# Multistate Survival Models and Their Extensions in Program MARK

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## Abstract

*Program MARK provides >100 models for the estimation of population parameters from mark–encounter data. The multistate model of Brownie et al. (1993) and Hestbeck et al. (1991) allows animals to move between states with a probability of transition. The simplest multistate model is an extension of the Cormack–Jolly–Seber (CJS) live recapture model. Parameters estimated are state-specific survival rates and encounter probabilities and transition probabilities between states. The multistate model provides a valuable framework to evaluate important ecological questions. For example, estimation of state-specific survival and transition probabilities between the biological states of breeders and nonbreeders allows estimation of the cost of reproduction. Transitions between physical states, such as spatial areas, provide estimates needed for meta-population models. The basic multistate model uses only live recaptures, but 3 extensions are included in MARK. A multistate model with live and dead encounters is available, although the dead encounters are not state specific. Robust-design multistate models are also included in MARK, with both open and closed robust designs. These models assume that animals move between states only between primary sessions of the robust design. For the closed robust design, we can specify 12 different data types for the modeling of encounter probabilities during the primary session, including 6 versions of the closed model likelihood incorporating population size (*N*) directly in the likelihood, and 6 versions of the Huggins model in which* N *is estimated as a derived parameter outside the likelihood. One assumption that is generally necessary to estimate state-specific survival rates in the multistate model is that transitions take place immediately before encounter occasions. Otherwise, survival rates over the interval between encounter occasions are a mix of survival rates over multiple states. Advantages of using MARK to estimate the parameters of the various multistate models include flexibility of model specification to include group, time, and individual covariates, estimation of variance components, model averaging of parameter estimates, and Bayesian parameter estimation using Markov chain Monte Carlo procedures on the logit scale.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1521–1529; 2006)

## Key words

*breeding probabilities, encounter histories, maximum likelihood estimation, multi-strata models, Program MARK.*

Program MARK (White and Burnham 1999) provides >100 different models to estimate survival ($S$) and other population parameters, such as population size ($N$) and population rate of change ($\lambda$), from the encounters of marked animals. This diversity of models is necessary to account for the various methods used to encounter marked animals (e.g., live recaptures, resightings of animals without actual capture, and recovery of dead animals), as well as the method of marking animals. For example, the fates of radiomarked animals are often presumed known and, hence, no nuisance parameter to model the encounter probability is necessary, whereas mark–resighting–recapture–recovery studies involving only leg-banded birds might require nuisance parameters to model the encounter probability of live recaptures, live resightings without actual capture, and encounters of dead birds (possibly through harvest but not exclusively so).

In this paper we review the estimation procedures provided in Program MARK and discuss a specific extension of the Cormack–Jolly–Seber (CJS) live recapture model (Cormack 1964, Jolly 1965, Seber 1965) extended to multiple areas or strata. The multistate model offers biologists a rich family of models with which to estimate survival and transition probabilities for a wide variety of situations, providing a convenient framework to model the spatial aspects and individual variation of population dynamics (Lebreton and Pradel 2002). Some of the most important applications of multistate models (Lebreton and Pradel 2002) have been the estimation of differences in survival between breeders and nonbreeders, in effect estimating a cost of reproduction or estimating the probability of breeding. In both cases, we define the states as breeders and nonbreeders. The multistate model provides the capability to implement the framework of Nichols et al. (1994). We describe the basic multistate model and 3 extensions (Table 1).

### *Estimation Methods in MARK*

Typically, researchers obtain parameter estimates in Program MARK by the method of maximum likelihood, first developed by the legendary statistician R. A. Fisher. The idea behind maximum likelihood estimation is to find the "most likely" parameter value given the observed data. Maximum likelihood estimates have good statistical properties that we will not discuss in detail. Likelihood theory is the cornerstone of estimation methods in statistics, and the likelihood function plays a major role in both frequentist and Bayesian statistical methodology. Theory has been developed based on the log of the likelihood function to

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*Table 1.* The 4 multistate models implemented in Program MARK.

| Model | Description |
|---|---|
| Basic multistate | Multistate model with single encounter occasion per primary session. Parameters to be estimates are $S$, apparent survival; $p$, live encounter probability; and $\psi^{rs}$, transition probabilities between strata. |
| Multistate with both live and dead encounters | Same model as the basic multistate extended to include information from dead encounters. One additional parameter is $r$, conditional reporting probability of a dead animal. |
| Robust design multistate with closed primary sessions | Same model as the basic multistate extended to handle multiple secondary encounter occasions for each primary encounter occasion. Primary sessions are closed. The closed capture model parameters: $p$, probability of first capture; $c$, probability of recapture, and possibly $\pi$ mixture probability for heterogeneity models; and $N$ for population size, replace the basic multistate $p$ parameter. Probability of animal misidentification ($\alpha$) can also be modeled. |
| Robust design multistate with open primary sessions | Same model as the basic multistate but with multiple secondary encounter occasions for each primary encounter occasion. Primary sessions are open. The open model parameters—*pent*, probability of entry to be available for live encounter; $\phi$, probability of remaining available for live encounter; and $p$, probability of live encounter on a secondary occasion—replace the basic multistate $p$ parameter. |

estimate the parameter value, its standard error, and profile likelihood confidence intervals.

