . In this context, the results will often be unstable, with boundary estimates and wide confidence intervals being very likely. This is a first reason to look for parsimonious models, based, for example, on assumptions of constancy over time of some parameters.

Secondly, the most general multistate models permit individuals to move from every state to every other state and are thus potentially much richer in biological terms than the usual survival models. This aspect is clear in the vole example with the emphasis on dispersal. The number of parameters in unconstrained models such as the JMV and CAS models grows rapidly with the number of states and occasions: the precision then deteriorates, while these models do not focus on specific biological questions. To retain reasonable parsimony and to address efficiently the many different biological questions that can be investigated using multistate models, the use of constrained models, as developed for single state models (Lebreton *et al.*, 1992), is even more important. The predictions above concerning the voles provide a clear basis for the development of appropriately constrained models.

In parallel with this double need for imposing constraints on the basic models, there is a need for generalizations, exactly as was the case for CJS models, for instance by considering variation in the parameters with the age of individuals. Age is sometimes viewed as time elapsed since initial capture, and this meaning of age will coincide with true age of the animal only for individuals marked at birth. Obviously, ages could be modeled as states, with deterministic transitions over time. However, in terms of computational efficiency, age is better treated as a separate attribute, and this is what is done in available software.

We show below with the vole example that the exact same strategy developed for single state models (Lebreton *et al.*, 1992) can be applied efficiently, namely:

- Check the fit of the CAS model, and possibly use an overdispersion factor;
- Build biologically plausible models as constrained models, and fit these models;
- Proceed to model selection based on AIC.

This state-of-the-art, exemplified with the vole data below, can now be implemented nearly routinely using programs MARK (White and Burnham, 1999) and M-SURGE (Choquet *et al.*, 2004). M-SURGE is specifically designed for multistate models, with refined algorithms (analytic gradient, improved rank calculations to determine the number and nature of identifiable parameters following Gimenez *et al.* (2003), fast calculations) and a model definition language that makes it possible to set up complex models easily and reliably. We use this language as an abbreviation for models in the examples below.

Based on our experience, the warning by Lebreton and Pradel (2002) on frequent convergence of iterative algorithms to local minima of the deviance can be emphasized and sharpened: local minima are common, in particular if the survival (JMV, CAS) and recapture (JMV) matrices are ill-conditioned (e.g., far from a diagonal structure), and if the model has many parameters. This is illustrated in Figure 4, concerning the CAS model for the vole data. Besides a detailed examination by profile likelihood (Gimenez *et al.*, 2005), we strongly recommend multiple runs of the same model with random initial values, as routinely proposed in M-SURGE, as currently the best protection against convergence to local minima.

With reliable determination of the deviance, D , of an estimated overdispersion factor, \hat{c} , if needed, and of the number of identifiable parameters n , model selection can be based on the QAIC = $D/\hat{c} + 2n$, or on other techniques such as likelihood ratio tests and analyses of deviance when preferable (Grosbois *et al.*, 2008).

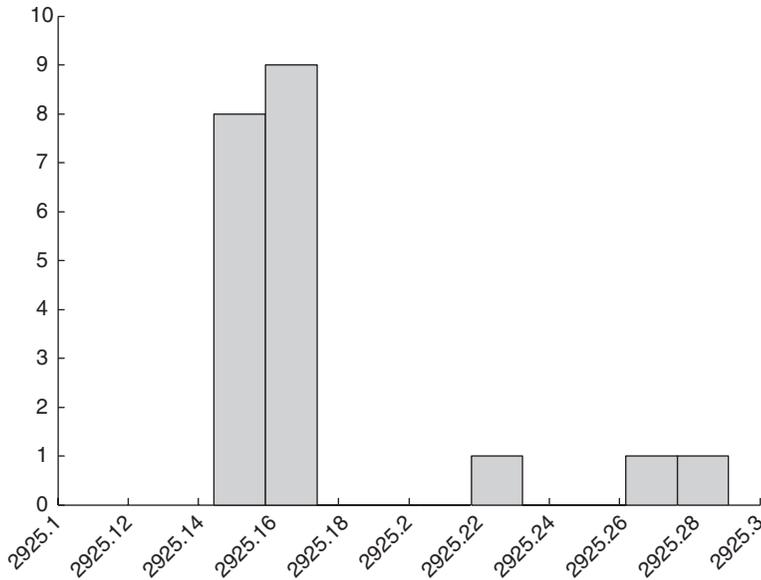


Figure 4 An example of convergence to local minima: histogram of the final deviance over 20 runs of the Conditional Arnason–Schwarz (CAS) model for the vole *M. pennsylvanicus* data, using random initial values.

C. Constrained Models for the Vole Case Study

Model selection is summarized in [Table 8](#), using the M-SURGE model definition language. From bottom to top, the AIC decreases, while a variety of plausible model structures are investigated by looking first at recapture probabilities, then survival, then transition. When investigating recapture probabilities, for example, we used relatively general parameterizations for the other two types of parameters, probabilities of survival and movement. Then when we settled on a model (in other cases it might be 2 or 3 models) for recapture probability, we focused on the modeling of survival while leaving movement probabilities relatively general, etc. This strategy does not cover all biologically reasonable models, because it does not cross all plausible structures over the three types of parameters, and we make no claims about the optimality of this strategy. However, it is a pragmatic approach for achieving parsimony, while keeping the overall number of models reasonably small ([Lebreton *et al.*, 1992](#)).

In the first step, as could be expected, there was some variation in capture probabilities over grids and occasions. The difference in capture probability between sexes could be reduced to an additive effect on a logit scale. A model with no sex-specific variation, but only temporal variation, in recapture

Table 8 Results of model selection for the vole *M. pennsylvanicus* data

Survival	Transition	Recapture	Deviance	np	AIC
sex + pop.t	sex + pop.period	sex + pop.t	3108.958	47	3202.958
sex + pop.t	sex + pop + period	sex + pop.t	3111.364	46	3203.364
sex + pop.t	(sex + pop).period	sex + pop.t	3107.864	48	3203.864
sex + pop.t	sex.pop.period	sex + pop.t	3106.809	50	3206.809
sex + pop.t	Pop(2) + sex(2) + pop(1).period	sex + pop.t	3111.951	48	3207.951
sex + pop.t	pop.period	sex + pop.t	3116.726	46	3208.726
sex + pop.t	sex.period	sex + pop.t	3123.630	46	3215.630
sex + pop.t	sex.pop.t	sex + pop.t	3075.488	79	3233.488
sex + pop.t	sex.pop.from.to.t	sex + pop.t	3044.272	121	3286.272
pop.t	sex.pop.from.to.t	sex + pop.t	3046.732	120	3286.732
(sex + pop).t	sex.pop.from.to.t	sex + pop.t	3035.690	130	3295.690
sex.pop.t	sex.pop.from.to.t	sex + pop.t	3023.822	140	3303.822
sex.pop.period	sex.pop.from.to.t	sex + pop.t	3131.118	107	3345.118
sex + pop.period	sex.pop.from.to.t	sex + pop.t	3133.991	106	3345.991
sex.pop.from.t	sex.pop.from.to.t	sex + pop.t	2990.464	179	3348.464
sex.pop.from.t	sex.pop.from.to.t	t	3010.873	169	3348.873
sex.pop.from.t	sex.pop.from.to.t	pop + t	3010.418	170	3350.418
sex.pop.from.t	sex.pop.from.to.t	sex.pop.to.t	2925.145	225	3375.145
sex.pop.from.t	sex.pop.from.to.t	I	3096.331	161	3418.331
sex.pop.from.t	sex.pop.from.to.t	Sex	3094.462	162	3418.462
sex.pop.from.t	sex.pop.from.to.t	pop	3095.388	162	3419.388
sex.pop.from.t	sex.pop.from.to.t	Sex + pop	3093.442	163	3419.442

Bold print model structure indicates the parameters of primary interest with that set of models. “Period” is a factor contrasting intervals 1–4 (before treatment) with periods 5–10. (after treatment); “pop”, for population, is a factor with two categories (Grid A and Grid B).

probabilities was close in terms of AIC, but the slightly more complex structure sex + pop.t (Table 8) was retained in order to protect from any further bias when modeling the two other types of parameters. The sex + pop.t notation refers to a model in which capture probability varied fully (full interaction) by grid (“pop” notation) and sampling occasion (*t*), with an additive or parallel effect of sex. Thus, capture probability varied over time for each grid, but it varied in parallel over time for the two sexes within each grid.

After the structure for recapture probability was reduced to sex + pop.t, the survival and transition probabilities were modeled with specific attention to the factor “period”, contrasting intervals 1–4 (before treatment) with periods 5–10 (after treatment). This order in considering the three types of parameters corresponded to the order of biological interest and specificity of *a priori* hypotheses. Specifically, the biological thinking followed a gradient going from no predictions for recapture probabilities, to fairly detailed predictions for movement probabilities. Because grid and time effects were

present in the recapture probability structure, we considered it unlikely that structure on recapture probabilities could produce spurious inferences about grid and time effects on transition probabilities.

In the final model, the estimated recapture probabilities that were identifiable varied from 0.5979 to 0.8552, 0.5496 to 0.9800, 0.4986 to 0.9697, and 0.5599 to 0.9762, for males in A, females in A, males in B, females in B, respectively, over occasions 2–10.

Concerning survival, the effect of time on survival could not be reduced to the period effect (models not shown). Model selection provided evidence of more complex variation over time than just variation before/after treatment (Figure 5). In other words a simple model with fixed effects of grid, sex and period appropriately combined is rejected in favor of a more complex variation over time. The variation over time is sufficiently erratic that we are tempted to consider it as random, as if all the multiple causes of variation were sufficiently randomized. This line of thought has led over the last several years to the use of random effects in capture–recapture models. We will, thus, defer tests of survival predictions to Section V, dealing with random effects.

As expected, the transition (movement) probabilities could be modeled symmetrically between the two halves of each grid (removal of the M-Surge model language term “from.to”; in terms of parameter constraints, $\psi_k^{12} = \psi_k^{21}$). Then, the effect of time on the transition probabilities could be reduced to the period effect, that is, to two levels, in interaction with sex and population (grid). Model selection results thus supported models with sex-specific movement parameters (Table 8), and point estimates were consistent with the predictions of greater movement by males (Table 9).

The estimated probabilities of transition in the final model, with a single parameter for movement from one state (grid half) to the other irrespective of the state considered, are given in Table 9. In accordance with general recommendations for the treatment of experiments, we looked neither at the change in parameter estimates on the treatment grid over time, nor at the absolute difference in estimates between grids A and B during the post-treatment period, with grid B seen as a baseline level. Rather, in order not to confound seasonal changes in movement with treatment effects, we compared the change in movement probability before and after the date of treatment on grids A and B. The estimated difference in the probability of movement before/after treatment was -1.67 on a logit scale in grid A, irrespective of sex (treated as an additive effect in this model). This drop in the natural logarithm of the odds of movement, or log-odds-ratio, of 1.67 corresponded in turn to a drop in the probability of movement from 0.1010 to 0.0206 in males and 0.0502 to 0.0098 in females. However, there was also a drop in the probability of movement on grid B, estimated on a logit scale as -0.68 . The difference (-1.00) indicates that the estimated decrease in movement was indeed stronger on grid A than on grid B. Was it stronger to a significant extent?

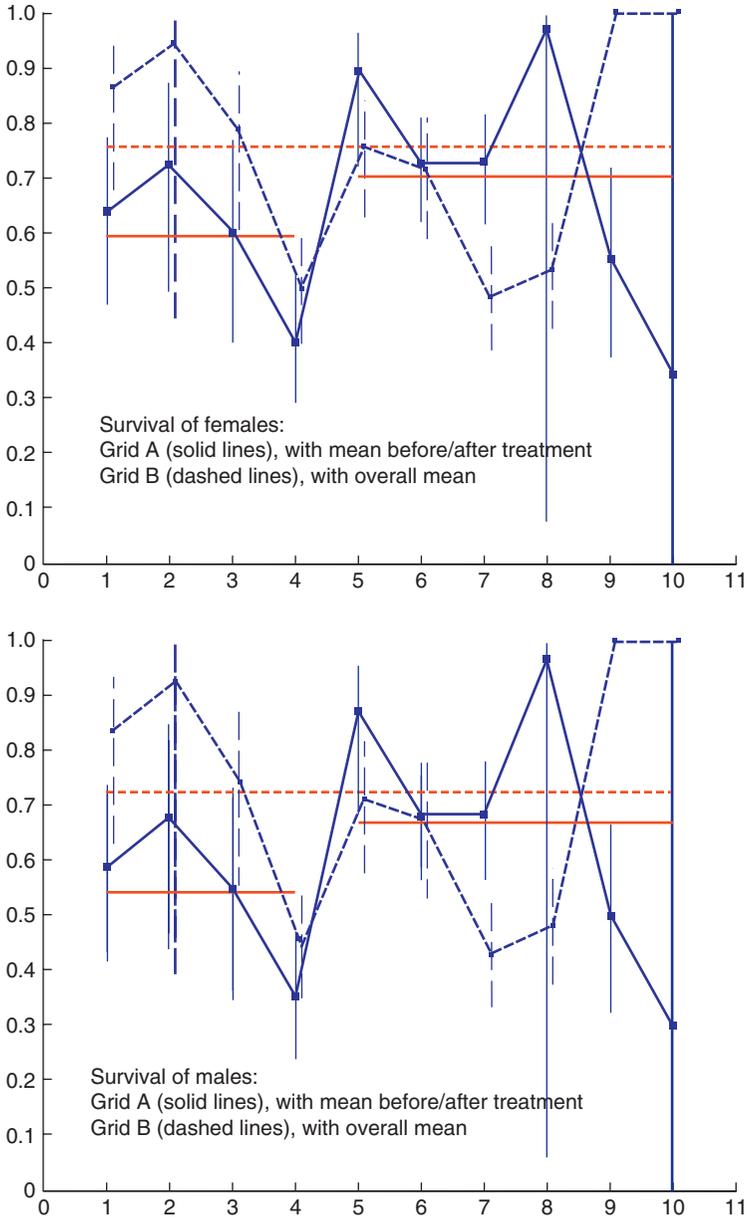


Figure 5 Estimated probabilities of apparent survival by sex, for the two grids, with an emphasis on the fragmentation treatment by plowing that took place in grid A.

