

Estimating Reproductive Costs with Multi-State Mark-Recapture Models, Multiple Observable States, and Temporary Emigration

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Abstract Multi-state mark-recapture models have seen increased use in recent years for studies of reproductive costs. When individuals in both breeding and non-breeding states can be observed, multi-state models can be used to directly estimate reproductive costs by comparing state-specific estimates of survival and breeding probabilities. The method assumes that each state that an animal occupies is observable, an assumption that is violated if some animals are absent for one or more breeding seasons and are thus, unobservable due to temporary emigration. Previous research on the case of a single observable state and a single unobservable state has shown that non-random (Markovian) temporary emigration can, if not accounted for, bias estimates of survival. Here, simulation is used to study effects of non-random (Markovian) temporary emigration on estimates of survival and breeding probabilities for the case of two observable states and one unobservable state. Results clearly show that temporary emigration can cause estimates of survival and breeding probability to be biased if the unobservable state is ignored. Bias was either positive or negative depending on circumstances, and was sometimes severe (percent relative bias was as high as 67% for estimates of breeding probability). Accordingly, the strengths and limitations of including an unobservable state in analyses are also considered. For some situations, simply including an unobservable state will be an adequate solution. But, for those studies particularly interested in temporal variation in costs of reproduction, it will be necessary to collect other information to avoid problems of parameter constraints. Additional information can consist of data from sub-sampling during primary sampling occasions, radio telemetry, or ring recoveries.

1 Introduction

An organism's lifetime reproductive output determines its fitness. To maximize output, individuals must optimize their life-history decisions because producing

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and caring for offspring in one year may decrease energy available for subsequent reproductive opportunities and reduce longevity. Thus, organisms are expected to have to balance current reproduction against future survival and reproduction (Williams 1966). The trade-off between current reproductive effort and future reproductive value is known as the cost of reproduction. The trade-off is expressed through decreased survival, future probability of reproduction, and/or offspring quality and is hypothesized to be an important factor shaping life-history strategy for many species (Roff 1992; Stearns 1992). Accordingly, evolutionary ecologists have devoted a great deal of effort to empirically measuring reproductive costs.

In testing for reproductive costs, it is common to be interested in whether breeding at time t negatively affects an individual's probability of surviving from time t to time $t+1$ or its probability of breeding at time $t+1$, although delayed costs can certainly be of interest as well (Nichols et al. 1994; Clobert 1995). To estimate possible effects, survival and breeding probabilities are often compared between breeders and non-breeders. As shown by Nichols et al. (1994), mark-recapture methods provide a useful approach for comparing these probabilities and allow one to deal with possible differences in the probabilities of individually marked breeders and non-breeders appearing in samples. In particular, one can use a multistate modeling approach (Darroch 1961; Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993) to estimate reproductive costs while accounting for possible time- and age-specific variation in sampling probabilities across K successive potential breeding periods (Nichols et al. 1994). When applying multistate modeling to questions of costs of reproduction when breeders and non-breeders can be observed, it is common to define each observed individual as being in either the breeder or non-breeder state for each sampling occasion (breeding period), and to estimate and compare state-specific probabilities of survival (probability of being alive at time $t+1$ given being alive and in a particular state at time t) and breeding (probability of being in the breeder state at time $t+1$ given being in a particular state at time t and conditional on being alive at time $t+1$). Transitions between the breeder and non-breeder state are typically treated as a first-order Markov process (state at time $t+1$ depends only on state at time t) (Brownie et al. 1993).

Since Nichols et al. (1994) first described the multistate modeling approach for studying reproductive costs, the details and benefits of the approach have been further discussed (Clobert 1995; Nichols and Kendall 1995; Viallefont et al. 1995; Boulinier et al. 1997; Doligez et al. 2002; Lebreton and Pradel 2002; Williams et al. 2002; Sandercock 2006), and the multistate modeling approach has been used to assess costs of reproduction in numerous studies of diverse taxa (e.g., Viallefont et al. 1995; Cam et al. 1998; Sandercock et al. 2000; McElligot et al. 2002; Yoccoz et al. 2002; Rivalan et al. 2005; Barbraud and Weimerskirch 2005; Tavecchia et al. 2005; Beuplet et al. 2006; Hadley et al. 2007). Although there are certainly other approaches to studying costs of reproduction (e.g., Reznick 1985; 1992; Golet et al. 2005), results from multistate modeling can provide rigorous empirical estimates of potential costs of reproduction under certain circumstances and have contributed much to our understanding of life history evolution.