Most of the models in MARK are structured from a multinomial distribution, an extension of the binomial distribution. We will not discuss exceptions here. The multinomial distribution describes the probability of the outcome when the outcome has to be one of a fixed set of possibilities. As an example, consider a duck banded at the start of year 1, and what we might expect as possible outcomes of the fate of this band. A hunter could shoot the duck in interval 1 and return the band, or similarly in interval 2, and so forth for the duration of the study. However, to make the set of multinomial classes complete, a category of "never seen again" must be included. Therefore, the set of possible fates is for the return of the band in year $i$, $i = 1, \ldots, t$, or else never seen again. These fates are mutually exclusive and all encompassing (i.e., the fate of the duck's band must fall in one of these categories).

The encounter histories of the marked animals are the input data to Program MARK. As an example for the CJS model, consider the encounter history of an animal marked in year 2, recaptured in years 4 and 5 of a 5-year study: 01011, which is just one of $2^3 = 8$ possibilities conditional on animals first captured on occasion 2. Zero represents "not captured," and 1 represents "captured." We can construct the log-likelihood from the encounter histories for each animal because of the structure of the multinomial distribution. We computed the probability of observing the 01011-encounter history based on the current parameter values. For the CJS time-specific model, the probability of this encounter history, conditional on first being captured in period 2, is $\phi_2(1 - p_3)\phi_3 p_4 \phi_4 p_5$, where $\phi_i =$ the probability an animal in the population in period $i$ is alive and in the population in period $i + 1$, and $p_i =$ the probability an animal is captured in period $i$, given that it is in the population. Suppose that we observed 22 animals with this identical encounter history. The contribution to the log-likelihood for these 22 animals would be

$$22 \times \log[\phi_2(1 - p_3)\phi_3 p_4 \phi_4 p_5].$$

Because of the properties of the log-likelihood function derived from the multinomial distribution, the log-likelihood for all the animals is proportional to the sum of the numbers of animals with a specific encounter history times the log of the probability of that encounter history. For $k$ encounter histories of those first captured in period 2, each with $n$ animals observed with that history, the symbolic log-likelihood is

$$\log L(\phi_2, p_3, \phi_3, p_4, \phi_4, p_5 | n_i, X_i, i = 1, \cdots, k) \propto \sum_{i=1}^{k} n_i \log[\Pr(X_i)] \, ,$$

the log of the likelihood of the parameters $\phi_2$, $p_3$, $\phi_3$, $p_4$, $\phi_4$, and $p_5$, given $n_i$ animals with encounter history $X_i$ for the $k$ observed encounter histories, is proportional to the sum of the encounter history frequency times the log of the probability of this history for all $k$ encounter histories. The strategy used in Program MARK to obtain the estimates of the unknown parameters ($\phi_2$, $p_3$, $\phi_3$, $p_4$, $\phi_4$, and $p_5$) is to numerically maximize the log-likelihood function by adjusting the values of the unknown parameters until the log-likelihood reaches a maximum (i.e., no matter how the parameters change, a value of the log-likelihood cannot be obtained that is greater than the current maximum).

The flexible model-building capabilities of MARK, provided by the ability to manipulate parameter indices through the parameter index matrices (PIMs) and the design matrix, provide linear logistic models of the biological and nuisance parameters (the $\phi$'s and $p$'s in the above example, denoted as "real" parameters in MARK). The PIMs provide the capability to equate parameters. For example, to equate estimates of $\phi_1$, $\phi_2$, $\phi_3$, and $\phi_4$, the indices of these 4 parameters would all be set equal in the PIM for the $\phi$ parameters, so that a single estimate replaces the 4 estimates. The design matrix provides additional capabilities to develop models of the estimated parameters, such as modeling the estimates as functions of temporal and attribute group covariates. As an example, the design matrix can specify a linear model on the logit scale to force a trend in the estimates of $\phi_1$, $\phi_2$, $\phi_3$, and $\phi_4$. In addition, MARK provides the capability to incorporate individual covariates into models of the biological parameters through the design matrix. White et al. (2001) and White and Burnham (1999) provide further descriptions of these capabilities.

Described above is the typical estimation method researchers most commonly use in Program MARK. In addition, the Bayesian paradigm using the Markov chain Monte Carlo (MCMC) is included in MARK. The main use of this estimation method is to obtain estimates of process variances and covariances, although nothing precludes using MCMC to obtain estimates of fixed effect parameters as well.