Table 9 Estimated probabilities of transition in the final model for the meadow vole *M. pennsylvanicus* data, with a single parameter for movement from one half to the other, irrespective of the half considered

Transition probability	Maximum likelihood estimate	Bounds of 95% CI	Estimated standard error
A males Before	0.1010	0.0512 0.1895	0.0339
A males After	0.0206	0.0084 0.0494	0.0093
A females Before	0.0502	0.0241 0.1013	0.0184
A females After	0.0098	0.0038 0.0250	0.0047
B males Before	0.1739	0.1135 0.2570	0.0364
B males After	0.0966	0.0622 0.1472	0.0213
B females Before	0.0901	0.0526 0.1502	0.0242
B females After	0.0479	0.0291 0.0780	0.0121

Before and after refer to the two periods before and after treatment, that is, intervals 1–4 and 5–10, respectively.

There are several ways to answer this question. The model-oriented answer is based on the fact that this difference is an estimated interaction term. One may then compare the selected model (Table 8, first row), with structure “sex + grid.period” for transition probabilities with the same model without the grid.period interaction (“sex + grid + period”, Table 8, second row). This latter model assumes there was no difference between grids in the change in movement between the two periods. The difference of deviance between these two models (2.4088 on a single df) can be used in a one-sided test, which is close to significance ($z = -1.5520$, $P = 0.0603$). Equivalently, a Wald test could be done, after having obtained an estimated standard error of the estimated difference, as a linear combination of the original parameters in the model. Lastly, the model with interaction is marginally preferable in terms of AIC, the fully additive structure corresponding to a difference in AIC of 0.406. One should realize that this difference is relevant to address the effect of treatment because the difference above is negative; were it not, the model with interaction would have to be discarded, as an *ad hoc* way of making the AIC “one-sided”. For the sake of clarity we preferred in this case to base inference on a few tests of some effects, in combination with AIC-based model selection.

The vole example thus provides some evidence of a decrease in movement probabilities associated with the fragmentation treatment. While this example hopefully provides a good illustration of the strategy of model building and selection, it does not lead to strong inferences, primarily because of the absence of replication (the example is based on a subset of the available data). A comprehensive treatment is provided by Nichols *et al.* (in preparation).

V. RANDOM EFFECTS

A. Fixed and Random Effects in Capture–Recapture Models

The use of linear constraints on transformed parameters that we just used for the vole data is not at all restricted to multistate models, and indeed just expands on a now classical approach for single state survival models (Lebreton *et al.*, 1992). This approach can be summarized for the typical situation in which, among the parameters, there are n time-dependent parameters $\theta_1, \theta_2, \dots, \theta_n$, in vector notation $\theta = (\theta_1, \theta_2, \dots, \theta_n)$, in general already transformed by a link function such as the logit transform. We will focus on variation in $\theta_1, \theta_2, \dots, \theta_n$, and we denote as ξ the vector of the m other parameters. The overall vector of the $n + m$ parameters is denoted thus as (θ, ξ) . In MSMR and other capture–reencounter models, the parameters are estimated through a likelihood denoted as $L(CR_data, \theta, \xi)$. The MLEs, possibly not unique in case of identifiability problems, are denoted as $\hat{\theta} = (\hat{\theta}_1, \hat{\theta}_2, \dots, \hat{\theta}_n)$ and $\hat{\xi}$. $\text{Dev}(\theta, \xi) = -2L(CR_data, \theta, \xi)$ is the deviance of the model, as a function of the n parameters of specific interest, θ , and the m other ones, ξ . As mentioned earlier, the deviance will often be relative, that is, be defined up to an additive constant, as only differences in deviance will be used.

The simplest model forces the parameters of interest to be constant over time:

$$\theta_i = a \tag{3}$$

The time-dependent model considers a particular fixed value at each date, and is, as such, a “fixed effect” model:

$$\theta_i = a + b_i \tag{4}$$

Time-dependence is usually investigated by a likelihood ratio test or by comparing AIC between these two models, since the only variability considered is that induced by the capture–recapture sampling scheme.

As an alternative way to treat temporal variation, each θ_i can be treated as a realization of a random variable inducing a variation around the mean

(as mentioned above, possibly logit transformed) survival a (with $\text{var}(\varepsilon_i) = \sigma^2$, $E(\varepsilon_i) = 0$ and the ε_i identically and independently distributed):

$$\theta_i = a + \varepsilon_i \tag{5}$$

With respect to temporal variation, the main parameter of interest is now σ^2 , the variance over time in the generic parameter of interest θ . The categories of the time factor (in the ANOVA meaning) are not considered associated with a particular year, but as random realizations arising from an underlying distribution of year effects. Thus, the time factor has been treated as a random effect: “Conceptualizing mark–recapture parameters as random variables is a natural and logical step in mark–recapture models” (Barker *et al.*, 2002). There is a huge literature on random effects in linear models (Searle *et al.*, 1992), and we will concentrate here only on the application to capture–recapture models, in particular MSMR.

1. Estimation Procedures

To produce a likelihood as a function of a , σ^2 , and ξ which are now the only parameters, one has to integrate the probability of the data with respect to the probability density of the $\varepsilon_i, f(\varepsilon_i, \sigma^2)$, which in general will be assumed to be a normal distribution probability density. With subscripts F and R denoting the fixed and random effect model likelihoods, respectively:

$$\begin{aligned} \log L_R(Cr_data, a, \sigma^2, \xi) = \\ \log \left(\int_{\varepsilon_1} \dots \int_{\varepsilon_n} f(\varepsilon_1, \sigma^2), \dots, f(\varepsilon_n, \sigma^2) L_F(Cr_data, \theta(a, \varepsilon_1, \dots, \varepsilon_n), \xi) d\varepsilon_1, \dots, d\varepsilon_n \right) \end{aligned} \tag{6}$$

Estimation using this likelihood is totally impractical by standard approaches with capture–recapture models because of its complexity. Two main approaches have been used in the literature to approximate this likelihood.

The first one uses a normal approximation to the likelihood of the time dependent fixed effect model (already used in the context of capture–recapture methods by Lebreton *et al.*, 1995), based on asymptotic results of ML theory (e.g., Mood *et al.*, 1974). In a first approximation, one replaces in $(\hat{\theta}, \hat{\xi}) \overset{\text{asympt}}{\approx} N((\theta, \xi), \Sigma)$ the unknown covariance matrix Σ by its estimate $\hat{\Sigma}$, obtained as a by-product of fitting the fixed effect time-dependent model, to obtain $(\hat{\theta}, \hat{\xi}) \overset{\text{asympt}}{\approx} N((\theta, \xi), \hat{\Sigma})$. Geometrically speaking, in this first step, one approximates the deviance, viewed as a function of the parameters of the fixed model, by the paraboloid tangent to the deviance in $\hat{\theta}$. Under the

random effect model $\theta = N((a, \dots, a), \sigma^2 I_{n \times n})$, the previous distribution is conditional on θ . Integrating over the distribution of θ produces

$$(\hat{\theta}, \hat{\xi}) \approx N\left(\left((a, \dots, a), \xi\right), \hat{\Sigma} + \sigma^2 \begin{pmatrix} I_{n \times n} & 0_{n \times m} \\ 0_{m \times n} & 0_{m \times m} \end{pmatrix}\right)$$

The probability density of this distribution, viewed as a function of the parameters, is an explicit and simple approximation of the likelihood of the random effect model, from which MLEs of a , σ^2 , and ξ can be obtained. One thus applies a ML procedure to ML estimates. This two-stage procedure initially appears to be *ad hoc*, but, as just explained, it does provide an approximation of the integral for the likelihood of the random effect model. It is inherent in the approximate calculations proposed by [Burnham *et al.* \(1987\)](#), [Link and Nichols \(1994\)](#), and [Gould and Nichols \(1998\)](#). The two-stage approach to inference under a random effect model was proposed by [Krementz *et al.* \(1997\)](#) in a case where $\hat{\Sigma}$ is diagonal, and by [Barker *et al.* \(2002\)](#) and [Schaub and Lebreton \(2004\)](#).

The second approach uses stochastic integration, by algorithms derived from Bayesian statistical theory, a subject of intense recent development. The two main methods are Markov Chain Monte-Carlo (MCMC) methods ([Brooks *et al.*, 2002](#); [Clark *et al.*, 2005](#); [Link *et al.*, 2002a](#)) and recursive filtering ([Buckland *et al.*, 2004](#)). MCMC methods, in particular, have seen use in estimation using multistate models ([Dupuis, 1995, 2002](#); [King and Brooks, 2002, 2003a,b, 2004](#)).

B. Mixed Models

Although useful and interesting, a model with just a single effect fails to consider a more general and biologically interesting situation where parameters of interest, such as survival probabilities, vary as a function of both a fixed factor or covariate that can be identified (such as “period” in the vole example) and other unidentified factors or sources of variation. Part of the variation in survival (that not explained by the identified factor) can thus remain unexplained. A straightforward model to cover this situation considers simultaneously the fixed factor and a random source of variation; that is, a random effect, which adds its effects to that of the fixed factor. Such a model is referred to as a mixed model. A relevant model when survival varies over time in relation with an environmental covariate would be $\text{logit}(\phi_i) = a + bx_i + \varepsilon_i$. The usual fixed effect model $\text{logit}(\phi_i) = a + bx_i$ is certainly a reasonable first approach, and the only approach technically within reach in the past ([Clobert and Lebreton, 1985](#); [North and Morgan, 1979](#)), but should be considered at best as a first approximation. The fixed model seems to

provide a useful approximation to the processes that generated the data only when sampling uncertainty is high because of small sample size. Such uncertainty tends to mask the process variation represented in the mixed model by ε_i . Mixed models are also relevant when the fixed effect is a categorical variable, a factor in the ANOVA sense, rather than a continuous covariate. For the vole data, for instance, one can consider, for grid A, a fixed period effect (intervals 1–4 vs. 5–10) and a random time effect: $\theta_i = b_{\text{period}} + \varepsilon_i$

Because of the random effect, the overall variation in survival is that of the time-dependent model (i.e., the time-dependent model includes all of the temporal variation). The approaches presented above for models with a single random effect also apply to mixed models with multiple fixed and random effects.

A further simple and efficient approach can be presented in this context. Lebreton and Gimenez (in preparation) show that the fixed effect cannot be tested by a standard likelihood ratio test when there is unexplained variation over time, that is, $\sigma^2 > 0$. They show further (see also simulations by Grosbois *et al.*, 2008), that the analysis of deviance (Skalski *et al.*, 1993) is an adequate test procedure. As an example, for the vole data, we consider three models. Denoting again as n the number of parameters of direct interest that will be modeled and as m the number of remaining parameters, these three models are:

- The constant parameter model, $M_c : \theta_i = a$ with $m + 1$ parameters
- The model with a fixed period effect, $M_p : \theta_i = b_{\text{period}}$, with $m + 2$ parameters for the case with two periods.
- The time dependent model, M_t . In terms of overall variation, it can be expressed equivalently with a fixed or random time effect added to the period effect of an overall fixed time effect: $\theta_i = b_{\text{period}} + c_i = b_{\text{period}} + \varepsilon_i = d_i$. Under the fixed effect form it has $m + n$ parameters, leaving aside potential identifiability problems.

We denote as $\text{Dev}(M_C)$, $\text{Dev}(M_F)$, and $\text{Dev}(M_t)$, respectively, the deviance for each of these three models. Since the constant parameter model is nested within the fixed effect model, itself nested within the time dependent model, one has: $\text{Dev}_C > \text{Dev}_F > \text{Dev}_t$. The likelihood ratio test statistic is $B = \text{Dev}_C - \text{Dev}_F$. Variation over time not explained by the fixed effect is reflected in $W = \text{Dev}_F - \text{Dev}_t$. B and W are the counterparts of Between and Within ANOVA Sum of Squares, with 1 and $n-2$ degrees of freedom, respectively, obtained as differences between the number of identifiable parameters of the respective models. The analogs of the ANOVA Mean Square Errors are thus B and $W/(n-2)$. The analysis of deviance statistic is then the counterpart of the ANOVA F -statistic and is defined as $F = B/[W/(n-2)]$. This approach provides an approximate test for a period effect in the mixed model $\theta_i = b_{\text{period}} + \varepsilon_i$ in the presence of the random effect.