As discussed by Nichols et al. (1994), multistate modeling is especially applicable to studies directed at phenotypic correlations, but the approach can also be used in some field, experimental-manipulation studies and may be useful for dealing with possible genotypic variation in capture or observation probabilities in genetic field studies. However, it is important to note that multistate models based on live encounter data yield survival estimates that are commonly referred to as “apparent survival” rates in the mark-recapture literature because they combine the probability of survival and the probability of not permanently emigrating from the study area, i.e., apparent survival differs from true survival to an extent that depends on the level of permanent emigration. This has potentially important implications if breeders and non-breeders have different rates of permanent emigration: differences in apparent survival between animals in different breeding states could be due to variation in site fidelity and not true survival. Accordingly, the multistate modeling approach to estimating costs of reproduction is most appropriate for species in which site fidelity is high or for which permanent emigration occurs at similar rates for breeders and non-breeders.

When using multistate modeling to compare survival and breeding probabilities for breeders and non-breeders, one assumes that each state that an animal occupies is observable (for details of all assumptions, see Nichols et al. 1994; Williams et al. 2002). As reviewed by Kendall (2004), this assumption fails if some members of the population are unavailable for capture or detection when sampling occurs, i.e., heterogeneity in detection probability exists such that some individuals are in an unobservable state (probability of detection is zero). Failure of this assumption can lead to biased estimates.

In multistate modeling of reproductive costs, some individuals may temporarily emigrate and be absent for one or more breeding seasons. For example, in some species, both breeders and non-breeders may be present and observable on breeding sites, but some non-breeders may use non-breeding habitat and be unobservable (for an overview of the widespread nature of temporary emigration see Schaub et al. 2004). Estimates obtained from multistate modeling that ignores temporary emigration can be biased in the presence of some forms of temporary emigration (Kendall et al. 1997; Fujiwara and Caswell 2002; Kendall and Nichols 2002; Schaub et al. 2004), and consequently, estimates of costs of reproduction will also be biased. In particular, it is well known that survival estimates can be biased if the probability of temporary emigration depends on an individual’s state during the previous occasion, i.e., is non-random or Markovian (Kendall et al. 1997).

The existence of an unobservable state can be accommodated by incorporating it into multistate models. For the simplest case where individuals occur in either one observable state or one unobservable state (e.g., only breeders present on study sites; all non-breeders in an unobservable state; Reed et al. 2003), the effects of Markovian temporary emigration on parameter estimates have been well studied, methods for incorporating the unobservable state in mark-recapture modeling have been developed, parameter redundancies are quite well understood, suggestions for obtaining useful additional information have been provided, and comprehensive guidelines exist (e.g., Lebreton et al. 1999; Pradel and Lebreton 1999; Fujiwara and Caswell 2002;

Kendall and Nichols 2002; Schaub et al. 2004; Choquet et al. 2004; Kendall 2004). Of particular note, Schaub et al. (2004) used simulation and computer algebra to comprehensively evaluate the performance of the traditional Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965) and a multistate model that included one observable state and one unobservable state when Markovian temporary emigration occurred. Schaub et al. (2004) found that estimates of survival from the Cormack–Jolly–Seber model were biased in the presence of Markovian temporary emigration, whereas estimates from the multistate model were not. They concluded that when survival and recapture probabilities are high the multistate model works well when Markovian temporary emigration occurs and individual states can be well described with one observable and one unobservable state.

However, for situations with multiple observable states and at least one unobservable state, the complexity is much greater due to the increased number of states, possible transitions between the various states, and the increased number of parameters. For example, Kéry et al. (2005), in an investigation of parameter identifiability for a variety of multistate model for perennial plants with two observable states and one unobservable state, found that most models had identifiable parameters and that some models allowed for estimation of state-specific survival rates, including that of the unobservable state. However, they also found that several models contained no identifiable parameters, which highlights the additional complexity that arises when working with an unobservable state and multiple observable states. At this time, it is difficult to know how well information from the single-observable-state situation applies to the multiple-observable-state situation (Kendall 2004). Of particular relevance to studies of costs of reproduction, information from studies of single-observable states provides no information about how temporary emigration may bias estimates of transitions between observable states, which include breeding probabilities for breeders and for non-breeders. Consequently, it is not clear how one should proceed with multistate analyses of breeders and non-breeders if temporary emigration is suspected. If one includes the unobservable state, then additional constraints such as time constancy must be placed on demographic parameters (Kendall and Nichols 2002; Kendall 2004; Schaub et al. 2004) unless additional information about detection probability is available (Kendall 2004).