### *Multistate Model*

The main topic of this paper is the particularly useful class of models known as the multistate or multi-strata set of models, in which observations of marked animals occur in various mutually exclusive categories. The multistate model is a logical extension of the CJS live recapture model extended to multiple areas or strata. The first application of this model was for Canada geese (*Branta canadensis*) banded with individually identifiable neck bands wintering on the east coast of the United States in 3 discrete areas (Hestbeck et al. 1991). The 3 states of this model were 3 wintering areas: Mid-Atlantic, Chesapeake, and Carolinas. Brownie et al. (1993) provided a rigorous development of the model, in which they used matrix algebra to present the probability of an observed encounter history. Three sets of parameters form the basic multistate model, all of which can be time-specific: $S_i^s$ is the probability an animal survives the time interval $i$ to $i+1$ if in stratum $s$ ($s=1, \ldots, k$) at time $i$ and remains available for recapture on occasion $i+1$, $p_i^s$ is the probability of capture at time $i$ for an animal in stratum $s$ at time $i$, and $\psi_i^{rs}$ is the probability that an animal in stratum $r$ moves to stratum $s$ at the end of the interval starting at time $i$, conditional on the animal remaining alive and available for capture. They designated the $\psi_i^{rs}$ as the transition probabilities, with $\psi_i^{rr}$ as the probability of remaining in a stratum a possible result. Therefore, the sum of the transition probabilities equals 1; that is, $\sum_{s=1}^{k} \psi_i^{rs} = 1$. To maintain this required constraint, one of the transition probabilities is normally obtained by subtraction; for instance, we estimate the probability of remaining in stratum $r$ as $\psi_i^{rr} = 1 - \sum_{s \neq r} \psi_i^{rs}$.

Program MARK uses the information (data) from the encounter histories to form the log of the likelihood function of the estimable parameters given the observed data. A simple example will make this model clearer. Assume a sample of 3 strata: A, B, and C, analogous to the 3 wintering areas in Hestbeck et al. (1991). Encounter histories must include the information of from which stratum researchers captured an animal. Thus, instead of using a "1" to indicate capture, the stratum code is used to identify the encounter stratum. For 5 encounter occasions, a history such as

BCACC

might result. That is, the animal was initially released in stratum B, resighted in stratum C during the second occasion, resighted in stratum A on the third occasion, resighted in stratum C on the fourth occasion, and then again in stratum C on the fifth occasion. The probability of observing this encounter history given the parameters is

$$[S_1^B \psi_1^{BC} p_2^C]\,[S_2^C \psi_2^{CA} p_3^A]\,[S_3^A \psi_3^{AC} p_4^C]\,[S_4^C (1 - \psi_4^{CA} - \psi_4^{CB}) p_5^C]\,,$$

where brackets, for the sake of clarity, separate the 4 intervals between the 5 occasions. In the multistate model, the encounter history is conditional on first capture, so there is no $p_1$ encounter probability. Note that for the fourth interval, the probability of remaining in stratum C ($\psi_4^{CC}$) is just one minus the sum of the probabilities of leaving stratum C. Transitions in the above equation are assumed Markovian; that is, the next transition depends only on the current state and does not depend on the previous state.

The complexity that results when an animal is not captured (i.e., a zero is in the encounter history) is difficult to demonstrate without matrix algebra. However, to provide a glimpse of the construction of the encounter history probabilities, consider the encounter history

BC0CA.

Three possibilities can explain the zero on occasion 3: the animal remained in C and was not captured:

$$S_2^C (1 - \psi_2^{CA} - \psi_2^{CB})(1 - p_3^C) S_3^C (1 - \psi_3^{CA} - \psi_3^{CB}) p_4^C;$$

or the animal moved to stratum A and was not captured and then moved back to C:

$$S_2^C \psi_2^{CA} (1 - p_3^A) S_3^A \psi_3^{AC} p_4^C;$$

or the animal moved to stratum B and was not captured and then moved back to C:

$$S_2^C \psi_2^{CB} (1 - p_3^B) S_3^B \psi_3^{BC} p_4^C.$$

In the first case, the animal has to remain in stratum C at the end of both interval 2 and interval 3 to be captured in stratum C on occasion 4. For both of the cases where the animal moved, it has to return to stratum C because the capture occurred in stratum C on the fourth occasion.

The above example of an encounter history probability demonstrates an arbitrary assumption of the multistate model as implemented in MARK based on the Brownie et al. (1993) formulation: they modeled survival with the survival rate for the stratum where the capture of the animal took place, and then movement to a new stratum takes place. That is, all mortality takes place before movement. An animal cannot move to a new stratum where a different survival rate pertains and then die. If it dies, it must do so on the current stratum. If it lives, then it can move to a new stratum. This assumption is critical if survival rates are different between the strata, with violation of this assumption resulting in estimated survival being a weighted average across strata. If survival is the same across all the strata, then the assumption is not important because survival is the same regardless of the stratum currently occupied. Where geographic areas define strata, as in a metapopulation study, this assumption is often difficult to meet or validate, and limits the usefulness of the model in that strata-specific survival estimates are not obtainable unless the transitions between strata take place immediately before an encounter occasion. Note that different assumptions about when the transitions take place could be made (e.g., just after an encounter occasion, or at any time during the interval), but different assumptions result in a different model from that currently available. The implemented assumption is not draconian where breeding status defines the state. In fact, it is ideally formulated for evaluating cost of reproduction, where survival probability is hypothesized to be affected not by where the animal is between breeding seasons (in fact many breeders and nonbreeders intermix between seasons for many species), but the fact that the animal is participating in breeding and incurring the potential costs in survival.