C. Treatment Effect and Time Variation in Survival in Voles

The models needed to test for a period effect on grid A, in the presence of a random time effect, are the first three models in Table 10. The time effect itself was highly significant based on a likelihood ratio test between the model with only a period effect and the full time model ($\chi^2_{17} = 91.876, P = 0.0000$). It would thus be totally inadequate to test for a period effect without accounting for the additional time variation. The analysis of deviance for a period effect on grid A leads to $F = 26.292/(91.876/17) = 4.8648 \cong F(1, 17)$, best expressed as $t_{17} = 2.206$ once account is taken of the positive sign of the variation in mean survival in grid A after treatment (Figure 5). An increase in survival was expected to result from a decrease in permanent emigration (a component of the complement of capture–recapture survival estimates; also see Coffman *et al.*, 2001). Based on a one-sided test, this statistic is certainly significant, providing strong evidence in favor of the prediction.

Similar results were obtained by the two-stage ML procedure (Table 11), although there is some instability caused by the near singularity of the covariance matrix and by boundary estimates. In particular, this instability affects the estimated standard errors.

A Wald test on period effect in grid A leads to $z = 1.714$, to be compared with $t = 2.206$ by analysis of deviance. Similarly, a Wald test of the hypothesis

Table 10 Models for survival of meadow voles *M. pennsylvanicus* used for an analysis of deviance on survival, with reference to the final model with 47 parameters

Survival	Deviance	np	AIC
Sex + pop.t	3108.958	47	3202.958
Sex + pop(1).period+pop(2)	3200.834	30	3260.834
Sex + pop	3227.125	29	3285.125
Sex + pop.period	3198.856	31	3260.856
Sex + pop+period	3221.635	30	3281.635

The model structure for Transitions is sex + pop.period and for Recapture sex + pop.t.

Table 11 Mixed models for survival of meadow voles *M. pennsylvanicus* used in the two-stage ML procedure to test for a period effect on survival in grid A

Survival	DEV	np	AIC
Sex + pop(1).period + pop(2) + TIME	69.426	31	131.426
Sex + pop + TIME	78.323	30	138.323

Effects in lower case are fixed effects. “TIME” in capitals is a random effect. The model structure for Transitions is sex+pop.period and for Recapture sex + pop.t.

of a temporal process variance equal to zero ($z = 2.2240$, $P = 0.053$) is not as strongly significant as the LRT ($\chi^2(1) = 78.823-69.426 = 8.497$, $P = 0.036$).

The change in survival on grid A is significant ($P = 0.0433$) if considered as a one-sided test, again indicating a significant increase in survival. Once again, the relevant issue is whether or not the change differed between the two grids. A treatment effect in the expected direction would translate as a larger increase in survival on grid A than on grid B. This amounts to a test for a period by grid interaction in the presence of a time effect. The analysis of deviance statistic for this test, based on rows 1, 3, and 4 in Table 10 is $F(1,16) = 4.0542$. The estimated probability of survival increased after treatment from 0.5227 to 0.7475 on grid A, while it decreased from 0.6574 to 0.5950 on Grid B after period 4.

In conclusion, survival varied over time as expected because of the experimental treatment. The results support the prediction that fragmentation resulted in a decrease in animal movement and permanent emigration, and thus in an increase in apparent survival.

Even if this example is only illustrative, it is clear that addressing different levels of variation such as the time and period within time variation is a key feature offered by mixed models. One may thus expect strong development of these approaches, at a pace that will largely depend on the development of user-friendly software, in particular for implementation of Bayesian approaches. The ability of mixed models to take into account subtle design features links naturally with the potential of multistate models to address detailed biological questions. We note that this set of analyses was directed at *a priori* hypotheses and their associated predictions. Although such an approach is natural for experimental work directed at treatment effects, we also believe it to be appropriate for observational studies. In particular, it would be very unusual to study a system so unique that no ecological theory or empirical generalization or studies of similar systems provided any basis for prediction.

VI. RECRUITMENT MODELS AS AN EXAMPLE OF GENERAL MULTISTATE MODELS

A. The Rapid Development of MSMR

Based on the development above, it seems clear that multistate capture–recapture models (MSMR) can be used to draw inferences about state-specific survival and state transitions in the same way that CJS models have been used to provide inferences about survival over the last 20 years. The general strategy of model selection, starting from a general umbrella model that fits the data and then considering biologically plausible models

focusing on the biological questions, works in a similar fashion. Adequate constraints make MSMR models less data hungry than one may guess based on an initial look at the most general models. This general approach simply underlines, in a reassuring fashion, the similarity of MSMR models and CJS models focused on survival.

In addition to this similarity, we believe that because MSMR models accommodate movement of individuals between states, the potential utility of MSMR to population biology is much greater than that of survival models. Taken strictly as multisite models, MSMR models provide an ideal tool to study breeding dispersal (Greenwood and Harvey, 1982) as shown, for example, by Spendelov *et al.* (1995), Lindberg *et al.* (1998), Blums *et al.* (2003a), Brown *et al.* (2003), Cam *et al.* (2004), Drake and Alisauskas (2002) and Skvarla *et al.* (2004). MSMR models have also proved useful for testing ideas from metapopulation ecology (Hanski, 1999), for example, about predicted relationships between the probability of dispersing from one location to another and the distance between the two locations (Martin *et al.*, 2006; Spendelov *et al.*, 1995; Skvarla *et al.*, 2004).

Expanding on the initial idea of using these models for state variables characterizing individual animals rather than just for geographical sites (Nichols *et al.*, 1992, 1994), a variety of states has been considered in the literature. Consideration of “dead” as a state made it possible to recast the analysis of dead recoveries (e.g., Brownie *et al.*, 1985) and of mixtures of dead recoveries and live recaptures (Barker, 1997; Burnham, 1993) as specific MSMR models (Lebreton *et al.*, 1999; see also Fujiwara and Caswell, 2002a). Initial efforts to deal with temporary emigration in capture–recapture modeling (Kendall and Nichols, 1995; Kendall *et al.*, 1997; Schwarz and Stobo, 1997) used the robust design (Pollock, 1982). Although not labeled as such, these models were multistate models in which an organism within the studied population could be in either of 2 states, observable (with nonzero probability of capture) or unobservable (zero probability of capture). More recently, it was recognized that standard open-model data can be used with MSMR models that include “unobservable” states to deal effectively with temporary emigration (Hunter and Caswell, 2009; Fujiwara and Caswell, 2002b; Kendall and Nichols, 2002; Schaub *et al.*, 2004b). In studies of plant populations, dormancy represents a specific form of temporary emigration that can be investigated using MSMR models (Kéry *et al.*, 2005).

Breeding propensity, or the probability that an individual of reproductive age breeds in a given year, is one of the least studied demographic parameters. In cases where animals are sampled on breeding grounds and non-breeders are not present at these areas, MSMR models with unobservable states can be used for inference about breeding propensity (Bailey *et al.*, 2004; Fujiwara and Caswell, 2002b; Kendall and Nichols, 2002; Schaub *et al.*, 2004b). In situations where both breeding and nonbreeding individuals can

be observed and classified as to reproductive state, MSMR models provide a direct means of estimating breeding propensity and investigating mechanisms (Cam *et al.*, 1998; Nichols *et al.*, 1994).

An inference problem related to that of breeding propensity involves age at first reproduction and accession to reproduction. In many species, all individuals do not begin reproduction at the same age, leading to an interest in the probability that an individual of a particular age that has not yet reproduced will be recruited into the breeding population and breed for the first time. For some species, both breeders and nonbreeders are observable, so that addition of age-specificity to standard MSMR models permits inference about age-specific probabilities of recruitment to the breeding population (Hadley *et al.*, 2006). In many other species, such as colonial birds, the estimation problem is made more difficult by the fact that prebreeders are not observable. Pradel and Lebreton (1999) showed that the recruitment models proposed by Clobert *et al.* (1994) for analyzing resightings or recaptures of breeding individuals, without being able to see or recapture nonbreeders, could be written as a partially age-dependent MSMR model with an unobservable state for nonbreeders. For such situations involving multiple state variables (e.g., age and breeding status), Lebreton (1995) recommended combining multiple types of states in the same model structure. Following this suggestion, Spendelov *et al.* (2002) combined age and breeding status (observable = breeding, unobservable = prebreeding) to estimate age-specific breeding probabilities for individuals at a single breeding location. Lebreton *et al.* (2003) further extended such models by considering a model that combined age, geographical sites, and breeding/nonbreeding status (observable/unobservable states).

Here, we revisit the multisite recruitment model presented by Lebreton *et al.* (2003) to study dispersal and recruitment in the roseate tern, based on the long term study by Spendelov and collaborators (Nichols *et al.*, 2004; Spendelov, 1982, 1991; Spendelov and Nichols, 1989; Spendelov *et al.*, 1994, 1995, 2002). This example will emphasize the rapid progress over the last few years on topics such as goodness-of-fit, detection of identifiability problems, and flexibility in modeling, as well as the influence of this progress on our ability to address biological questions efficiently.

B. The Roseate Tern Case Study

The data used in Lebreton *et al.* (2003) and here concern three breeding sites of the roseate tern from Long Island Sound between New York and Connecticut, extending east to Buzzards Bay, Massachusetts. The three colony sites are Falkner Island, Connecticut (denoted as site A), Bird Island, Massachusetts (B), and Great Gull Island, New York (C). Capture–recapture–resighting data used here are from a coordinated study across

the three sites and cover the years 1988–1998, $K = 11$. Estimated numbers of breeding adult terns at these sites over the period of study varied from 240–380 (A), 2140–3560 (B), and 2200–3700 (C) (Spindel *et al.*, 1995; Spindel *et al.*, unpublished). Descriptions of the study sites and the techniques used to mark, recapture, and resight terns are provided by Spindel *et al.* (1995, 2002). Data were restricted to individuals identified at nests by trapping at all three colony sites and also by resighting at site A. Breeding status could not be confirmed at sites B or C for resighted birds, so these data were not used. Many birds were marked as chicks, such that exact age was known at any subsequent year of resighting or recapture. When unmarked breeding adults were encountered, they were marked as well. The models developed below consider age of prebreeders (unobservable state for ages > 1) and first-time breeders (new recruits to the breeding population), but do not otherwise distinguish ages of adult breeders.

Hypotheses and predictions about results of these analyses followed those presented by Lebreton *et al.* (2003). Natal dispersal is thought to be more prevalent than breeding dispersal in many bird species (Greenwood and Harvey, 1982), including seabirds (Bradley and Wooller, 1991). Despite this widely held belief, avian studies of natal dispersal that adequately deal with variation in detection probabilities over time and space are rare (but see Blums *et al.*, 2003b; Hénau *et al.*, 2007; Lindberg *et al.*, 1998). Our basic prediction was that for any pair of colony sites, u and v , the probability of young birds dispersing from natal site u to recruitment site v would be greater than the probability of a breeder at u in year t moving to site v at year $t+1$. We also tested the prediction that the relative attractiveness of colony sites would be similar for young and adult birds. Our knowledge of the behavior of the terns led to several hypotheses. The simplest prediction was that natal and breeding dispersal probabilities varied in parallel between the different pairs of colony sites. However, fledglings and adults from one site may visit other colony sites before true fall migration takes place, and both surviving prebreeders and experienced adults have the opportunity to assess several potential sites before choosing where to nest each year. Thus, for birds that do move, differences in their experience and level of knowledge of local conditions at these sites could lead to differences in the relative rates of movements to destination sites between first-time breeders and more experienced adults. For example, natal-dispersing first-time breeders might be more likely simply to move to a nearby colony site, whereas more experienced birds that disperse might be more likely to move to a higher-quality site even though it may be farther away.

Based on the sizes and histories of the colony sites, colony A is believed to have been the least successful colony. Thus, we predicted that the probability of returning to (not dispersing from) a colony should be greater for sites B and C than for A, for both young birds and adult breeders. A hurricane in

August of 1991 (Hatch *et al.*, 1997) passed over important premigratory staging areas for this population (Trull *et al.*, 1999), and we considered the possibility that rates of dispersal increased following this event. The hurricane effect was modeled as a single-year effect for breeding dispersal, and as a two-year effect for natal dispersal given breeding starts at age 2 and two cohorts could be affected.

Because of the importance of age at first reproduction to fitness (Cole, 1954; Charnov and Schaffer, 1973), we expected probabilities of recruitment to the breeding population to increase with age. If substantial variation in individual “quality” exists (see Cam *et al.*, 2002; Cooch *et al.*, 2002; Link *et al.*, 2002b), then this prediction would still be expected to hold within individuals, but not necessarily at the population level (the level of our modeling).

The suspected loss/degradation of breeding habitat and the relative saturation at the Bird Island colony site (B) led to the prediction that recruitment probabilities at this site might be lower than those at the other two sites because of intraspecific competition and interspecific competition with common terns (*S. hirundo*) for suitable nesting sites. More specifically, we predicted that there would be higher recruitment of natal-dispersers from site A to the closer and presumably less-saturated site C than from site A to the more distant site B.