As clearly articulated by Kendall (2004:100), “To be forced to assume a priori that parameters are equal over time or group is unsatisfactory. In fact, testing that hypothesis might be of interest.” Alternatively, one can choose to ignore the temporary emigration and risk having some level of bias in the resulting estimates. Analysis choices have been recently considered for a situation with multiple observable states and a single unobservable state in orchids (Kéry et al. 2005). However, to date, I am aware of only two papers that have discussed these choices with respect to estimates of reproductive costs based on multistate analyses of breeders and non-breeders. Beauplet et al. (2006) chose to incorporate an unobservable state at the cost of additional parameter constraints and numerical convergence issues. In contrast, Hadley et al. (2007) chose to ignore the unobservable state in their primary analyses after preliminary analyses provided evidence that temporary emigration was not having important effects on estimates of reproductive costs for their situation. Until better information becomes available on how best to proceed in such situations,

researchers will continue to face difficult decisions when designing studies of reproductive costs and analyzing resulting data.

Given the rapid increase in the use of multistate modeling to study reproductive costs in recent years and the possibility that temporary emigration has been, or will be, an issue in at least some multistate studies, the objectives of this paper are to stimulate thinking about how to handle temporary emigration in multistate modeling of reproductive costs by (1) using simulated data to illustrate how temporary emigration, if ignored, can cause important levels of bias in estimates of survival, breeding probability, and reproductive costs, (2) using simulated data to show that the inclusion of an unobservable state into multistate models imposes modeling constraints that can limit one’s ability to fully estimate reproductive costs, and (3) reviewing suggestions for additional information that can be collected to improve future multistate comparisons of survival and breeding probabilities in breeders and non-breeders. The results have implications that reach beyond multistate modeling of reproductive costs as they are also relevant to a variety of other studies containing multiple observable states or sites and at least one unobservable state or site (e.g., dispersal among sites when some sites are not monitored, Lebreton et al. 2003; demography of perennial plants with observable vegetative and flowering states and unobservable below-ground rhizomes, Kéry et al. 2005).

2 Methods

To assess the effects of Markovian temporary emigration on estimates of survival and breeding probabilities for breeders and non-breeders, I conducted simulations using M-SURGE (Choquet et al. 2004) and an expected-values approach for a variety of multistate modeling scenarios that might be encountered. Choquet et al. (2005) and Devineau et al. (2006) provide details regarding the process for generating expected data using M-SURGE. Devineau et al. (2006) provide additional details about the expected-values approach, its benefits, and how it relates to Monte Carlo simulation. For the simulations done here, all analyses considered one group with three states: breeders (B), non-breeders in an observable state (N), and non-breeders in an unobservable state (U). Individuals in state N and U were assigned the same reference parameters except that detection probability (p) was zero for those in state U. Because it is a fairly common real-world scenario, I created data for a situation where only breeders could be captured but in which field-readable markers could be observed on breeders and non-breeders.

For the multistate model with states B, N, and U, the transition matrix and associated vectors of survival and capture probabilities were

$$\begin{bmatrix} \psi^{BB} & 1 - \psi^{BB} - \psi^{BU} & \psi^{BU} \\ \psi^{NB} & 1 - \psi^{NB} - \psi^{NU} & \psi^{NU} \\ \psi^{UB} & 1 - \psi^{UB} - \psi^{UU} & \psi^{UU} \end{bmatrix}_t \begin{bmatrix} S^B \\ S^N \\ S^N \end{bmatrix}_t \begin{bmatrix} p^B \\ p^N \\ 0 \end{bmatrix}_t,$$

where ψ_t^{rs} is the probability that an individual which is still alive and present in the study population at the end of period t will move from state r to state s ; S_t^r is the

probability that an individual in state r survives and remains in the study population through period t , where non-breeders are assigned the same survival rate on a given occasion regardless of whether they are in state N or U; and p_r^t is the probability that a marked individual alive in state r at time t is captured or observed (zero for those in state U). The matrix and vector subscript t denotes that time dependence was possible: in the actual modeling, parameters were held constant for some scenarios and allowed to vary with time in others (see below).