The number of types of time-specific parameters in this simple example is already large. There are 3 stratum-specific survival rates ($S_i^A$, $S_i^B$, $S_i^C$) for each time interval ($i = 1, \ldots, 4$) and 3 stratum-specific capture probabilities ($p_i^A$, $p_i^B$, $p_i^C$) for the last 4 occasions ($i = 2, \ldots, 5$). In addition, each interval $i$ has transition probabilities $\psi_i^{AB}$, $\psi_i^{AC}$, $\psi_i^{BC}$, $\psi_i^{BA}$, $\psi_i^{CA}$, and $\psi_i^{CB}$. Thus, Program MARK creates 12 sets of parameters, each with 4 time-specific values, resulting in 48 total parameters. However, not all of the parameters are identifiable in the fully time-specific model, so that only the product of the last $S$ and last $p$ is estimable, resulting in 45 estimable parameters for the example demonstrated here. Note, however, that all of the transition probability parameters are identifiable if the confounding of the last $S$ and $p$ product is rectified (e.g., by fixing the last $p$ value to 1 for each stratum so that the last estimate of $S$ is actually an estimate of the product of $S$ and $p$). Typically, however, more biological approaches to handling this confounding are desirable, such as using biologically important covariates to model either or both of the $S$ and $p$ parameters to remove the confounding of parameters, as well as modeling the $\psi$ parameters with covariates.

At this time, Program MARK only includes the movement model without memory. Brownie et al. (1993) describe models that are more complex, in which the animal remembers where it was on the previous occasion. This memory model requires a very large amount of data to provide reasonable estimates because the number of parameters grows quickly, even more so than the model considered above.

Under the basic multistate model, all states must be observable (i.e., animals must have encounter probabilities $p^s > 0$ for all strata $s$). If movement out of the set of observed states is inherently permanent, then this movement is confounded with survival (Burnham 1993). If this movement is temporary (i.e., if there is a chance the animal will return to a study area), then this movement is partly or completely confounded with capture probability (Barker 1997, Kendall et al. 1997). The multistate model incorporating dead encounters described below incorporates permanent emigration. The closed or open robust design multistate models described below incorporate temporary emigration. That is, parameters are estimable when an unobservable state is included in the model.

The multistate model can display some heinous behavior when there are >2 states, most notably multiple optima in the likelihood function (Lebreton and Pradel 2002). That is, depending on the starting values used to maximize the likelihood function, the solution can vary. Most models in MARK have a single maximum, and so researchers do not encounter this behavior. However, the multistate models occasionally seem to behave very poorly, particularly when one or more of the transition probabilities reach a parameter boundary, such as $\psi = 0$. An alternative optimization procedure has been included in Program MARK to manage such behavior. Simulated annealing (Goffe et al. 1994) is less efficient than the default optimization algorithm in finding the maximum of the function, typically requiring 10 times as many evaluations of the likelihood to reach a solution. However, the reason for this "inefficiency" is why simulated annealing is provided in MARK. Periodically, the simulated annealing algorithm makes a totally random jump to a new parameter value, and this characteristic is what allows the algorithm more flexibility in finding the global maximum instead of a local maximum. Besides simulated annealing, for similar reasons, the MCMC estimation procedure also provides a useful tactic to finding the global maximum.

Another consideration of the multistate model is the need for the multinomial logit link function. The logit link is commonly used in MARK to model real parameters (the biologically meaningful parameters such as $S$, $p$, or $\psi$) as functions of beta parameters, $\beta_i$. The logit link constrains the values of the real parameters to the range [0, 1]. With the logit link function $\log(S_i/[1 - S_i]) = \beta_i$, maximization of the likelihood occurs without restriction on the value of the $\beta$'s. The estimates for these parameters are then back-transformed to real parameters, using the inverse link function $S_i = \exp(\beta_i)/[1 + \exp(\beta_i)]$. However, the $\psi$ parameters require additional constraints (i.e., $\psi_i^{rr} = 1 - \sum_{s \neq r} \psi_i^{rs}$). That is, the sum of the $\psi$ estimates must be $\leq 1$, and each of the $\psi$ values must be $0 \leq \psi \leq 1$. MARK provides the multinomial logit link to enforce this constraint because the alternative approach of using a penalty function does not always perform satisfactorily, especially when the probability of remaining in a stratum is zero or near zero. Consider the 2 transition probabilities in the 3-strata example above. For stratum A, each time-specific set of transitions, $\psi_i^{AB}$ and $\psi_i^{AC}$, must meet the above constraints. The following set of link functions in terms of the beta parameters $\beta_1$ and $\beta_2$ generate estimates of the transition probabilities from the beta parameters and enforce the constraints:

$$\psi_i^{AB} = \frac{\exp(\beta_1)}{1 + \exp(\beta_1) + \exp(\beta_2)},$$

$$\psi_i^{AC} = \frac{\exp(\beta_2)}{1 + \exp(\beta_1) + \exp(\beta_2)},$$

*Table 2.* Model selection results from Program MARK for the meadow vole data from grid 1 of Nichols et al. (1994) fit with the multistate model.