We expected both death and permanent emigration to be greater for very young birds and thus predicted that annual apparent survival rates for the first two years of age would be lower than apparent survival at later ages (e.g., Loery *et al.*, 1987; Ricklefs, 1973). The hurricane in 1991 led to the prediction that survival would be lower in 1991 than other years for both young and adult birds.

C. General Umbrella Model

The initial states of chicks at banding, that is, as age-0 prebreeders, in the three sites were coded as a, b, c. Recaptures of these birds as breeding adults and initial captures of breeding adults were coded as A, B, C. Typical capture histories are a0AB0A000 for a bird marked as a chick, 00CC0ACC0 for a bird marked as an adult. Since the models are conditional on first capture, initial ringing as a prebreeder (in state a) is quite compatible with the impossibility of recapturing prebreeders: there will never be a reobservation in states a, b, or c. The general structure of the model is based on a directional move from the set of states (a, b, c) to (A, B, C), that is, recruitment. The data set can thus be summarized as two m -arrays (Tables 12 and 13): one from banding as chick to the first observation as breeder, the second starting from the first observation as a breeder for birds banded as chicks and from

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Table 12 *m*-Array for the roseate terns *S. dougalli*, from ringing as chick to the first recapture as breeder, by site of banding as a chick and site of first recapture

Time	Site	Time	3	3	3	4	4	4	5	5	5	6	6	6	7	7	7	8	8	8	9	9	9	10	10	10	11	11	11	
		Site	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
1	1	206	0	0	0	17	1	1	9	0	0	3	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
1	2	983	0	0	0	0	28	1	0	6	0	1	8	1	0	7	1	0	3	3	0	3	1	0	0	0	0	0	1	0
1	3	355	0	0	0	1	1	3	1	0	1	2	0	3	0	1	2	0	0	1	0	0	1	0	0	4	0	0	3	
2	1	136				0	0	0	9	0	0	6	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
2	2	1158				0	5	0	0	2	0	1	13	0	0	21	0	0	6	0	0	10	0	0	6	0	0	1	2	
2	3	508				0	0	0	1	1	4	1	1	9	0	3	11	0	0	4	0	0	4	0	0	2	0	0	1	
3	1	142							0	0	0	9	0	2	7	0	1	3	0	1	2	0	1	0	0	0	0	0	2	
3	2	1128							1	2	0	4	8	2	1	20	1	0	15	5	1	13	1	0	6	1	0	5	2	
3	3	560							0	0	1	0	1	10	3	3	13	1	0	5	0	1	3	0	0	8	0	0	5	
4	1	158										0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
4	2	538										0	0	0	0	2	0	1	5	0	0	4	0	0	2	1	0	0	1	
4	3	918										0	0	0	1	0	2	1	0	1	1	0	2	0	0	1	0	0	0	
5	1	103													0	0	0	17	0	0	4	0	0	4	0	0	1	0	1	
5	2	657													0	0	0	0	23	1	0	18	0	0	13	2	0	5	1	
5	3	772													1	0	1	2	0	6	10	3	2	3	2	7	0	0	9	
6	1	189																0	0	0	26	1	1	13	0	0	7	0	1	
6	2	911																0	0	0	0	8	0	0	11	0	1	7	2	
6	3	1139																0	0	0	7	0	4	3	4	15	0	4	23	
7	1	186																			0	0	0	15	0	1	8	0	1	
7	2	1168																			0	0	0	0	10	0	0	26	2	
7	3	1116																			1	0	1	2	1	4	1	2	29	
8	1	122																						0	0	0	10	0	2	
8	2	1154																						0	0	0	0	1	1	
8	3	1116																						0	0	0	2	0	13	
9	1	82																									0	0	0	
9	2	829																									0	0	0	
9	3	797																									0	0	0	

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Table 13 *m*-Array for breeding roseate terns *S. dougallii* from the first recapture or from banding as a breeder to the next, by site and occasion

Time	Site	Time Site	2			3			4			5			6			7			8			9			10			11			Total
			1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3				
1	1	160	57	1	2	20	0	1	3	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	89	
1	2	254	0	6	0	0	6	0	0	3	0	0	4	0	0	7	1	0	8	0	0	1	0	0	4	0	0	0	0	1	0	41	
1	3	200	2	1	3	2	1	2	2	0	9	0	0	3	0	0	5	1	1	3	0	0	1	1	0	1	0	0	4	0	0	1	43
2	1	193				115	0	0	13	0	2	2	2	2	0	0	2	1	0	2	1	0	1	0	0	1	0	0	2	0	0	1	147
2	2	213				0	4	0	1	2	1	0	3	1	0	6	0	0	8	0	0	4	0	0	1	0	0	3	0	0	0	0	34
2	3	153				1	0	6	0	0	4	0	0	2	1	0	3	0	0	2	0	0	3	0	0	2	0	0	2	0	0	1	27
3	1	243							173	0	0	10	1	0	0	0	1	4	0	0	0	0	1	1	0	0	0	0	0	1	0	0	192
3	2	247							0	14	0	0	6	0	0	8	0	0	14	0	0	2	0	0	3	0	0	3	0	0	1	0	51
3	3	138							0	0	9	0	2	4	0	0	5	0	1	9	2	0	5	0	0	3	0	0	0	0	0	1	41
4	1	278										152	0	0	11	0	2	3	0	0	2	0	0	1	0	0	0	0	1	0	0	172	
4	2	315										0	6	0	0	12	0	0	8	0	0	3	1	0	4	0	0	2	1	0	0	0	37
4	3	253										1	0	7	2	0	9	0	0	8	1	0	9	0	0	3	0	0	5	0	0	2	47
5	1	213													174	0	0	7	0	1	2	0	0	0	0	1	0	0	0	0	1	186	
5	2	201										0	31	1	0	13	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	31	
5	3	179										3	0	10	3	1	7	2	0	9	0	0	0	1	0	3	0	0	0	5	44		
6	1	277																205	4	0	6	0	1	1	1	0	0	2	0	0	0	220	
6	2	225																0	18	0	0	8	1	0	11	0	0	7	0	0	2	0	47
6	3	278																2	3	20	0	0	12	0	2	5	0	0	3	1	0	1	49
7	1	262																			193	0	1	7	0	0	2	0	0	0	0	1	204
7	2	447																			0	16	0	0	19	0	0	8	2	0	7	0	52
7	3	280																			0	0	10	3	1	7	0	0	7	0	0	2	30
8	1	245																						182	2	0	16	0	0	2	0	0	202
8	2	200																						0	13	0	2	21	1	0	4	1	42
8	3	193																						0	0	7	1	0	5	0	0	3	16
9	1	265																								182	0	3	8	0	3	196	
9	2	237																							3	26	0	1	13	0	43		
9	3	110																							0	0	5	0	0	1	6	6	
10	1	257																											181	1	0	182	
10	2	247																											0	12	0	12	
10	3	188																											0	0	5	5	

banding for those first captured as breeders. These two m -arrays are sufficient statistics for the models that follow, that is, the models can be fit using these data summaries alone: the first one contains information on immature survival, natal dispersal and recruitment, the second on breeding dispersal and adult survival. The delay in reproduction and the progressive accession to reproduction are clearly visible in the first of these tables, the first diagonal being empty and the next ones filling in progressively.

The transitions within (a, b, c) will model natal dispersal, those within (A, B, C) breeding dispersal. Age dependence is present in the transitions from a, b, c to all states. The transitions from A, B, C can only be to A, B, C and are assumed to be independent of age. This absence of an age effect makes it possible to consider simultaneously birds of unknown age marked as breeders. We emphasize that the assumption of no movement from A, B, C to a, b, c (i.e., from breeder to prebreeder) does not imply that all recruited individuals are assumed to breed every year. The absence of reproduction by previously recruited birds in some years will be accounted for in the probability of recapture, and the recruitment probabilities will be relative to breeding probabilities of adults. In accordance with the general assumption of nonobservability of prebreeders, the probability of recapture in a, b, c is fixed to 0. Further features of the model are that the survival of prebreeders from age 2, that is, the age at first reproduction at the population level, onwards is the same as that of breeders, and that natal dispersal takes place between birth and age 1. The latter assumption is not restrictive: since no further movement is considered within the three unobservable states a, b, c, the resulting transition probabilities will indeed model the overall natal dispersal, that is, dispersal between locations of birth and first breeding. The model structure is given in further detail in [Lebreton *et al.* \(2003\)](#). We summarize it in [Table 19](#), based on the model definition language of M-SURGE briefly illustrated in [Table 14](#).

In accordance with our general philosophy, it is natural to start from a detailed umbrella model for which goodness-of-fit can be assessed. We will thus consider that the various parameters, with all of their described sources of variation (such as age-dependence in the transitions from a, b, c to A, B, C), also vary over time. [Lebreton *et al.* \(2003\)](#) used an *ad hoc* approach to assessing model fit, assumed to be conservative and based on reduction of the data to single state data. They obtained a lack-of-fit coefficient $\hat{c} = 4.011$ that was used to protect model selection by QAIC ([Burnham and Anderson, 2002](#)). Since there is no age-dependence from the first observation in A, B, C, onwards, that part of the model is exactly like the CAS model. Its fit can be tested in the two steps described earlier that are now available: goodness of fit of JMV plus assessment of difference in quality of fit between JMV and CAS. This will provide the first two components of our assessment of fit. [Crespin *et al.* \(2006\)](#) describe for a single site model how the first part of the capture

Table 14 A few formulas illustrating the model definition language of M-SURGE for the recruitment models of roseate terns *S. dougalli*

Short name	Notation in M-SURGE model definition language	Comments
Age(2, ≥3)	a(2,3:10)	Second year, >Second year
Ads	[a(1).f(1,2,3)&a(2:10).f(1 4,2 5,3 6)]	Adult survival: Breeders in first year after marking and Breeders and non breeders aged at least 2
Ims	a(1).f(4,5,6)	First year survival, concerning non-breeders only
	ld(3).a(2,3,4).to(1,2,3)	Recruitment at ages 2,3,4; ld(3) = lower diagonal #3, that is, transitions from nonbreeder states 1,2,3, to breeder states 4,5,6, respectively
	ld(3).a(5)	Recruitment at age 5 (fixed at 1 for full recruitment at age 5)
	ld(3).[a(2,3:10) + to(1,2,3)]	Additive age (2 and >2 years) and site effect on recruitment
	ld(3).a(2,3:10).to(1,2,3)	Constant recruitment from age 3 onwards, by site
	to(1,2,3)	Site effect for breeders
	f(1,2,3).to(1,2,3)	Breeding dispersal (between breeder states 1, 2, and 3)
	a(1).f(4,5,6).to(4,5,6)	Natal dispersal (as dispersal before recruitment, i.e., among non breeder states 4, 5, 6)
Hurricane(3)	t(1:3;5:10,4)	Hurricane effect (before, after, year of hurricane)

The short names in first column are used in [Tables 16–19](#) presenting model selection.

history (such as a0A. . .) brings no information on goodness of fit provided the corresponding part of the model is sufficiently time and age dependent. This reduces the assessment of fit of a recruitment model to a goodness-of-fit test of the CAS model on the breeder portion of the capture histories. In the multisite context, the situation is a bit more complex, since the model further assumes the independence between the two parts of the capture history. We obtain thus a third component in the form of a test “Where before—Where after,” conditional on the state at the first observation as a breeder.

The results of this goodness-of-fit procedure are given in [Table 15](#). While the model clearly does not fit the data, the lack of fit is somewhat balanced among test components, with the exception of the component concerning the “memory” of the birth site by breeders. The relatively large value of χ^2/df for this component implies, for example, that birds born in site 2, after having bred for the first time in site 1, have a greater tendency to come back to site 2 for further breeding than birds born elsewhere. Such dependence could only

Table 15 Goodness of fit results of the recruitment model for the roseate tern *S. dougallii* data

Component	χ^2	<i>df</i>	χ^2/df
W Before W After	41.367	9	4.5963
3G.SR	132.794	27	4.9183
3G.Sm	103.338	44	2.3486
M.ITEC	213.636	45	4.7475
M.LTEC	38.485	43	0.9450
JMV	529.620	168	3.1525
W Born–W After	66.206	8	8.2758
JMV/CAS	66.168	51	1.2974
Total	661.994	227	2.9163

The overall χ^2 -squared statistic (661.994, $df = 227$) is highly significant ($P = 0.0000$) as are all components but M.LTEC if tested by themselves. The components being reasonably balanced, the lack-of-fit will be accounted for by an overdispersion coefficient $\hat{c} = 2.9163$,

be taken into account using an age-dependent generalization of the memory model proposed by [Brownie *et al.* \(1993\)](#); see also [Pradel, 2005](#)). While further modeling could consider such structural features to remove part of this lack of fit, we considered for the time being that it could be summarized as an overdispersion coefficient, \hat{c} . Compared with the *ad hoc* measure of fit used by [Lebreton *et al.* \(2003\)](#), this overdispersion coefficient drops from $\hat{c} = 4.011$ to $\hat{c} = 2.9163$ showing indeed that multistate modeling did remove a portion of the heterogeneity, as expected.