The key steps in the process used here were to (1) define a set of reference parameter values, (2) obtain the expected data (i.e., expected values for encounter histories) using the Arnason–Schwarz model (Arnason 1972, 1973; Schwarz et al. 1993), (3) obtain maximum-likelihood estimates of parameters for models of interest (see below); and (4) derive relevant measures of bias and precision. Expected data were generated based on (1) the reference values (see below), (2) the number of breeders released on the first occasion ($n = 10,000$), and (3) the population growth rate for the number of breeders between successive occasions. I released a large number of breeders to minimize possible rounding errors that may have been associated with working with fractional numbers of animals that result from using expected data in the encounter histories (trials with even larger numbers of released individuals indicated that the number used was adequate to avoid rounding errors; smaller numbers may have sufficed). The population growth rate for breeders was set to one between all successive occasions. Thus, as breeders died or transitioned to other states, an adequate number of breeders was injected into the population to maintain 10,000 breeders on each occasion, and all new individuals were captured and released. Thus, there was a staggered entry of newly marked individuals in state B, and there were resightings of individuals in states B and N. The reference parameters determined the actual survival, transition, and detection rates for animals in each state on each occasion (see below).

For multistate modeling, it may not be possible to estimate all parameters because some may be aliased and not separately identifiable, and the parameter redundancy is not always intuitive (Gimenez et al. 2003, 2004). Therefore, parameter redundancy was evaluated for each model considered here using the numerical version of the Catchpole, Morgan, and Freeman approach as implemented in M SURGE and described by Choquet et al. (2005). After checking that all parameters were identifiable for a given model, parameter estimates were compared to the reference parameter values and, where applicable, between competing models applied to a given dataset. Absolute bias was computed as the difference between a given parameter estimate and the true underlying reference parameter value, and percent relative bias was the absolute bias divided by the reference parameter value and multiplied by 100. Percent coefficient of variation was calculated for each parameter as the estimated standard error divided by the parameter estimate and multiplied by 100.

The scenarios that were simulated were not meant to encompass the extremely broad range of sampling scenarios that might be encountered in actual studies. Rather, they were chosen to illustrate some estimation problems that can arise if Markovian temporary emigration is not dealt with properly and to motivate future work on the problem. The situations were limited to scenarios where only breeders

were captured and where breeders were always resighted at a higher rate than were non-breeders. However, within these constraints, and as explained in more detail below, I did bracket conditions such that reproductive costs to survival, future fecundity, or both were large, small, or absent and for which recapture rates were high or low. The actual parameter values used were arbitrarily chosen. As detailed below, I considered scenarios in which parameters were constant over time or time-varying.

2.1 Simulations to Evaluate Effects of Ignoring Markovian Temporary Emigration when Estimating Reproductive Costs

Based on published information regarding factors affecting bias in survival rates estimated with multistate models of one observable and one unobservable state in the presence of temporary emigration (e.g., Kendall 2004; Schaub et al. 2004), I chose to consider simulations with (1) Markovian temporary emigration, (2) high versus low capture probabilities ($p^B = 0.9$ or 0.3 ; $p^N = p^B - 0.2$), (3) high versus low survival rates ($S^B = 0.9$ to 0.2 , $S^N = 0.9$ or 0.3), (4) presence or absence of reproductive costs to survival rate ($S^B = S^N \times 0.667$ or $S^B = S^N$), and (5) presence or absence of reproductive costs to breeding probability ($\psi^{BB} = \psi^{NB} \times 0.445$ or $\psi^{BB} = \psi^{NB}$) (Table 1). In all scenarios, the temporary emigration rate was higher for breeders ($\psi^{BU} = 0.4$) than for non-breeders ($\psi^{NU} = 0.1$), which could occur if (1) breeders have a propensity to move to an alternate habitat for replenishing body reserves in the year after a breeding attempt such that $\psi^{BU} > \psi^{NU}$, but (2) non-breeders can also gain benefits from being present on breeding sites, e.g., for evaluating site quality, such that ψ^{BU} and $\psi^{NU} < 1$. In all simulations, parameters were constant across time and age, and data were generated for eight occasions.

For each scenario, two models were run. First, the true generating model (a model that included state U) was used to estimate parameters from the expected data. Results from the generating model were checked to ensure that the model converged on the reference parameters and that all parameters were estimable. Second, a simplified version of the generating model (included states B and N but ignored state U and held parameters constant across time and age) was used and the resulting estimates were evaluated for absolute bias and precision (percent coefficient of variation), with emphasis on the estimates of S^B , S^N , ψ^{BB} , and ψ^{NB} , i.e., those used to estimate costs of reproduction.