| Model | $AIC_c$[a] | $\Delta AIC_c$ | $AIC_c$ weights | Model likelihood | No. of parameters | Deviance |
|---|---|---|---|---|---|---|
| {$S$(.[b]) $p$(strata[c]) ψ(strata × $t$[d])} | 520.255 | 0.000 | 0.30362 | 1.0000 | 11 | 88.724 |
| {$S$(.) $p$(.) ψ(strata × $t$)} | 520.465 | 0.210 | 0.27330 | 0.9001 | 10 | 91.145 |
| {$S$(strata) $p$(strata) ψ(strata × $t$)} | 521.407 | 1.152 | 0.17066 | 0.5621 | 12 | 87.645 |
| {$S$(strata) $p$(.) ψ(strata × $t$)} | 522.148 | 1.894 | 0.11780 | 0.3880 | 11 | 90.618 |
| {$S$(.) $p$(t) ψ(strata × $t$)} | 523.014 | 2.760 | 0.07640 | 0.2516 | 13 | 87.000 |
| {$S$(t) $p$(.) ψ(strata × $t$)} | 523.608 | 3.354 | 0.05677 | 0.1870 | 13 | 87.595 |
| {$S$(strata) $p$(strata × $t$) ψ(strata × $t$)} | 531.684 | 11.430 | 0.00100 | 0.0033 | 18 | 84.083 |
| {$S$(strata × $t$) $p$(strata) ψ(strata × $t$)} | 533.655 | 13.401 | 0.00037 | 0.0012 | 18 | 86.054 |
| {$S$(strata × $t$) $p$(strata × $t$) ψ(strata)} | 537.251 | 16.997 | 0.00006 | 0.0002 | 18 | 89.650 |
| {$S$(strata × $t$) $p$(strata × $t$) ψ(strata × $t$)} | 540.047 | 19.792 | 0.00002 | 0.0001 | 22 | 82.765 |
| {$S$(strata) $p$(strata) ψ(strata)} | 590.987 | 70.732 | 0.00000 | 0.0000 | 6 | 170.306 |

[a] Akaike's Information Criterion adjusted for small sample sizes.
[b] Estimates constant across strata and time.
[c] Estimates differ by strata.
[d] Time-specific estimates.

and

$$\psi_i^{AA} = \frac{1}{1 + \exp(\beta_1) + \exp(\beta_2)}.$$

Researchers should always consider the multistate model a candidate for analysis of data when animals occur in multiple states. The example above of animals moving between spatial areas is common. However, other biologically interesting examples are breeding versus nonbreeding, poor condition versus good condition, etc.

Breeding versus nonbreeding are presumably discrete states that can be determined upon capture. A complexity that commonly occurs with this categorization is that nonbreeding animals are not observable, e.g., nesting albatrosses (*Diomedea* spp.) versus the nonbreeders that remain at sea. In such cases, researchers could use the robust design multistate model described below or dead recoveries to account for the unobservable state.

Animal condition is generally a time-varying continuous covariate that researchers can measure upon capture of the animal. However, because researchers do not know the condition of the animal if they do not capture the animal, they cannot use a continuous individual covariate to model this phenomenon. Therefore, the multistate model is appropriate, in which discrete categories classify condition, because we do not need to know the condition of the animal at occasions in which the animal is not captured to use this model. The price we pay for not knowing condition at all times is that we have to categorize the variable and hence lose some information, although this loss is typically small. Typically, a common line of reasoning that leads to a multistate model is 1) we know a time-varying covariate would make a great individual covariate to predict survival; 2) however, we know this covariate is only when the animal is captured; and 3) therefore, we categorize the covariate and use this information in a multistate model.

## Multistate Model Example

The multistate model is illustrated using capture–recapture data on female meadow voles (*Microtus pennsylvanicus*) derived from Nichols et al. (1994). The 25 occasions were 5 primary trapping sessions, with 5 secondary occasions each. Here, we collapsed the data across the secondary occasions within each primary session to create 5 occasions to illustrate the multistate model. Multistate capture–recapture models are useful for determining the proportion of a population that is breeding, given that we can determine the breeding status at the time of capture. Importantly, the multistate model allows differences in capture or sighting probabilities for breeding and nonbreeding individuals, which we would generally not consider the same for the 2 types of individuals. We can also estimate the cost of reproduction on survival as the difference between the survival rates of the breeding and nonbreeding strata.