D. Model Selection

Starting from a full time dependent model, with an overdispersion coefficient $\hat{c} = 2.9163$, we examined potential variation over time in natal and breeding dispersal. Constancy was preferred both to full time variation and to a hurricane effect ([Table 16](#)). Starting from this new model, survival both during the first year and after the first year was shown to be affected by the hurricane ([Table 17](#)). One should note that survival probability is estimated over the whole immature period, that is, from birth to age 2. Under the reasonable assumption that survival of second year birds (age 1–2) is the same as that of older birds, one can produce an estimate of survival for first year birds.

We then modeled recruitment by looking at various alternatives. A constant recruitment rate from age 3 onwards, with additive effects of site, appeared as preferable ([Table 18](#)), and there was no indication that the

Table 16 Modeling breeding and natal dispersal in roseate terns *S. dougallii* starting from full time-dependent model

Breeding dispersal	Natal dispersal	Dev	np	QAIC
time	time	19754.832	266	7 305.94
constant	time	19855.413	212	7 232.43
hurricane(3)	time	19828.493	224	7 247.20
constant	constant	19905.521	170	7 165.61
constant	hurricane(3)	19892.401	182	7 185.11

The notation of effects is detailed in Table 14. Hurricane(3) considers a variation with three levels: years 1–3 (before hurricane), 4 (year of hurricane), 5–10 (after hurricane). Based on Q-AIC with $\hat{c} = 2.9163$, the model with constant breeding and natal dispersal is strongly preferable to others.

Table 17 Modeling survival in roseate terns *S. dougallii* under constant breeding and natal dispersal

np	Survival Model	Result		
		Dev	np	QAIC
60	ads.t + ims.t	19 905.521	170	7 165.61
39	ads.hurricane + ims.t	19 969.365	150	7 147.50
18	ads.hurricane + ims.hurricane	19 999.741	132	7 121.92
12	ads + ims.hurricane	20 047.812	126	7 126.40
12	ads.hurricane + ims	20 108.705	126	7 147.28

Recruitment and recapture are fully time-dependent. Notation of effects, detailed in Table 14, is as follows: ads = adult survival, ims = immature survival, hurricane considers a variation with three levels: years 1–3 (before hurricane), 4 (year of hurricane), 5–10 (after hurricane). Based on Q-AIC with $\hat{c} = 2.9163$, the model with constant breeding and natal dispersal is by far preferable to others.

hurricane had a significant effect on the rate of accession to breeding. As expected at that stage, the time and site dependence in capture probabilities could not be removed. In our final round of model selection we found, as shown previously by Spendelov *et al.* (2002), that the hurricane in 1991 had a greater impact on the survival of young from that year than it had on the survival of adults (Table 19). We also were able to reduce the “hurricane effect” from 3 to 2 levels, that is, the average survival in all “before hurricane” years was not significantly different from the average survival in all “after hurricane” years (Table 20). Using data from just Falkner Island,

Table 18 Modeling recruitment in roseate terns *S. dougallii* under constant breeding and natal dispersal

Transition model	Result		
	Dev	np	QAIC
age(2, 3, 4, 5).site.t	19999.741	132	7 121.92
age(2, ≥3).site	20182.515	66	7 052.59
age(2, ≥3).site.t	20039.005	111	7 093.38
age(2, ≥3).site.hurricane(3)	20134.668	78	7 060.18
age(2, ≥3) + site	20204.844	65	7058.25

Recapture is site and time-dependent. Notation of effects, detailed in Table 14 is as follows: hurricane(3) considers a variation with three levels: years 1–3 (before hurricane), 4 (year of hurricane), 5–10 (after hurricane); age is age in years. Based on Q-AIC with $\hat{c} = 2.9163$, the model with a specific recruitment probability at age 2, constant recruitment probability from age 3 onwards, by site (with. $2 \times 3 = 6$ recruitment parameters).

Spendelow *et al.* (2002) found that young from the two cohorts (1992 and 1993) immediately following the hurricane had above-average survival estimates, but we did not examine this particular model in our analysis. The estimates of the dispersal parameters in Table 22 are similar to those given by Lebreton *et al.* (2003; Tables 7 and 8).

Compared to the analysis in Lebreton *et al.* (2003), this analysis takes full advantage of the recent availability of goodness-of-fit procedures, since, relying on a lower overdispersion coefficient, it is less conservative (Tables 19–23). It also takes advantage of the flexibility and numerical reliability of M-SURGE: all models were run from several initial values to avoid problems with local minima, and the QAIC calculations use reliable estimates of the number of estimable parameters. Finally, the analysis benefited from the flexibility and user friendliness of the model definition language in M-SURGE, illustrated by the simplicity of the model formulas (Table 14). The refined definition of states and the progress in statistical methodology and software clearly have great potential for population biology. It is often advantageous in such a context to incorporate various sources of information in the same analysis, not only to improve precision or power, but also to estimate parameters and thus investigate mechanisms that would otherwise be inaccessible. Several promising approaches exist. Hénaux *et al.* (2007) incorporated a state “alive elsewhere” and a state “dead” to generalize the type of recruitment model we used to incorporate information from dead recoveries and estimate permanent emigration out of the set of sites studied. More general approaches for combining information are developed in the next section.

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Table 19 Final exploration of specific effects in roseate tern *S. dougallii* recruitment models

Survival model	Recruitment model	Recapture model	Results		
			Deviance	np	QAIC
ads.hurricane(3) + ims.hurricane(3)	age(2, ≥3).site	site.time	20182.515	66	7052.589
ads.hurricane(3) + ims.hurricane(3)	age(2, ≥3).site	site	20379.101	37	7061.999
ads + ims + hurricane(3)	age(2, ≥3).site	site.time	20233.338	56	7050.017
ads + ims + hurricane(2)	age(2, ≥3).site	site.time	20236.104	55	7048.965
ads+ims+hurricane(2)	age(2, ≥3). site.hurricane(3)	site.time	20188.424	73	7068.616
ads.hurricane(2) + ims.hurricane(2)	age(2, ≥3)+site	site.time	20225.896	59	7053.465
ads + ims + hurricane(2)	age(2, ≥3)+.site	site.time	20257.652	54	7054.354
ads.hurricane(2) + ims.hurricane(2)	age(2, ≥3).site	site.time	20203.307	60	7047.719

The notation of effects is detailed in [Table 14](#). The main features of this final model selection were as follows:

The recapture probabilities did vary by site and occasion (i.e., the time variation could not be removed from the model).

The hurricane effect could be reduced from 3 to 2 levels (hurricane year against before after, without need to separate the last two categories).

The effects of hurricane on adult and immature survival were not identical on a logit scale (i.e., the hurricane effect could not be considered as additive to age).

Recruitment was not affected by hurricane.

Table 20 Estimates of survival probabilities under the final model of [Table 19](#) for the roseate tern *S. dougallii* data

Age	Site	Period	Estimated survival probability	Lower bound 95% CI	Upper bound 95% CI	S.E.
Adults	A	Before and after hurricane	0.9115	0.8659	0.9427	0.0192
Adults	B	Before and after hurricane	0.7777	0.7219	0.8250	0.0263
Adults	C	Before and after hurricane	0.8363	0.7748	0.8835	0.0276
First year	A	Before and after hurricane	0.4538	0.3538	0.5576	0.0527
First year	B	Before and after hurricane	0.6091	0.4566	0.7428	0.0750
First year	C	Before and after hurricane	0.5962	0.4449	0.7311	0.0750
Adults	A	Hurricane year	0.7126	0.6394	0.7762	0.0351
Adults	B	Hurricane year	0.6290	0.4750	0.7607	0.0748
Adults	C	Hurricane year	-			Not identifiable
First year	A	Hurricane year	0.0670	0.0271	0.1561	0.0302
First year	B	Hurricane year	0.2458	0.1375	0.3998	0.0676
First year	C	Hurricane year	0.0838	0.0412	0.1628	0.0296

The estimate of first year survival probability is obtained by dividing the estimate of survival probability over the first two years of life by that of adults, that is, under the assumption that second year birds have the same survival probability as adults.

Table 21 Estimates of recruitment probabilities under the final model of [Table 19](#) for the roseate tern *S. dougallii* data

Site	Age	Estimated recruitment probability	Lower bound 95% CI	Upper bound 95% CI	S.E.
A	2	0.0098	0.0031	0.0302	0.0057
B	2	0.0236	0.0106	0.0517	0.0096
C	2	0.0181	0.0056	0.0573	0.0108
A	> = 3	0.5411	0.4598	0.6203	0.0413
B	> = 3	0.5117	0.3474	0.6734	0.0863
C	> = 3	0.5377	0.3322	0.7311	0.1077

The probability of recruitment is the transition probability from a nonbreeder state to a breeder state.

Table 22 Estimates of dispersal probabilities under the final model of [Table 19](#) for the roseate tern *S. dougallii* data

From	To	Estimated dispersal probability	Lower bound 95% CI	Upper bound 95% CI	S.E.
(A) Breeding dispersal					
A	A	0.8454	0.7838	0.8892	0.0189
B	A	0.0012	0.0006	0.0027	0.0005
C	A	0.0069	0.0049	0.0096	0.0012
A	B	0.0273	0.0152	0.0486	0.0081
B	B	0.9831	0.9691	0.9908	0.0048
C	B	0.0110	0.0063	0.0192	0.0031
A	C	0.1274	0.0957	0.1676	0.0183
B	C	0.0156	0.0086	0.0282	0.0047
C	C	0.9822	0.9713	0.9888	0.0034
(B) Natal dispersal					
A	A	0.5654	0.2792	0.7358	0.0666
B	A	0.0027	0.0012	0.0064	0.0012
C	A	0.0158	0.0097	0.0258	0.0039
A	B	0.0645	0.0179	0.2072	0.0410
B	B	0.9308	0.8827	0.9598	0.0179
C	B	0.1035	0.0618	0.1684	0.0266
A	C	0.3701	0.2464	0.5136	0.0697
B	C	0.0664	0.0391	0.1109	0.0178
C	C	0.8807	0.8059	0.9286	0.0275

(A) Breeding dispersal, that is, from a breeding site to next breeding site. (B) Natal dispersal, that is, from the birth site to the first breeding site (all denoted here as capital letters A, B, C).

VII. MULTISTATE MODELS FOR MIXTURES OF INFORMATION

A. Recoveries and Recaptures

[Burnham \(1993\)](#) developed a model for the joint analysis of live-recapture and ring-recovery data when all animals in the study are exposed to both types of sampling. This model was extended by [Catchpole *et al.* \(1998\)](#) to allow age- and time-dependent parameters. [Szymczak and Rexstad \(1991\)](#) used Burnham's model to estimate survival and site fidelity probabilities of a gadwall (*Anas strepera*) population. [Barker \(1997\)](#) generalized [Burnham's \(1993\)](#) model to include information from resightings of live animals obtained between marking occasions. This model extends the resighting models of [Cormack \(1964\)](#) and [Brownie and Robson \(1983\)](#) to allow resighting to occur any time between marking occasions and to also include live-recapture and dead-recovery data. Interestingly, [Jolly's \(1965\)](#) earlier suggestion for

Table 23 Estimates of recapture probabilities under the final model of [Table 19](#) for the roseate tern *S. dougallii* data

Site	Occasion	Estimated recapture probability	Lower bound 95% CI	Upper bound 95% CI	S.E.
A	2	0.5621	0.4543	0.6643	0.0544
B	2	0.0391	0.0195	0.0766	0.0137
C	2	0.0258	0.0107	0.0608	0.0115
A	3	0.8147	0.7324	0.8760	0.0365
B	3	0.0327	0.0180	0.0588	0.0100
C	3	0.0275	0.0142	0.0525	0.0092
A	4	0.8878	0.8192	0.9326	0.0283
B	4	0.0829	0.0615	0.1108	0.0124
C	4	0.0625	0.0430	0.0900	0.0118
A	5	0.8832	0.8146	0.9288	0.0287
B	5	0.0433	0.0296	0.0630	0.0084
C	5	0.0267	0.0172	0.0412	0.0060
A	6	0.9254	0.8705	0.9582	0.0216
B	6	0.0768	0.0586	0.1001	0.0105
C	6	0.0577	0.0430	0.0769	0.0085
A	7	0.9529	0.9074	0.9766	0.0166
B	7	0.1304	0.1052	0.1605	0.0141
C	7	0.0656	0.0507	0.0845	0.0085
A	8	0.9408	0.8908	0.9687	0.0190
B	8	0.0694	0.0540	0.0888	0.0088
C	8	0.0551	0.0421	0.0718	0.0075
A	9	0.9000	0.8499	0.9346	0.0213
B	9	0.0940	0.0732	0.1200	0.0119
C	9	0.0302	0.0216	0.0422	0.0052
A	10	0.9295	0.8740	0.9616	0.0215
B	10	0.0873	0.0662	0.1142	0.0121
C	10	0.0490	0.0360	0.0664	0.0077
A	11	0.8861	0.7848	0.9431	0.0390
B	11	0.0600	0.0438	0.0817	0.0095
C	11	0.0627	0.0460	0.0851	0.0099

augmenting live-recapture data with resightings leads to the maximum likelihood estimators for capture and survival probabilities, but only under the assumption of no, or random, emigration ([Barker, 1997](#)).