2.2 Simulation of Time-Varying Reproductive Costs in the Presence of Markovian Temporary Emigration

When no additional information about movements, capture probabilities, or survival rates is available, parameter estimation for a model that includes states B, N, and U is only possible if at least one of the following constraints is applied: the order of Markovian transition probabilities is reduced to make them random, partial determinism is imposed on transition probabilities (e.g., probabilities of transition

Table 1 Absolute bias and coefficient of variation (%CV) for estimates of survival and breeding probabilities for breeding and non-breeding individuals for different MSMR modeling scenarios using an expected-values approach in M-SURGE where data were generated in the presence of Markovian temporary emigration and analyzed with a model that ignored temporary emigration

Reference parameter values		S^B			S^N			ψ^{BB}			ψ^{NB}		
p^B	p^N	S^B	S^N	ψ^{BB}	Bias	%CV	Bias	%CV	Bias	%CV	Bias	%CV	
0.9	0.7	0.6	0.9	0.267 ¹	-0.01	0.5	0.00	0.3	-0.02	1.0	-0.07	0.6	
0.3	0.1	0.6	0.9	0.267 ¹	-0.03	3.0	-0.06	2.8	-0.10	17.3	-0.25	17.3	
0.9	0.7	0.2	0.3	0.267 ¹	-0.01	2.2	0.03	2.4	-0.02	2.6	-0.11	2.7	
0.3	0.1	0.2	0.3	0.267 ¹	-0.02	15.4	-0.04	6.0	-0.18	15.7	-0.40	14.9	
0.9	0.7	0.9	0.9	0.267 ¹	-0.01	0.3	0.01	0.2	-0.02	0.8	-0.09	0.5	
0.3	0.1	0.9	0.9	0.267 ¹	-0.02	2.1	0.01	1.2	-0.08	10.7	-0.21	11.5	
0.9	0.7	0.3	0.3	0.267 ¹	-0.01	1.8	0.03	2.0	-0.02	2.2	-0.12	2.2	
0.3	0.1	0.3	0.3	0.267 ¹	-0.02	12.9	0.00	7.2	-0.17	102.2	-0.40	102.5	
0.9	0.7	0.6	0.9	0.4 ²	0.09	0.4	0.10	0.0	0.35	0.6	0.12	1.2	
0.3	0.1	0.6	0.9	0.4 ²	0.13	1.1	0.10	0.0	0.43	2.2	0.17	4.2	
0.9	0.7	0.2	0.3	0.4 ²	0.03	2.4	0.13	3.1	0.33	2.9	0.06	5.6	
0.3	0.1	0.2	0.3	0.4 ²	0.05	6.2	0.13	13.2	0.43	7.0	0.10	16.1	
0.9	0.7	0.9	0.9	0.4 ²	0.00	0.2	0.04	0.3	0.32	0.6	0.11	1.3	
0.3	0.1	0.9	0.9	0.4 ²	0.00	0.7	0.07	1.8	0.39	2.4	0.14	4.4	
0.9	0.7	0.3	0.3	0.4 ²	0.01	1.4	0.10	2.6	0.28	2.6	0.02	4.8	
0.3	0.1	0.3	0.3	0.4 ²	NA ³	NA	NA	NA	NA	NA	NA	NA	

¹ Reproductive costs to fecundity present; probabilities for other transitions were: $\psi^{BN} = 0.333$, $\psi^{BU} = 0.4$; $\psi^{NN} = 0.3$, $\psi^{NU} = 0.1$.

² Reproductive costs to fecundity absent; probabilities for other transitions were: $\psi^{BN} = 0.2$, $\psi^{BU} = 0.4$; $\psi^{NN} = 0.5$, $\psi^{NU} = 0.1$.

³ Estimates from the generating model did not converge to reference parameter values so no results reported for scenario.

from non-breeder to breeder are assumed to be 0 before a certain minimum age and all animals are assumed to begin breeding by a certain age), or parameters are constrained to be constant over time or to follow a temporal trend (Kendall and Nichols 2002; Kendall 2004). For some species Markovian temporary emigration is expected and partial determinism in transitions is not. For example, breeders in year t may be more likely to be absent from the breeding site in year $t+1$ than are non-breeders in year t , but the organisms do not follow a set temporal pattern of breeding and non-breeding. In such cases, one is only left the option of making some parameters constant.