We show the ranking of a set of models estimated with Program MARK for animals captured on grid 1 (Nichols et al. 1994) in Table 2. The models with transition probabilities varying with time receive the most support because the proportion of reproductively active females showed strong seasonal variation, as expected, with low breeding proportions in midwinter (Nichols et al. 1994). The data suggest no evidence of reproductive costs in survival, in that the top model has survival constant across both time and strata. There is evidence of a difference in capture probability between the strata because for models differing only in $p$(.) versus $p$(strata), the stratum-specific model always ranks higher of the pair.

## Dead Encounters in the Multistate Model

A logical extension of the multistate model is to include encounters of dead animals (e.g. band recoveries) in the model. Encounters of dead animals tells much about survival in the sense that the animal had to survive up to the dead encounter and then is "removed" from the encounter history with probability $1 - S$. The multistate live and dead encounter model in Program MARK is a merger of the band recovery models of Seber (1970) and the multistate model of Brownie et al. (1993). Barker et al. (2005) developed this model for a mark–recapture analysis combining data from live recaptures of paradise shelduck (*Tadorna variegata*) at multiple banding sites (molting sites that are the strata of the multistate model) with reported recoveries from birds shot by hunters. The transition probabilities provided estimates of the movement of paradise shelduck between molting sites. The model allows survival, recapture, and movement probabilities to depend on the possibly unknown (because not recaptured) location of the birds at the time researchers make live recaptures. We do not assume band recoveries are stratum-specific. We can include temporary emigration in the model using unobserved states in which capture cannot occur because the band recovery portion of the model provides an estimate of survival across all strata. Thus, the apparent survival of the basic multistate model is now true survival, if survival for the unobservable state is constrained to equal survival for one of the observable states, and if the banded birds cannot escape the sampling mechanism responsible for the recovery of dead birds. For this example, harvesting of shelduck occurs throughout New Zealand, so band recoveries take place throughout the range of the population of interest.

The incorporation of dead encounters into the basic multistate model adds one additional type of parameter, the probability that a dead bird will be reported, $r$. That is, the parameter $r$, or conditional reporting rate (Otis and White 2002), is the probability that the band is reported given that the bird has died, and is equivalent to the $\lambda$ parameter of Seber (1970). The relationship between $r$ and the recovery rate, $f$, of Brownie et al. (1985) is $f = (1 - S)r$.

We do not classify dead recoveries into strata, as are the live encounters in this model, because dead recoveries come from a completely different sampling process, and the strata applicable to live encounters through recaptures are not appropriate for dead encounters. Thus, we enter dead encounters as a 1 in the live–dead encounter history, ignoring the live encounter strata. However, the conditional reporting rates are a function of the stratum which the bird occupied during the last live capture occasion, even if we did not encounter the bird alive on that occasion. Thus, the conditional reporting rates are still stratum- and time-specific, so that for an example with 3 strata, 3 sets of time-specific parameters are required: $r_i^A$, $r_i^B$, and $r_i^C$.

For the paradise shelduck in New Zealand, Barker et al. (2005) found that both survival and conditional reporting rates were a function of molting site and sex but that transition probabilities between molting sites were just a function of site. That is, ducks transitioned between sites depending on their current molting site. Some molting sites were preferred sites from which ducks seldom transitioned.

### *Robust Design Extension for Closed Primary Occasions*

Kendall and Nichols (1995) and Kendall et al. (1995, 1997) extended the simple CJS model to include multiple secondary capture occasions within each primary occasion. That is, for the simple example above with 5 primary occasions, each primary occasion would consist of 2 or more secondary occasions for which we assume demographic and geographic closure. The set of secondary occasions within a primary occasion is a closed population, and thus the closed captures models of MARK into the robust design model.

Therefore, we apply the maximum likelihood closed captures models of Otis et al. (1978) and White et al. (1982). In addition, the closed captures and robust design models of Program MARK have incorporated the closed captures models of Huggins (1989, 1991) and Alho (1990), allowing the use of individual covariates to estimate capture probabilities. Further, Pledger (2000) extended the closed capture models by modeling heterogeneity of probabilities with mixture distributions, and this capability has been added to the closed capture models of both Otis et al. (1978) and Huggins (1989, 1991). Finally, all of these parameterizations can include animal misidentification (Lukacs and Burnham 2005), so 12 different parameterizations of the closed captures models are available in MARK, and all are available in the robust design extensions that we discuss below for the closed robust design multistate models.

The closed robust design extension of the multistate model is available in MARK, although the literature has not formally described the model as such. This model provides considerable advantages over the simple multistate model without secondary encounter occasions. First, the robust design provides estimates of the population size for each of the primary occasions in each stratum. Second, the multiple secondary occasions within a primary occasion increase the probability that an animal will be encountered during the primary session, and so improve the precision of the estimates of survival, $S$, and transition probabilities, $\psi$. Even for a fixed amount of effort, the information across secondary occasions used by robust design models increases the precision of $\psi$ over pooling those occasions. Third, the estimate of the probability that an animal is encountered during the primary occasion can be produced from just the encounters within the primary occasion. This result means that the confounding of the last survival rate and last encounter probability is no longer present (although other confounding occurs if there is an unobservable state).