[Lebreton *et al.* \(1999\)](#) demonstrated that [Burnham's \(1993\)](#) model could be expressed as a special case of a multistate mark–recapture model. They developed a multistate representation of the CJS model in which two states “Alive” and “Dead” are defined. In the CJS model, animals can only be observed in the “Live” state but in [Burnham's](#) model, information is also obtained from recoveries of marked individuals that have died (dead recoveries). To develop the multistate representation of [Burnham's \(1993\)](#) model, [Lebreton *et al.* \(1999\)](#) defined a new state “Newly dead”; animals can be

observed in the states “Alive” and “Newly dead” but not in the state “Dead”. An animal alive at i may remain alive at $i + 1$ or it may move into the state “Newly dead”. An animal in the state “Newly dead” at i makes the transition to the absorbing state “Dead” at $i + 1$. Because the state “Dead” is not observable, it can be suppressed; the likelihood requires only that the two states “Alive” and “Newly dead” be explicitly expressed.

Burnham (1993) also considered the case of two forms of emigration: permanent emigration where animals may move away from the region where they are at risk of capture, but not return, and a second form “random temporary emigration” where animals may leave and return. For random temporary emigration the probability of being at risk of capture at i is the same regardless of whether the animal was at risk of capture at $i - 1$. In this case of random temporary emigration, the probability that an animal is at risk of capture in sample i , is confounded with the recapture parameter p_i . Thus, the model as described above is valid for situations in which either no emigration or random temporary emigration occurs. On the basis of standard open model encounter history data we cannot distinguish between these two models, although discrimination is possible under the robust design (Kendall *et al.*, 1997).

Permanent emigration (with probability denoted as $1 - F_i$, the complement of fidelity) can be accommodated in the multistate framework by including a second unobservable “Alive” state. Animals in the state “Unobservable alive” are alive but not at risk of capture. If the state “Observable Alive” is state 1, the state “Unobservable alive” is state 2 and the state “Newly dead” is state 3, then the multistate representation of Burnham’s (1993) model with permanent emigration is obtained by constraining the CAS likelihood so that:

$$\Phi_i = \begin{bmatrix} S_i F_i & S_i(1 - F_i) & 1 - S_i \\ 0 & S_i & 1 - S_i \\ 0 & 0 & 0 \end{bmatrix} \quad \text{and} \quad \mathbf{P}_i = \begin{bmatrix} p_i & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & r_i \end{bmatrix} \quad (7)$$

This development utilizes the MSMR framework with states corresponding to animals that are alive and dead. The state space can also be extended to incorporate multiple banding and recovery locations, bringing both sources of information to bear on the estimation of movement probabilities. Kendall *et al.* (2006) combine these information sources to estimate survival and movement probabilities for Canada geese wintering in the Atlantic Flyway, US.

B. Modeling Live Resightings Between Capture Occasions

A dead recovery is not the only way that information can be obtained from animals between capture occasions. Animals may also be resighted alive. Barker (1995) extended Burnham’s (1993) model in two ways: (1) to allow modeling of live resighting of animals between samples i and $i + 1$ in addition to dead

recoveries and (2) to allow temporary emigration to be described by a Markov chain, relaxing the assumption that temporary emigration is random (where “random” is defined as above; see also Burnham, 1993 and Kendall *et al.*, 1997).

1. *The First Model Considers No, or Random, Temporary Emigration*

In a dead recovery model, an animal found dead is no longer available for recapture or recovery. Thus, at time i , the indicator can only take the value 1 if the animal was caught alive at i or 2 if it was found dead in $(i, i + 1)$. With live resightings an animal can be both seen alive in $(i, i + 1)$ and caught at i , and so coding is more complicated. To develop the multistate representation of the model with resightings we modify the data format used by program MARK (White and Burnham, 1999) in which events in the interval $(i, i + 1)$ are recorded using pairs of indicator variables ($LiDi$). Here we adopt a similar approach with the indicators defined as follows:

- $L_i = 0$ (not captured in sample i)
- $L_i = 1$ (captured in sample i)
- $D_i = 0$ (not resighted alive nor found dead between samples i and $i + 1$)
- $D_i = 2$ (resighted alive in between samples i and $i + 1$)
- $D_i = 3$ (found dead between samples i and $i + 1$).

For example, an animal with the history 00 10 02 13 was first released at sample time 2, was not caught at time 3 but was resighted alive between sample times 3 and 4, was caught at time 4 and then was found dead between samples 4 and 5.

Assuming no or random temporary emigration, we define three pseudo-states: “Alive and not resighted”, “Alive and resighted”, and “Dead and recovered”. These are not states in the usual sense of the multistate model in that they include resighting/recovery events. However, by expressing the model in this way, the CAS model generates the correct likelihood. The survival-movement matrix that governs the transition from a L_i sample to a D_i sample is given by:

$$\Phi_i = \begin{bmatrix} S_i(1 - R_i) & f_i v_i & f_i(1 - v_i) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \text{ with capture matrix } \mathbf{P}_{i+1} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \tag{8}$$

where

$$f_i = S_i R_i + (1 - S_i)(r_i + (1 - r_i)R'_i)$$

$$v_i = 1 - \frac{(1 - S_i)r_i}{f_i}.$$

and

R_i is the probability that an animal that is alive at i and at $i + 1$ is seen in $(i, i + 1)$,

R'_i is the probability that an animal that dies between i and $i + 1$ and is not reported dead is seen in $(i, i + 1)$ before it died,

r_i is the probability that an animal that dies between i and $i + 1$ is reported dead.

For transitions from a D_i sample to a L_{i+1} sample, the survival-movement matrix is given by:

$$\Phi_i = \begin{bmatrix} 1 & 0 & 0 \\ \frac{S_i R_i}{f_i v_i} & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \text{ with capture matrix } \mathbf{P}_{i+1} = \begin{bmatrix} p_{i+1} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \quad (9)$$

Barker (1997) showed that under random emigration, the probability of temporary emigration (i.e., the probability that an animal is at risk of capture at $i + 1$) is confounded with p_{i+1} as in Burnham's (1993) model.

2. Permanent Emigration or Markovian Temporary Emigration

The CAS and JMV models are Markovian in the sense that events in the interval between sample i and sample $i + 1$ depend only on the state of the animal at sample i . If emigration is random the multistate model as described above is Markovian; that is, the encounter history can be regarded as an observed realization of a Markov chain and the probability of transitions from states occupied during L sample to states occupied during D samples depends only on the state occupied for the L sample. Similarly, transitions from D to L samples depend only on the state occupied for the D sample.

When the model is generalized to allow permanent or Markovian temporary emigration the fate of an individual depends on whether it is "at risk of capture" or "not at risk of capture".

To model joint live-recapture/live-resighting data under permanent or temporary Markovian emigration we thus have to split the "Alive and not resighted" state into two states according to whether or not the animal is at risk of capture. Thus, we now have four states:

1. Alive and available for capture
2. Alive but not at risk of capture (unobservable)
3. Resighted alive
4. Resighted dead

The survival-movement matrix that governs the transition from an L_i sample to a D_i sample is then given by:

$$\Phi_i = \begin{bmatrix} S_i(1 - \gamma''_i)(1 - R_i) & S_{ii}\gamma''_i(1 - R_i) & f_i v_i & f_i(1 - v_i) \\ S_i(1 - \gamma'_i)(1 - R_i) & S_{ii}\gamma'_i(1 - R_i) & f_i v_i & f_i(1 - v_i) \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \text{with capture matrix}$$

$$\mathbf{P}_{i+1} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \tag{10}$$

where γ''_i is the probability that an animal that is at risk of capture at i is not at risk of capture at $i + 1$ (i.e., it has temporarily emigrated) and γ'_i is the probability that an animal that is not at risk of capture at i is not at risk of capture at $i + 1$ (i.e., it remains a temporary emigrant).

For transitions from a D_i sample to an L_{i+1} sample the survival-movement matrix depends on when the animal was last captured. If the last capture occasion is indexed by h :

$$\Phi_i^h = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ \frac{\alpha_{hi+1} S_i R_i}{\delta_{hi} f_i v_i} & \frac{\alpha'_{hi+1} S_i R_i}{\delta_{hi} f_i v} & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \text{with capture matrix}$$

$$\mathbf{P}_{i+1} = \begin{bmatrix} p_{i+1} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \tag{11}$$

The functions α , α' , and δ are functions of γ'' and γ' : α_{hj} is the probability that an animal last caught at h and alive at j is at risk of capture at j and has not been caught after h , α'_{hj} is the probability that an animal last caught at h and alive at j , is not at risk of capture at j and has not been caught after h , and δ_{hj} is the probability that an animal last caught at h and alive at j is not caught between k and (including) j . Note the distinction between the function δ_{kj} and the functions α_{hj} and α'_{hj} is that with δ_{hj} animals can be either at risk of capture or not at risk of capture at j . Computation of the likelihood is carried out as for the CAS model except that the appropriate survival-movement matrix must be substituted according to when the animal was last caught.

In order to make the model identifiable additional constraints are required on the parameters γ''_i and γ'_i . One option is permanent emigration (i.e., $\gamma'_1 = \gamma'_2 = \dots = \gamma'_{t-1} = 1$); another is to have stationary Markovian temporary

emigration by applying the constraints $\gamma''_1 = \gamma''_2 = \dots = \gamma''_{t-1}$ and $\gamma'_1 = \gamma'_2 = \dots = \gamma'_{t-1}$ (Barker *et al.*, 2004).

Note that constraining $\gamma''_i = 0$ for all i will result in a random (or no) emigration model being fitted (Barker and White, 2001). Under this constraint, γ'_i can be constrained to any value as it does not enter into the likelihood.

Because the JMV model is not adequate to describe permanent emigration or Markovian temporary emigration, the goodness of fit tests described in Section D are no longer appropriate. However, the JMV goodness of fit test will be sensitive to permanent or Markovian emigration. Because permanent or Markovian emigration describe a particular type of memory in the model it might be feasible to construct a test specifically for the random (or no) emigration assumption.

C. Other Mixtures of Information

The above two information mixtures are relatively general and well-developed, but additional MSMR models with multiple sources of information have been developed for specific problems. Conn *et al.* (2004) combined all of the above sources of information, capture–recapture data, resightings and band recoveries into a single MSMR model designed to estimate tag loss. Specifically, all neck-banded lesser snow geese (*Chen caerulescens caerulescens*) were classified by whether they still retained their neck band. Tag loss was modeled as a change of state, moving from with tag to without. Kendall *et al.* (2006) considered the combination of capture–recapture data, incidental resightings and band recoveries from multiple locations into a single MSMR model. Data from a subset of animals with radio tags have been used with special MSMR models to estimate temporary emigration from the central study location exposed to capture–recapture efforts (Powell *et al.*, 2000). Similarly, genotypic data can be used with genetic assignment tests (e.g., Manel *et al.*, 2005; Waser and Strobeck, 1998) to jointly model multi-site capture–recapture and gene frequency data (Nichols, Pollock, and Waser, unpublished) with MSMR models.

VIII. DISCUSSION

A. Multistate Models as a General Framework

As recalled in our historical account, multistate models first appeared as multisite generalizations of single state models (Arnason, 1972, 1973). Their full use started only with the progressive settling of statistical issues and the development of computational algorithms (Brownie *et al.*, 1993; Schwarz

et al., 1993). Hestbeck *et al.* (1991) showed in a seminal paper the huge interest of these models by providing the first real field application, together with a number of new ideas such as the role of memory of sites occupied in the past on dispersal. Our review shows that multistate models have considerably enriched the set of biological processes that can be accommodated by mark–recapture methodology, and are becoming a key tool for addressing biological questions based on data from individually marked animals (Cam, 2009; Conroy, 2009).

Significant progress has been recently made (Gimenez *et al.*, 2003; Pradel *et al.*, 2003, 2005) on resistant statistical issues, such as local minima in the likelihood and goodness-of-fit issues (Lebreton and Pradel, 2002). This progress has thus brought multistate capture–recapture models to a level of utility and flexibility comparable to that of survival models of the CJS family (Lebreton *et al.*, 1992), widely used by biologists (Schwarz and Seber, 2000). Software is now available (M-SURGE, Choquet *et al.*, 2004; MARK, White and Burnham, 1999) to apply in a flexible, reliable and quick way the same general approach that has been recommended for the CJS model, that is, starting from a general “umbrella” model that fits the data, and proceeding to model selection among a set of biologically plausible models obtained by constraining the general model. In the two examples we presented, this approach could be applied efficiently. In particular, constraints make it possible to greatly reduce the number of transition probabilities. As a consequence, multistate models, provided they are adequately constrained, do not appear as strongly data hungry. Given the number of excellent and rich data sets obtained in long term programs of study on marked animal and plant populations, and the tendency for biologists to focus on sources of variation among individual organisms, it seems clear that multistate models will see the same type of wide use as CJS models.