To illustrate some of the potential problems with this solution, I generated expected data for the following scenario. Survival and breeding probabilities varied by state and environmental conditions ($S^B = 0.8$ [good year] or 0.6 [bad year], $S^N = 0.8$ [all years], $\psi^{BB} = 0.6$ [good year] or 0.3 [bad year], and $\psi^{NB} = 0.7$ [good year] or 0.5 [bad year]). Temporary emigration was Markovian in bad years ($\psi^{BU} = 0.1$ [good year] or 0.5 [bad year], and $\psi^{NU} = 0.1$ [good year] or 0.3 [bad year]). The simulated study encompassed six breeding seasons, and conditions for survival and breeding probabilities were good, bad, good, bad, and good, respectively. Capture probabilities varied by occasion around different state-specific means (values of p^B had a mean of 0.7 and were drawn from a uniform distribution bounded between 0.6 and 0.8, whereas values of p^N had a mean of 0.5 and were drawn from a uniform distribution bounded between 0.4 and 0.6). This scenario was chosen to illustrate performance limitations of the multistate model with multiple observable states and a single unobservable state for a mildly challenging situation. Specifically, survival and detection rates were moderate to high, and temporary emigration was Markovian in only some years; under such circumstances, the multistate model as applied to a one observable and one unobservable state performs quite well (Schaub et al. 2004).

A single model was used to estimate parameters from the simulated data (S^B , S^N , p^B , and p^N allowed to vary by time; ψ^{BB} and ψ^{NB} constant through time). This model assumes that researchers were aware that parameters might vary by time but were not aware of the true underlying pattern of good and bad years and the effects of those changing conditions on parameters. Results from the model were evaluated for absolute bias and percent coefficient of variation, again with emphasis on the estimates of S^B , S^N , ψ^{BB} , and ψ^{NB} .

3 Results

3.1 Effects of Ignoring Markovian Temporary Emigration when Estimating Reproductive Costs

For time-constant reference parameters and Markovian temporary emigration, parameters in the models evaluated were separately identifiable, and estimates obtained from the generating model converged on reference parameters for all but

one of the scenarios simulated (Table 1). However, convergence was typically not achieved unless repeated random initial values were used, and local minima were apparent in the output, especially when reference values of p^B and p^N were low. When a model that ignored temporary emigration (i.e., a model that included states B and N but not U) was employed, the resulting estimates of survival and breeding probabilities typically had low coefficients of variation ($\%CV \leq 7\%$ for 24 of 30 estimates) (Table 1). However, the level of bias varied quite substantially depending on the simulation scenario and ranged from strongly negative to strongly positive. When costs of reproduction to breeding probability were present, bias was low for survival estimates and higher for estimates of breeding probability (average % relative bias = -4.4 , 0.2 , -28.2 , and -34.2 for estimates of S^B , S^N , ψ^{BB} , and ψ^{NB} , respectively), any bias tended to be negative, and absolute bias was always greatest for estimates of ψ^{NB} . In contrast, when costs of reproduction to breeding probability were absent, bias tended to increase (average % relative bias = 11.4 , 22.2 , 90.3 , and 25.7 for estimates of S^B , S^N , ψ^{BB} , and ψ^{NB} , respectively), was always positive, and was always highest for estimates of ψ^{BB} .

Given the bias in estimates of S^B , S^N , ψ^{BB} , and ψ^{NB} , estimates of reproductive costs were also typically biased: sometimes at low levels and sometimes severely so (Table 2). Estimates of reproductive costs to survival were typically over-estimated, whereas estimated costs to breeding probability were always negatively biased. Absolute bias was always greater for estimates of costs to breeding probability. Of particular note, when true ψ^{BB} was equal to ψ^{NB} , estimates indicated that ψ^{BB} was greater than ψ^{NB} by 0.22 – 0.33 (absolute difference between the rates).

3.2 Difficulties of Estimating Time-Varying Reproductive Costs in Presence of Markovian Temporary Emigration

Results from the simulation with full time-varying parameters, which could be separately identified for the data and model evaluated, illustrate some of the limitations that can arise when one is forced to impose time constraints on some parameters. Even for a scenario with moderately high values for survival rate (>0.6) and capture probability (>0.4), random and low values of temporary emigration in good years (0.1), and Markovian temporary emigration only in bad years, the time-varying multistate model that considered states B, N, and U was not able to fully characterize several key features of the reference parameters. As this is but one possible scenario out of a broad set of circumstances that could be considered, the results are kept brief and only a few highlights are mentioned.