Another major advantage of the robust design approach is that researchers can model the individual heterogeneity of the capture probabilities, as well as behavioral response to capture, with the closed captures models available in MARK. In contrast, the basic multistate model is only using the recaptures across occasions, and so individual heterogeneity of capture probabilities can cause difficulty in the model fitting the data. Of course, obtaining population estimates from the robust design is a useful benefit.

However, the additional parameters can greatly increase the complexity of the model selection process. The range of possible models that can be built within the robust design framework increases probably 10 times compared to the basic multistate model because of the wide range of potential models to model the capture and recapture probabilities. Therefore, the practitioner must be judicious in selecting the set of models for evaluation. One approach to this would be to identify the most parsimonious model structure for capture probabilities separately for each primary period

*Table 3.* Model selection results from Program MARK for the vole data from grid 1 of Nichols et al. (1994) fit with the robust design multistate model assuming closed populations during trapping sessions.

| Model | $AIC_c$[a] | $\Delta AIC_c$ | $AIC_c$ weights | Model likelihood | No. of parameters | Deviance |
|---|---|---|---|---|---|---|
| {$S$(.[b]) $\psi$(strata[c] × session[d]) $\pi$(session) $p$(session) = $c$(session) + constant $N$(strata × session)}[e] | 779.683 | 0.000 | 0.69109 | 1.0000 | 35 | 705.733 |
| {$S$(.) $\psi$(strata × session) $\pi$(strata × session) $p$(strata × session) = $c$(strata × session) + constant(strata) $N$(strata × session)} | 781.956 | 2.273 | 0.22183 | 0.3210 | 51 | 671.429 |
| {$S$(strata) $\psi$(strata × session) $\pi$(strata × session) $p$(strata × session) = $c$(strata × session) + constant(strata) $N$(strata × session)} | 783.882 | 4.199 | 0.08468 | 0.1225 | 52 | 671.006 |
| {$S$(strata) $\psi$(strata × session) $\pi$(strata × session) $p$(strata × session) $N$(strata × session)} | 792.186 | 12.503 | 0.00133 | 0.0019 | 50 | 683.999 |
| {$S$(strata) $\psi$(strata) $\pi$(strata × session) $p$(strata × session) = $c$(strata × session) + constant(strata) $N$(strata × session)} | 792.640 | 12.956 | 0.00106 | 0.0015 | 46 | 693.743 |
| {$S$(strata) $\psi$(strata) $\pi$(strata × session) $p$(strata × session) $N$(strata × session)} | 802.878 | 23.195 | 0.00001 | 0.0000 | 44 | 708.582 |
| {$S$(strata) $\psi$(strata × session) $p$(strata × session) = $c$(strata × session) $N$(strata × session)} | 812.636 | 32.953 | 0.00000 | 0.0000 | 30 | 749.743 |
| {$S$(strata) $\psi$(strata) $p$(strata × session) = $c$(strata × session) $N$(strata × session)} | 861.130 | 81.447 | 0.00000 | 0.0000 | 24 | 811.281 |
| {$S$(strata) $\psi$(strata × session) $p$(strata) = $c$(strata) $N$(strata × session)} | 868.646 | 88.963 | 0.00000 | 0.0000 | 22 | 823.091 |
| {$S$(strata) $\psi$(strata) $p$(strata) = $c$(strata) $N$(strata × session)} | 926.995 | 147.312 | 0.00000 | 0.0000 | 16 | 894.167 |

[a] Akaike's Information Criterion adjusted for small sample sizes.
[b] Estimates constant across strata and time.
[c] Estimates differ by strata.
[d] Estimates differ between primary sessions.
[e] We used 3 different closed captures data types to model the capture and recapture probabilities, with the minimum $AIC_c$ model based on the Pledger (2000) formulation that includes both individual heterogeneity and behavioral responses.

(using separate runs the closed population model feature of MARK). Researchers would then use the combination of these best models as the beginning point for model selection on survival and transition probabilities.

Another major advantage of the robust design multistate model is that the ability to estimate the probability of encounter from just the secondary encounter occasions means one of the states of the model can now be unobservable, and the transition probabilities to and from this state can be estimated (Kendall and Nichols 2002, Schaub et al. 2004). In the simplest case, researchers construct the multistate model with one observable state in which researchers encounter animals and one unobservable state in which researchers cannot encounter animals. This multistate model is exactly the robust design model described by Kendall et al. (1997). The transition from observable ($O$) to unobservable ($U$) states, $\psi_{i-1}^{OU}$ corresponds to their $\gamma_i$, the probability of the animal being off the study area unavailable for capture on occasion $i$, given that the animal was on the study area during the previous occasion $i-1$. Likewise, the transition $\psi_{i-1}^{UO}$corresponds to $1-\gamma_i$, the probability that an animal off the study area on occasion $i-1$ and unavailable for capture will be available for capture on occasion $i$. However, one key assumption still cannot be relaxed—the survival rate of animals in the unobservable state must be the same as the survival rate of animals in the observable state (i.e., $S^U = S^O$).