The key feature of multistate models is that any set of mutually exclusive and identifiable events in the life cycle of the population under study can be treated as states (Lebreton and Pradel, 2002). The recruitment model we presented for the roseate tern data illustrates this point by using a combination of breeding status and geographical sites. Among these states, some can be nonobservable. The price to pay concerns the identifiability of parameters. However, adequate techniques now exist to determine minimal and biologically reasonable constraints that make the maximum number of parameters estimable. It is still difficult to measure the potential utility of models based on complex combinations of elementary states. For instance, Henaux *et al.* (2007) combined states for multisite recruitment as in our tern example together with a state “alive elsewhere” and a state “dead” to analyze simultaneously colony-specific recruitment and large scale recoveries in the Cormorant. This model made it possible to estimate age-dependent survival and permanent emigration out of the set of colonies studied, and thus to draw

inferences about many of the key biological processes important to the understanding of recruitment mechanisms. Many different types of such models are possible, using states based on the biological questions, the sampling design and type of data available. Thus, it seems possible to customize MSMR for analyzing CR data from any long term program, losing as little information as possible and, at the same time, addressing as precisely as possible the biological questions that motivated the study. As mentioned above, such models are very appealing for studying a variety of biological and practical questions:

- Dispersal (states = geographical sites, [Bechet *et al.*, 2003](#); [Blums *et al.*, 2003a,b](#); [Coffman *et al.*, 2001](#); [Hestbeck *et al.*, 1991](#); [Martin *et al.*, 2006](#); [Nichols and Coffman, 1999](#); [Spendelov *et al.*, 1995](#); [Skvarla *et al.*, 2004](#)).
- Direct estimation of state transition probabilities for use in stage-based population projection matrices ([Fujiwara and Caswell, 2002a](#); [Leirs *et al.*, 1997](#); [Nichols *et al.*, 1992](#)).
- Trade-offs between reproductive status and survival (states = reproducer/nonreproducer, ([Cam *et al.*, 1998](#); [Church *et al.*, 2007](#); [Hadley *et al.*, 2007](#); [Nichols *et al.*, 1994](#)).
- Rate of accession to reproduction (states = prebreeder/breeder: [Hadley *et al.*, 2006](#); [Lebreton *et al.*, 2003](#); [Pradel and Lebreton, 1999](#)).
- Proportional contributions of different demographic components to population growth rate ([Nichols and Hines, 2002](#); [Nichols *et al.*, 2000](#)).
- Combination of different types of demographic information, such as live recaptures and recoveries of dead individuals by the public, that can be analyzed simultaneously using adequate multistate models ([Hénaux *et al.*, 2007](#); [Lebreton *et al.*, 1999](#); [Powell *et al.*, 2000](#)).
- Estimation in the face of temporary emigration (unobservable state) for some open population models in the absence of robust design data ([Fujiwara and Caswell, 2002b](#); [Hunter and Caswell, 2009](#); [Kendall and Nichols, 2002](#); [Schaub *et al.*, 2004b](#)).
- Investigation of the relative roles and interplay of different sources of mortality ([Schaub and Pradel, 2004](#)), even if parameters for MSMR models with several causes of mortality are often weakly identifiable.
- Reduction of heterogeneity in model parameters (e.g., capture and survival probabilities) by using states in order to get less biased estimates of demographic parameters and flows.

While the linear constraint approach derived from generalized linear models is efficient, progress is expected in dealing with random effects. Although the Bayesian techniques are strongly promising, their full benefit for customized models of the type we just mentioned will require sufficiently user-friendly software for an efficient transfer of these approaches to biologists. Meanwhile

we showed that simple techniques such as the analysis of deviance can be extremely helpful and can be carried out using existing computational methods.

Multistate models appear thus as a synthetic class of models, in particular because they generalize some existing powerful model families. They can be viewed alternatively as generalizations of the CJS models to more than one state, or as Markov chain models with incomplete detection of individuals. Specific applications of MSMR models also cover a wide range of models, notably all models for combinations of information, including the dead recovery models and models for mixtures of recoveries and recaptures. General states of any kind can indeed be considered and combined, provided that the states considered are mutually exclusive alternatives for each individual at each time step. As noted above, in a study of the Danish population of the Cormorant, *Phalacrocorax carbo*, Hénau *et al.* (2007) considered in a multisite recruitment model a state “alive elsewhere” and a state “just dead”. This combination made it possible to separately estimate survival and fidelity by taking into account dead recoveries that could occur even for individuals that permanently emigrated out of the set of colonies studied. We expect such combinations of information sources to be used increasingly in the future.

MSMR models require assignment of individuals to discrete states even when there are continuous criteria (e.g., quantitative indices for body condition) by which individuals can be classified. Such discretization is often viewed as a limitation. There is in fact no reason why continuous variables such as body mass cannot be categorized into discrete states such as “underweight”, “normal,” and “overweight”. It seems to us that the reluctance to discretize quantitative covariates, or to “group individuals” into discrete states, can often be attributed to some hidden feeling that the model should be as faithful a representation of reality as possible. Instead, we view models as the result of deliberate efforts at simplification for the purpose of facilitating understanding of complicated processes. If one fully accepts this view that models are tools, and if one checks the consequences of discretization for some real world examples, it becomes apparent that little is lost, despite a potential cost in number of parameters. Moreover, this cost is not always present: for example, in the case of body mass one could use three survival parameters for three mass categories instead of a quadratic continuous relationship between mass and survival which also requires three parameters. Discretization has the advantage of inducing within-state variability. Even if this variability is partly related to the systematic change of the discretized covariate within each state, it can be at least partly considered as reasonably randomized over individuals. It can then serve as a benchmark for assessing the significance of “between-state” variation, as is usual in Fisherian/frequentist statistics. Such variability can be detected, as when goodness of fit tests provide evidence of overdispersion, or it can be considered as hidden within the residual multinomial variability of the model.

An advantage of covariate discretization in some situations is the absence of a need to specify, *a priori*, a parametric relationship between the covariate and a parameter of interest (e.g., survival or transition probabilities). MSMR permits separate estimation of parameters for each state (set of covariate values), with no necessary relationship between parameters for different states (Nichols *et al.*, 1992; Pollock, 2002). If specific parametric forms are of interest, then they can be investigated by imposing a structure on the state-specific parameters. The point of this discussion is not to claim that the MSMR approach to time-varying covariates is necessarily superior to approaches based on continuous covariates (e.g., Bonner and Schwarz, 2005), but to emphasize that both approaches have advantages and disadvantages, and to suggest that these be considered when selecting an approach for a particular question.

As noted by Lebreton and Pradel (2002), “MSMR models can thus be viewed as canonical models for individual covariates changing over time”. They also provide a natural way of estimating parameters of stage-classified matrix models (Fujiwara and Caswell, 2002a; Nichols *et al.*, 1992). Indeed, as noted by Caswell (personal communication), by classifying individuals by state in a fully statistical context, MSMR models incorporate into a statistical estimation framework the *i*-state idea (Caswell, 2001; Metz and Diekmann, 1986) which is fundamental to structured population modeling.

B. Perspectives

Given this degree of generality, MSMR models thus represent a major step towards the general “mother-of-all” models envisaged by Barker and White (2004). However, MSMR models do not represent an endpoint in generality, as illustrated by the recent appearance of a further generalization, the uncertain state models, or “multievent models” (Pradel, 2005), discussed below.

In Figure 6, we summarize the links of MSMR models with a variety of statistical models, and their resulting role in providing a general framework. When all marked individuals are detected, MSMR models reduce to models for follow-up or known-fate data, namely Markov chains when there are several states, and binomial chains used in survival models in the single state case (upper right part of Figure 6). As discussed earlier, MSMR models reduce directly to single-state capture–recapture models when the number of states, s , equals 1. There is thus a direct link (right part of Figure 6) with the Jolly–Seber and CJS models, depending on whether interest is focused on population size estimation or not, respectively. Among many specific developments, considering unobservable states (left part of Figure 6) opened the way to a variety of possibilities. Multisite-recruitment models for colonial birds in which nonbreeders cannot be observed, as illustrated with the roseate

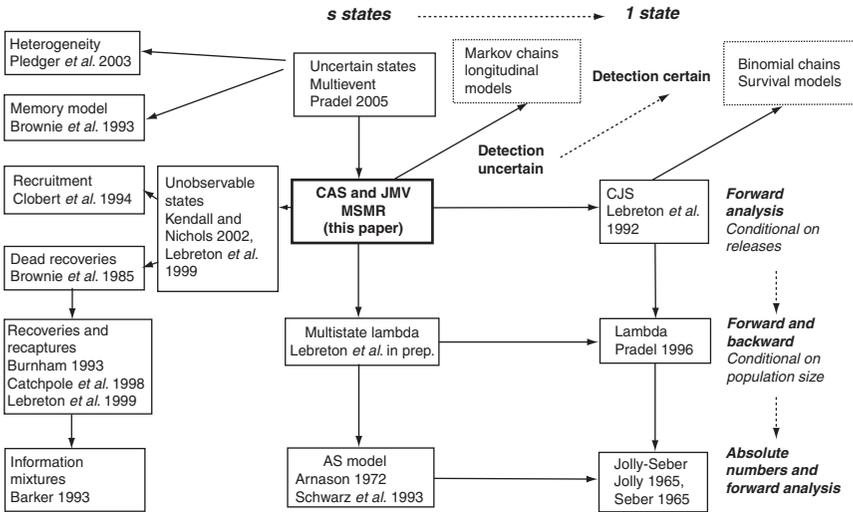


Figure 6 The Conditional Arnason–Schwarz (CAS) and Jolly–Move (JMV) models and their relationships with single state models, models with certain detection, and generalizations based on unobservable states and multievent models, as discussed in perspectives.

tern, are a good example of such a possibility. We discuss below a further promising generalization, multievent models, in which the states among which the individuals move are not known with certainty, even when the individuals are observed. These models cover as particular cases some existing models such as memory models and open population capture–recapture models with heterogeneity (upper left part of Figure 6).

1. State-Specific Abundance

Another advantage of the standardization of the framework we propose for MSMR models is that they can be easily combined with a number of other developments or generalized in several promising fashions. While we have focused on models conditional on the first capture (and marking) of individuals, analogous to the CJS survival model (Lebreton *et al.*, 1992), the number of unmarked individuals captured in each state at every occasion can also be modeled in a fashion analogous to the full JS model (Jolly, 1965; Seber, 1965) and can be used to estimate population size (e.g., see Williams *et al.*, 2002). For example, let $n_i(u)$ be the total number of animals captured at occasion i that are found to be in state u at that time; that is, $n_i(u) = m_i(u) + u_i(u)$, the sum of marked and unmarked animals, respectively, captured in

state u at occasion i . If $p_i(u)$ is the time-specific capture probability associated with animals in state u , and if this probability is similar for marked and unmarked animals, then we can estimate state-specific abundance, based on the usual Horwitz–Thompson type of estimator, as:

$$\hat{N}_i(u) = \frac{n_i(u)}{\hat{p}_i(u)} \quad (12)$$

Overall abundance for animals in all states is naturally estimated as the sum of state-specific abundances:

$$\hat{N}_i = \sum_u \hat{N}_i(u) \quad (13)$$

Finally, the probability that a member of N_i is a member of state u can be estimated as $\hat{N}_i(u)/\hat{N}_i$. Such probabilities can also be viewed as the expected proportions of animals in a particular state, u , and are of interest with respect to breeding proportions (e.g., [Nichols *et al.*, 1994](#)), proportion of animals infected by a particular disease, etc. Nonparametric bootstrap ([Efron and Tishirani, 1993](#)) appears then as a natural way to get confidence intervals for population sizes and associated parameters ([Marucco *et al.*](#), in preparation), as the distribution of MSMR estimates of abundance and related derived parameters can be highly skewed, and classical explicit confidence interval limits behave poorly.

2. Reverse-Time MSMR Modeling

MSMR has also been useful in certain applications employing reverse-time modeling. [Pradel \(1996\)](#) noted that CJS estimation could be applied to standard single-state capture–recapture data that are reversed in time, in order to estimate parameters associated with the recruitment process (also see [Pollock *et al.*, 1974](#); [Pradel *et al.*, 1997b](#); [Williams *et al.*, 2002](#)). Two classes of applications for which reverse-time MSMR has been found to be useful involves the state variables of age and location. With respect to age, reverse-time MSMR at a single location frequently focuses on an adult state that actually includes many ages (e.g., all animals of age >1) and addresses the question, what fraction of adults at time i were young versus adults at time $i - 1$? For example, consider a population consisting of young and adults in which an animal that is young at the sample period in year i will be an adult at the sample period in year $i + 1$, if it happens to survive until then. As noted previously, age is a dynamic state variable with deterministic transitions in forward-time models. However, in reverse time, the investigator is basically asking, what is the probability that a randomly selected adult at time i was an adult versus young animal at time $i - 1$? Reverse-time models with age-specificity thus

entail stochastic transitions and require MSMR. Such modeling can address ecological questions about the relative contributions of (1) surviving adults, (2) surviving young animals produced on the area, and (3) immigrants to the growth of the adult component of the population in a study area (Nichols *et al.*, 2000). Estimates of these relative contributions are relevant to assessments of areas as sources or sinks (e.g., Pulliam, 1988).

When the capture–recapture study includes multiple locations, reverse-time MSMR permits inferences about the contributions of animals (adults only, or both young and adults) from some subpopulation, A, to growth of animals in a different subpopulation, B (Nichols *et al.*, 2000). These estimated contributions can be used, in turn, to estimate the contributions of each subpopulation of a metapopulation system to population growth of the entire metapopulation (Runge *et al.*, 2006). In cases of a metapopulation open to immigration from locations outside the entire study system, this approach also permits estimation of the contribution of such immigration from outside.