First, the time constraints that were imposed on breeding probabilities, made it impossible to identify the large changes in breeding probabilities between good and bad years, which simply emphasizes a known problem when considering an unobservable state in models with time-varying parameters. Second, in one of the good years (reference values: $S^B = S^N$), time-varying estimates of survival rate were higher for breeders than for non-breeders (estimated difference = 0.04). The model did perform reasonably well in some respects, however. Time-invariant estimates were

Table 2 Absolute bias in estimates of reproductive costs to survival and breeding probability estimated for breeding and non-breeding individuals for different MSMR modeling scenarios using an expected-values approach in M-SURGE where data were generated in the presence of Markovian temporary emigration and analyzed with a model that ignored temporary emigration

Reference parameter values					Costs of reproduction to survival probability			Costs of reproduction to breeding probability			
p^B	p^N	S^B	S^N	ψ^{BB}	ψ^{NB}	Actual	Estimate	Bias	Actual	Estimate	Bias
0.9	0.7	0.6	0.9	0.267 ¹	0.6 ¹	0.30	0.31	0.01	0.33	0.28	-0.05
0.3	0.1	0.6	0.9	0.267 ¹	0.6 ¹	0.30	0.27	-0.03	0.33	0.19	-0.14
0.9	0.7	0.2	0.3	0.267 ¹	0.6 ¹	0.10	0.14	0.04	0.33	0.24	-0.09
0.3	0.1	0.2	0.3	0.267 ¹	0.6 ¹	0.10	0.09	-0.01	0.33	0.11	-0.22
0.9	0.7	0.9	0.9	0.267 ¹	0.6 ¹	0.00	0.02	0.02	0.33	0.27	-0.06
0.3	0.1	0.9	0.9	0.267 ¹	0.6 ¹	0.00	0.02	0.02	0.33	0.20	-0.13
0.9	0.7	0.3	0.3	0.267 ¹	0.6 ¹	0.00	0.04	0.04	0.33	0.24	-0.09
0.3	0.1	0.3	0.3	0.267 ¹	0.6 ¹	0.00	0.02	0.02	0.33	0.10	-0.23
0.9	0.7	0.6	0.9	0.4 ²	0.4 ²	0.30	0.31	0.01	0.00	-0.22	-0.22
0.3	0.1	0.6	0.9	0.4 ²	0.4 ²	0.30	0.27	-0.03	0.00	-0.26	-0.26
0.9	0.7	0.2	0.3	0.4 ²	0.4 ²	0.10	0.20	0.10	0.00	-0.26	-0.26
0.3	0.1	0.2	0.3	0.4 ²	0.4 ²	0.10	0.18	0.08	0.00	-0.33	-0.33
0.9	0.7	0.9	0.9	0.4 ²	0.4 ²	0.00	0.04	0.04	0.00	-0.22	-0.22
0.3	0.1	0.9	0.9	0.4 ²	0.4 ²	0.00	0.07	0.07	0.00	-0.25	-0.25
0.9	0.7	0.3	0.3	0.4 ²	0.4 ²	0.00	0.09	0.09	0.00	-0.27	-0.27
0.3	0.1	0.3	0.3	0.4 ²	0.4 ²	NA ³	NA	NA	NA	NA	NA

¹Reproductive costs to fecundity present; probabilities for other transitions were: $\psi^{BN} = 0.333$, $\psi^{BU} = 0.4$; $\psi^{NN} = 0.3$, $\psi^{NU} = 0.1$.

²Reproductive costs to fecundity absent; probabilities for other transitions were: $\psi^{BN} = 0.2$, $\psi^{BU} = 0.4$; $\psi^{NN} = 0.5$, $\psi^{NU} = 0.1$.

³Estimates from the generating model did not converge to reference parameter values so no results reported for scenario.

quite accurate for ψ^{BB} (estimate = 0.46, true average = 0.48) and ψ^{NB} (estimate = 0.62, true average = 0.62) and accurately estimated the average cost of reproduction to breeding probability over the study as being 0.14. Finally, the model typically produced estimates of survival rates with low bias (range in absolute bias: $S^B = -0.01$ to -0.02 ; $S^N = -0.07$ to $+0.02$) such that estimates of costs of reproduction to survival had low bias in all but one year.

4 Discussion

For the special application of multistate modeling that was investigated here, i.e., comparing survival and breeding probabilities between breeders and non-breeders, the results obtained make it clear that estimated costs of reproduction, especially costs of reproduction to breeding probability, can be badly biased when temporary emigration occurs but is not properly accounted for. For some scenarios evaluated, estimates of costs of reproduction were only slightly biased. However, for other situations, biased estimates of costs of reproduction to both survival and breeding probability could lead to misleading conclusions. For example, when reproductive costs to breeding probability were absent, and Markovian temporary emigration was present but ignored, estimates of breeding probability were biased high for both breeders and non-breeders, and the bias was greater for breeders. Thus, it appeared that breeding probability was higher for breeders than non-breeders. Such a result is of great interest in studies of life-history evolution as it relates to important questions regarding effects of heterogeneity in individual quality (e.g., Cam et al. 1998; Wintrebert et al. 2005). It would be useful to have similar evaluations regarding permanent emigration to aid decision-making for investigations in which breeders, non-breeders, or both might permanently leave the study area.