The robust design implementation of the model does not eliminate another limitation of the basic multistate model—apparent survival. Apparent survival became true survival for the combined live multistate and dead recoveries model because the dead recoveries provided an alternative sampling mechanism to estimate survival outside the live encounters study areas. However, the robust design multistate model does not provide an alternative sampling mechanism but rather just a more intensive sample of the usual live encounters sampling. Therefore, permanent emigration from the live encounters study sites will result in the parameter $S$ being an estimate of apparent survival and not true survival.

### Robust Design Multistate Closed Model Example

We use the un-collapsed grid 1 data of Nichols et al. (1994) to illustrate this model. We use all 25 occasions in the analysis, with 5 primary sessions of 5 secondary occasions each. Note that MARK does not require that primary sessions have equal numbers of secondary occasions or even that the primary sessions have equal time intervals between them. Model selection results (Table 3) are the same as determined for the multistate example shown in Table 2. That is, there is no evidence of differences in survival between the strata, $\psi$ varies with time, and there are small differences in capture probabilities between strata.

Importantly, the standard errors of the survival and transition estimates are typically smaller for the robust design models than the simpler basic multistate model because of the additional information available from the secondary occasions. For example, the estimate of survival from the top model is 0.648 ($SE = 0.0366$) for the robust design and 0.727 ($SE = 0.0388$) from the simpler model. The point, however, is that the additional data obtained from the robust design generally produce more precise estimates.

### *Robust Design Extension for Open Primary Occasions*

Kendall and Bjorkland (2001), following on the work of Schwarz and Stobo (1997), extended the multistate model to a robust design where the primary sessions are considered to be open; that is, geographic closure is not assumed within the primary session. They present a model for estimating availability for detection that relaxes 2 assumptions required in previous approaches. The first is that no additions or deletions to the sampled population occur across samples within a period of interest (i.e., Kendall and Bjorkland [2001] do not assume geographic closure during the primary periods). The second is that each member of the population has the same probability of being available for detection in a given period because Kendall and Bjorkland (2001) model the probability of an animal's entry into and exit from the sampling area during the primary occasion. Program MARK implements this model as the open robust design multistate model.

Kendall and Bjorkland (2001) applied their model to estimate survival and breeding probability in a study of nesting hawksbill sea turtles (*Eretmochelys imbricata*). The previously described approach, in which closed models are assumed for the primary occasions, is not appropriate because the capture of turtles occurs when they come to the beach to lay eggs, the nesting period is >6 months, and individual turtles are only present to lay eggs approximately every 2 weeks for approximately 5 clutches. Individual turtles arrive and depart in a staggered fashion over the 6-month nesting period. The strata in the Kendall and Bjorkland (2001) example were that an individual adult female either nested or skipped nesting in year *i*.

Kendall and Bjorkland (2001) found that probabilities of arrival, detection, and leaving the site for the year were constant within and among seasons. At the primary occasion level, breeding probability in year $i$ for nonbreeders in year $i - 1$ varied by year but survival probability did not. They fixed the probability of returning to breed in a second consecutive year to zero in the model because they never found any females to nest 2 years in a row.

### *Additional Features of MARK Useful for Multistate Models*

Program MARK provides many additional features useful for the analysis of mark–encounter data with multistate models. Previously mentioned is the capability to model biological parameters as functions of time, group, and individual covariates. In addition, as illustrated by the sea turtle example of Kendall and Bjorkland (2001), researchers can fix parameters to specified values, a useful feature for the multistate models because of transitions that cannot occur or that occur with probability equal to 1. Model selection is performed with information–theoretic procedures (Burnham and Anderson 2002), and parameter estimates can be model-averaged to obtain unconditional standard errors (i.e., estimates and standard errors that take into account model selection uncertainty; Burnham and Anderson 2002).

Program MARK also provides the capability to estimate variance components, e.g., the underlying process variance in a time series of survival or transition probability estimates. Estimates of process variances are necessary to construct data-driven population viability analyses (White 2000). A feature just added to MARK in 2004 is Bayesian estimation using MCMC methodology. The main attraction of this feature is the ability to estimate process variances and covariances across series of parameters. As an example, researchers could estimate the process covariance between survival rates and probability of breeding, an important life-history trait, with the multistate models described.

## Management Implications

Effective management of wildlife populations or meta-populations requires monitoring programs that 1) are driven by management objectives, 2) are unbiased in the choice of sampling units across space, and 3) produce estimates of demographic parameters for a given study unit or set of units with minimal bias and good precision. Based on the methodology described above, Program MARK provides a tool for computing robust estimates of demographic parameters with good precision. However, these tools are most useful if researchers give the design of capture–recapture studies thoughtful consideration a priori. Estimation will be more robust if researchers can eliminate unobservable states (i.e., capture animals wherever they are). If this is not possible, it is important to develop a robust design, or monitor movements outside the study areas directly using telemetry, and to look for opportunities for free information such as recoveries. Even if unobservable states do not exist, the robust design or dead recoveries will increase the precision of estimates of demographic parameters.

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