

Multievent: An Extension of Multistate Capture–Recapture Models to Uncertain States

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SUMMARY. Capture–recapture models were originally developed to account for encounter probabilities that are less than 1 in free-ranging animal populations. Nowadays, these models can deal with the movement of animals between different locations and are also used to study transitions between different states. However, their use to estimate transitions between states does not account for uncertainty in state assignment. I present the extension of multievent models, which does incorporate this uncertainty. Multievent models belong to the family of hidden Markov models. I also show in this article that the memory model, in which the next state or location is influenced by the previous state occupied, can be fully treated within the framework of multievent models.

KEY WORDS: Arnason–Schwarz model; Breeding propensity; Canada goose; Hidden Markov model; Jolly–Move model; Memory model.

1. Introduction

Biologists intending to study the dynamics of free-ranging animal populations often resort to following individuals rendered identifiable by some marking technique (exceptional natural marks can be used). Observations are carried out on several field visits allowing the construction of an encounter history for each recognizable individual. This method is known as capture–recapture (CR). The data so gathered allow the estimation of vital rates in the wild (see Schwarz and Seber, 1999 for a review of applications).

It is only recently that attention has turned toward estimating movements among geographical locations (Hestbeck, Nichols, and Malecki, 1991). In certain studies, the same individuals may be observed successively at different sites. The corresponding models, stemming from the work of Arnason (1972, 1973), are said to be “multisite.” They may also be applied to the study of transitions among states. Used as multistate (sometimes multistrata) models, the original multisite models serve, for instance, to estimate the probability that a breeding animal in year t will breed again in year $t + 1$ (Nichols et al., 1994). However, a state is not as easy to ascertain as a geographical position. An animal only observed while feeding may or may not be breeding. Thus, the multistate data present two kinds of uncertainty: uncertainty of detection and uncertainty of state. The multistate models currently in use provide for uncertain detection but fail to recognize uncertainty in the assessment of state. Up to now, attempts at accounting for state uncertainty have been limited to situations where assignment probabilities are available either from another source of information (Fujiwara and Caswell, 2002) or using the robust design (Kendall, Hines, and Nichols,

2003) (suggestions can also be found in Lebreton, 1995 and Lebreton and Pradel, 2002).

The main aim of this article is to show how uncertainty in the assessment of state can be incorporated into the analysis of “multistate” CR data. The solution I propose puts an emphasis on the real nature of the data. Conceptually, it is not states that are observed but rather something, say an “event,” which reflects to some extent the underlying state, which is the ultimate object of the study. The new models are called “multievent” to reflect the nature of the data. In the next section, I present the general multievent model with time-dependent parameters. Then, Section 3 examines four situations of particular interest. It is first shown that the multistate model of Arnason–Schwarz (AS) can be retrieved as a particular case of the time-dependent multievent model. Then, I propose a model for the study of breeding propensity when only the state breeder can be ascertained. The Jolly–Move (hereafter JMV) model and the memory model (Brownie et al., 1993) are two important generalizations of the AS model where some parameters (the encounter probabilities and the transition probabilities, respectively) depend on the state occupied at $t - 1$. I show in the same section that they can be cast within the framework of multievent models. The memory model has been previously treated with a partial likelihood approach (Brownie et al., 1993). Section 4 compares the numerical estimates of transition probabilities of Canada geese *Branta canadensis* among wintering sites obtained with the full likelihood proposed here to those obtained with partial likelihood. The last section discusses the potential and limitations of multievent models.