Given the importance of studying reproductive costs and the potential for biased results if temporary emigration is not properly incorporated into analyses, it is important to consider the available analysis options. In some situations, researchers might choose to use multistate models without an unobservable state because temporary emigration is thought to be a non-issue in their study. In such cases, it would be helpful if authors would provide justification for ignoring possible temporary emigration in analyses based on the biology, the sampling situation, and any available supporting data. It may be less clear how best to proceed in some studies because (1) less may be known about possible levels of temporary emigration and whether or not it may be Markovian and (2) there is currently no specific goodness-of-fit test for detecting temporary emigration. For such studies, it might be useful to compare results obtained from analyses conducted with and without an observable state and to then consider how best to proceed (e.g., Hadley et al. 2007). For still others, it may be known that temporary emigration occurs and an unobservable state may be incorporated in analyses (e.g., Beauplet et al. 2006).

When an unobservable state is included in analyses, several options are available. The simplest approach is to include the unobservable state in the model (with zero capture probability) using recently described methods (Lebreton et al. 1999; Pradel and Lebreton 1999; Kendall and Nichols 2002; Kendall 2004; Schaub et al. 2004) and readily available software (White and Burnham 1999; Choquet et al. 2004). When an unobservable state is considered, numerical and statistical problems inherent to multistate models are increased, and it will be important to use recently developed software to help ensure convergence (Lebreton and Pradel 2002; Choquet et al. 2004). As was found in the simulation work reported on here, convergence was not always easy to achieve even when working with the generating model or a close approximation and knowing the values of reference parameters. With the multistate approach, parameter identifiability will be a problem for some models and datasets and be important to evaluate (Gimenez et al. 2003, 2004; Kéry et al. 2005).

When deciding whether to address temporary emigration by simply including an unobservable state, researchers should also carefully consider whether or not the parameter redundancy problems and limitations of the approach will prevent them from asking key questions of interest. As thoroughly explained by Kendall (2004) and shown here with a simple simulation with time-varying reference parameters, the approach will be inadequate if hypotheses of interest involve time-varying reproductive costs and other solutions to handling parameter redundancy (such as partial determinism in state transitions) are inappropriate. As recently discussed by Tavecchia et al. (2005), there are excellent reasons to be interested in time variation in reproductive costs because trade-offs may vary in stochastic environments, thus affecting optimal reproductive strategies.

The results presented here further emphasize previous recommendations to properly evaluate the magnitude and nature of temporary emigration in mark-recapture studies (e.g., Kendall et al. 1997; Fujiwara and Caswell 2002; Kendall and Nichols 2002; Kendall 2004; Schaub et al. 2004). Also, as had been shown previously for the case of a single observable and a single unobservable state (Schaub et al. 2004), it is possible to obtain relatively unbiased estimates of survival even when Markovian temporary emigration occurs if capture probabilities and survival rates are high.

Kendall (2004) and White et al. (2006) provide excellent reviews of options for gaining greater flexibility in multistate modeling in the presence of an unobservable state. The key idea is that various types of additional information can be used to make additional parameters estimable. If sub-sampling is done within each breeding season, the robust design (Pollock 1982) can be used, which allows estimation of time-varying probabilities (Kendall 2004). This approach still requires the assumption that the survival probability for individuals in the unobservable state is equal to that for one of the observable states. For the case of breeder and non-breeder states, it may be reasonable in some situations to assume that unobservable individuals are non-breeders and therefore, have the same survival rate as do observable non-breeders. However, in other studies such an assumption may be unreasonable or a question of biological interest. In such cases, further additional information will be needed. Simply put, it will be necessary to sample unobservable individuals through radio telemetry, ring recoveries, or combinations of approaches. Examples

of innovative approaches for estimating temporary emigration and combining sources of information now exist (e.g., Lindberg et al. 2001; Bailey et al. 2004; Barker et al. 2005) and should be valuable to future studies of reproductive costs.

An excellent set of analysis options and software now exist for estimating temporary emigration. With thoughtful study design and analysis, future comparisons of survival and breeding probabilities for breeders and non-breeders should provide valuable information regarding reproductive costs regardless of Markovian temporary emigration. In fact, estimates of temporary emigration rates may provide insights into the strategies used to avoid incurring reproductive costs. In planning future studies or choosing among analysis options, simulations, which can now be readily conducted in software such as M-SURGE (Choquet et al. 2004) and MARK (White and Burnham 1999), should prove useful (Schaub et al. 2004; Devineau et al. 2006).

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