3. Temporal Symmetry Models and Multistate Lambda

As in single state models, the forward and backward modeling approaches can be combined, with seniority probabilities and survival-transition probabilities as parameters (Lebreton and Pradel, 2002). A likelihood approach is then possible (Lebreton *et al.*, in preparation) as a full multistate generalization of Pradel's (1996) temporal symmetry approach. Pradel's scalar growth rate λ is replaced by a matrix reflecting the growth rate and change in population structure over the states. This approach may be particularly useful in the presence of strong environmental variation over time, a situation in which the calculation of a scalar growth rate cannot avoid the intricacies of the random variation over time in population structure (Tuljapurkar, 1990).

4. Robust Design

Pollock's (1982) robust design involves sampling at two different temporal scales, providing capture–recapture data over a relatively short interval in order to provide information on the estimation of detection probability and abundance, and over a longer interval in order to estimate survival. The robust design can be viewed as a combination of information from these two different temporal scales. At a minimum, the approach permits robust estimation of abundance and increased precision of all estimates (Pollock, 1982; Kendall *et al.*, 1995). In addition, the approach can permit estimation of quantities that cannot be estimated with standard open or closed model

analyses (e.g., Kendall and Bjorkland, 2001; Kendall *et al.*, 1997; Nichols and Pollock, 1990; Schwarz and Stobo, 1997).

Use of the robust design in conjunction with multistate models has been relatively recent. Nichols and Coffman (1999) and Coffman *et al.* (2001) studied the influence of habitat fragmentation and corridors on population dynamics of meadow voles. Multistate models permitted estimates of movement among habitat patches within the study system. The robust design provided estimates of capture probability for young meadow voles, permitting decomposition of recruitment into components associated with (1) surviving young from the same patch, (2) movement of young and adults from the other patch within the study system, and (3) immigration from outside the study system. Similarly, Nichols *et al.* (2000) used reverse-time modeling with MSMR models to directly estimate the contributions of (1) surviving adults, (2) surviving young produced via in situ reproduction, and (3) immigration to the adult population growth rate of a study area. As noted above, the robust design was needed in order to estimate capture probability of young, and MSMR models were needed because age-specific models require stochastic transitions in reverse time. More recently, Skvarla *et al.* (2004) used the robust design with MSMR to model banner-tailed kangaroo rat *Dipodomys spectabilis* dispersal probabilities between colonies as functions of such covariates as intercolony distance and intervening matrix habitat.

Bailey *et al.* (2004) developed a kind of open robust design MSMR model to deal with a special sampling situation commonly used in investigations of pond-breeding amphibians. Drift fences are placed around breeding ponds, with pitfall traps located at intervals along both the pond side and the outside of the fence. Amphibians are thus captured as they enter the pond to breed and exit it following breeding. Animals captured along the fence are examined, marked (if previously unmarked) and released on the side of the fence opposite to the one at which they were captured. States are observable (breeding) and unobservable (nonbreeding), so that transitions between these states are biologically meaningful. Survival probabilities of animals in the unobservable state are modeled as functions of survival probabilities of observable state animals, as the latter can be directly estimated. Interesting ecological findings based on application of gateway robust design MSMR models include the inference that breeding probability for adult-age amphibians is much lower than previously reported or expected (Church *et al.*, 2007).

5. *Multievent Models and State Uncertainty*

Early development of MSMR models assumed that if an animal is captured, then assignment to state occurs unambiguously and correctly. Recent work has focused on MSMR models in which assignment of detected animals to

state is itself the subject of uncertainty. Sex is a static state variable that can be difficult to ascertain in certain groups of animals. To our knowledge the first application of MSMR models to problems with uncertain state assignment involved situations in which sex of young animals cannot be determined, but sex of adults can be assigned with certainty. In a study of pig frogs (*Rana gryllio*) in Florida, Wood *et al.* (1998) marked young frogs of unknown sex and adult males and females. Sex was eventually known for young animals that were recaptured as adults. The transition probability from unknown-sex young to known-sex adults reflected sex ratio of marked animals at the age transition from young to adult. Conroy *et al.* (1999) used a similar approach with serins (*Serinus serinus*) in Spain. Again, sex of young birds cannot be ascertained with certainty, but sex of adults is determined unambiguously. Conroy *et al.* (1999) classified each young bird using a discriminant function to predict sex probabilistically. Subsequent recaptures of known-sex adults informed this classification probability. In addition, rather than modeling survival of young birds using a single parameter for young of unknown sex, they used sex specific survival and capture parameters for young weighted by the sex-specific classification probabilities. Their model included the additional complexity of parameters reflecting the probability that a new bird is a transient (e.g., Pradel *et al.*, 1997a), and they were able to obtain estimates.

Nichols *et al.* (2004) developed a 2-state model for open populations of roseate terns for which state assignment was not always possible. They included a true sex ratio parameter for new releases and a correct assignment parameter reflecting the probability that sex could be ascertained, given that the animal was captured in period i . This parameter was applied only to observations of bird behavior that were unambiguous with respect to state assignment, although they could have used probabilistic assignments based on other ambiguous behaviors as well. Capture histories of birds eventually observed to be males or females were modeled with the appropriate sex-specific probabilities, whereas birds that never received an unambiguous sex assignment were modeled as a mixture of probabilities associated with the two states. The approach was shown to yield unbiased estimates and to be far preferable to an ad hoc approach to analysis that is widely used.

Runge *et al.* (2007) developed an open population MSMR model for a situation involving estimation of species-specific parameters in the face of uncertain species classification. They focused on a 2-species system of microtine rodents, and every captured animal was assigned to a species based on pelage and other characteristics. Model parameters were required for the age-specific probabilities of correct assignment, conditional on true species identity. Although these initial species assignments were made with error (nonnegligible misclassification probability), a subset of animals died in traps. Tooth patterns of these trap-death animals were then used to identify

species without error, and these data appeared in the likelihood and basically informed the classification parameters associated with initial assignments. The model also required parameters for the probabilities that newly caught animals belonged to one or the other species. The study was conducted on 2-patch study systems, so patch- and species-specific survival and movement probabilities were of interest. Simulations again indicated reasonable performance of estimators.

Misclassification problems with static state variables such as sex and species have the advantage that if classification can be certain at any time during an animal's capture history, then the animal's state is known for all other periods in the history. Similarly, in the case of deterministic transitions (e.g., state variables such as age), knowledge of an animal's dynamic state at any observation period permits reconstruction of an animal's state at any other point in time. However, the situation is more difficult with dynamic state variables that exhibit stochastic transitions. One approach to dealing with such state variables involves use of ancillary information providing information on true state (and thus classification probabilities) for a subset of individual animals. Kendall *et al.* (2003 and 2004) used repeat observations of individuals from secondary periods of a robust design to deal with state uncertainty in photo-identified manatees. In order to parameterize projection matrix models, it was necessary to estimate the number of adult females with and without calves (young). Some observations were conclusive, in that a calf is so closely associated with a female that there is no uncertainty. However, calves may be "missed", either because they are not visible at the angle from which the photo is taken or they are far enough from the female to admit uncertainty. Because truth is assumed known for animals classified as "with calf", repeat observations on females within the season permit estimation of classification parameters.

The previous applications were all focused on specific study systems, whereas Fujiwara and Caswell (2002b) and Lebreton and Pradel (2002) discussed general approaches to dealing with state uncertainty in MSMR models. Fujiwara and Caswell (2002a) included "stage-assignment" matrices in their MSMR models specifying relative probabilities of individuals being in different stages. These probabilities were viewed as being estimated separately and then inserted into the MSMR estimation process. Lebreton and Pradel (2002) considered general multievent models, including matrices for the probability that an animal was in a specific true state conditional on an observation that provided a probabilistic state assignment. These latter observations are viewed as events that are related to true states, such that the probabilities associated with these relationships become part of the estimation problem.

This general multievent view of MSMR was developed more fully by Pradel (2005). Multievent models cover as particular cases several previously

published models including multistate models with memory (Brownie *et al.*, 1993) and finite mixture models for heterogeneity of capture (Pledger *et al.*, 2003). As argued by Pradel (2009), the treatment of such models within a general framework will be more powerful than their treatment as particular cases. One may expect to be able then to explore progressively issues of goodness-of-fit and identifiability; one may also expect that stochastically dynamic state variables will be difficult to handle without some external source of information that provides knowledge of true state at each occasion for a subset of individuals. However, the current exploration of multievent models (Pradel, unpublished results) reveals that the level of uncertainty associated with state classification is not radically different from other uncertainties already at the core of capture–recapture modeling. Program E-Surge (Choquet *et al.*, 2009), expanding on the philosophy of M-Surge, is indeed available for flexible fitting of multievent models. An optimistic view is that such models will evolve and become standard tools in the same fashion that multistate models have evolved up to now. Integrated modeling (e.g., Gauthier *et al.*, 2007 and Section 7 below), blending information from surveys of population size and/or structure, may play a key role to improve the robustness of multievent models when needed.

6. *Occupancy as a Multistate Problem*

Occupancy estimation and modeling concern the probability that a sample unit is occupied by a particular species (e.g., Mackenzie *et al.*, 2002, 2006). The study design involves detection–nondetection (frequently referred to as “presence–absence”) surveys in which sites or units are visited and surveys are made to try to detect one or more focal species. The units on which observations are obtained are sites, rather than individual animals, and sites are characterized as occupied by the species of interest or not. The problem is thus a simple case of MSMR with uncertainty in state assignment. True state is known for the sites at which the species is detected, but the sites at which no detections are made represent sites at which the species is either absent, or present but undetected. In single-season studies, repeat visits permit estimation of detection probability conditional on species presence, and these probabilities permit resolution of the ambiguity associated with nondetection.

Multiseason occupancy modeling focuses on the dynamics of this 2-state problem, using probabilities of local extinction and colonization to describe this Markov process. Nondetection in a given year is again ambiguous, but the ambiguity is resolved with a robust design in which repeat observations within a season permit direct estimation of detection probabilities (Mackenzie *et al.*, 2003, 2006). Recent modeling efforts have extended these

models to deal with multiple occupancy states (e.g., abundance categories, Royle, 2004; Royle and Link, 2005; sites that do and do not produce young, Nichols *et al.*, 2007) and ambiguity in state assignment even when animals are supposedly detected (Royle and Link, 2006).

Occupancy modeling can thus be viewed as a MSMR problem. Indeed, the initial work on multiseason occupancy modeling (Barbraud *et al.*, 2003) used mark–recapture software developed to deal with temporary emigration, a problem now viewed as MSMR with observable and unobservable states (Fujiwara and Caswell, 2002b; Kendall and Nichols, 2002; Schaub *et al.*, 2004b).

7. *Integrated Modeling*

A general estimation approach in population dynamics that has seen substantial development in the past 5 years involves use of multiple data sets providing information about either abundance or fundamental demographic parameters and combining these with population-dynamic models as a means of permitting the different data sources to contribute to the estimation. For example, state–space models for projecting abundance as a function of demographic parameters estimated from capture–recapture studies can be combined with direct estimates of abundance based on count data (e.g., distance sampling, Buckland *et al.*, 2001) to directly link data from these disparate sources to parameters under a common estimation framework. Estimation under the resulting joint models can be accomplished by maximum likelihood (e.g., Besbeas *et al.*, 2002, 2005; Gove *et al.*, 2002), least squares (White and Lubow, 2002), or using Bayesian approaches (e.g., Elliott and Little, 2000; Millar and Meyer, 2000; Newman *et al.*, 2006; Trenkel *et al.*, 2000; Thomas *et al.*, 2005). This general approach has been used for several years by fisheries scientists (e.g., Gallucci *et al.*, 1996; Quinn and Deriso, 1999; Schnute, 1994) and is beginning to see use in investigations of terrestrial animal ecology (Besbeas *et al.*, 2002; Gauthier *et al.*, 2007; Gove *et al.*, 2002; Trenkel *et al.*, 2000; Véran and Lebreton, 2008; White and Lubow, 2002). An even more intimate and fruitful relationship between capture–mark–recapture models and integrated modeling is provided by formulating the hidden Markov chain model inherent in MSMR models as a set of state equations (the multistate Markov chain, at the individual level) and observations equations (the recapture/detection process) (Gimenez *et al.*, 2007). Because MSMR models provide the natural methodological tool for estimating the parameters of state–based population projection matrices (e.g., Caswell, 2001; Fujiwara and Caswell, 2002a; Nichols *et al.*, 1992), thus providing close links with state–space models, we believe that they will assume a prominent role in future integrated population dynamic modeling.

C. Conclusion

Multistate mark–recapture models make it possible to address a variety of questions at the population level, in case where detected individuals can be organized into mutually exclusive states. They are thus extremely relevant to population biology. We thus expect that MSMR and their associated generalizations will become an integral part of the population biologists' toolbox and will in turn influence our knowledge of population dynamics and biology at least to the extent that single state, survival oriented, capture–recapture models has done so over the last 20 years. We hope that powerful and flexible user-friendly software will continue to develop, facilitating access to this broad class of incompletely observed Markov chains. In parallel, we recommend that multistate capture–recapture models be considered as part of the quantitative training of population biologists. Such training would provide young biologists with the ability to use this powerful tool, and prepare them for the spread and development of further generalizations, out of which the most immediately promising of which are integrated (state–space) models and multievent models.

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