2. The Time-Dependent Multievent Model

2.1 Data

The time-dependent multievent model assumes that the individuals in the population move independently over a finite set of N states, $E = \{e_1, \dots, e_N\}$, through a finite number of sampling occasions, T . For example, the states may be $e_1 = \text{“breeder,”}$ $e_2 = \text{“nonbreeder,”}$ $e_3 = \text{“dead.”}$ Note that, unlike the dominant practice in CR (but see Dupuis, 1995; Lebreton, Alm eras, and Pradel, 1999; Fujiwara and Caswell, 2002), the state “dead” (hereafter denoted \dagger) is explicitly included in E . For a given animal, the successive states occupied are not observed directly; rather, at each occasion t , an event o_t among L possible (set $\Omega = \{v_1, \dots, v_L\}$) happens and is recorded leading to an observed encounter history $h = (o_1, \dots, o_T)$. To keep with the example of breeding animals, we might have $v_1 = \text{“sitting on an egg,”}$ $v_2 = \text{“standing in the colony,”}$ $v_3 = \text{“feeding in a nearby field,”}$ $v_4 = \text{“not observed.”}$ Hence, a possible encounter history over three time steps is (v_3, v_4, v_1) . This encounter history may be concisely written as (301) with 0 standing for $v_4 = \text{“not observed”}$ in accordance with the common practice in CR. The important point here is to observe that the codes represent events, not the states.

2.2 Assumptions

Events and states are best seen as random variables denoted O_t and Q_t , respectively. I assume that the event of occasion t , O_t , depends only on the unobserved underlying state Q_t of the animal at the moment. I also assume that the successive states obey a Markov chain.

2.3 Parameters

The parameters of the multievent model are

- $\phi_{ij,t}$, the probability of being in state e_j at time $t + 1$ if in state e_i at time t ,
- $\pi_{i,t}$, the probability of being in state e_i when first encountered at time t ,
- $b_{uj,t}$, the probability of event v_u for an animal in state e_j at time t ,
- $b_{uj,t}^0$, the probability of event v_u for an animal in state e_j at time t , which is then encountered, i.e., $P(v_u | e_j \text{ and “encountered”})$.

The b^0 's are needed because the model conditions on the time of first encounter of each animal. I will use the following matrix and vector notations: $\Phi_t = (\phi_{ij})_t$, $\pi_t = (\pi_1, \dots, \pi_N)_t$, $B_t = (b_{uj})_t$, and $B_t^0 = (b_{uj}^0)_t$. Note that Φ_t is row stochastic because of the systematic inclusion of the state dead, while the columns of B_t and B_t^0 always sum to 1.

2.4 Likelihood

With these parameters, it is possible to write out the probability of any encounter history. For instance, the capture history (301) has probability

$$P(301) = \sum_{i,j,k} \pi_{i,1} b_{3i,1}^0 \phi_{ij,1} b_{4j,2} \phi_{jk,2} b_{1k,3},$$

where i , j , and k span all possible states. It may be useful to reflect on this example. A reasonable constraint here could be

that $b_{12} = 0$, i.e., a nonbreeder (the “2”) cannot be observed sitting on an egg (the “1”). Then, b_{11} would be the probability that a breeder is encountered sitting on an egg, and b_{11}^0 would be the probability that a breeder *that is encountered* is then sitting on an egg. $P(301)$ can be written in a more compact form using matrix notations. More generally, taking $D(\theta)$ to be the diagonal matrix with diagonal elements equal to the elements of the arbitrary vector θ , the probability of the generic encounter history h starting at time e can be written as

$$P(h) = \pi_e D(B_e^0(o_e, \cdot)) \left(\prod_{i=e+1}^T \Phi_{i-1} D(B_i(o_i, \cdot)) \right) \mathbf{1}_N.$$

In this expression, $B(o, \cdot)$ is the row vector of B corresponding to event o , and $\mathbf{1}_N$ is the column vector of N ones. If there are right-censored individuals (e.g., lost on capture), the T in $P(h)$ is to be replaced with the time of censoring. Finally, the likelihood is the product of the probabilities of all the encounter histories.

3. Some Particular Cases

3.1 The Arnason-Schwarz Model

The AS model is the model where, when an animal is observed, its state is known without error. Thus, in the formalism of the multievent model, $E = \{e_1, \dots, e_s, \dagger\}$ and $\Omega = \{v_1, \dots, v_{s+1}\}$ where v_i is the event “state e_i is observed” except for v_{s+1} which is “the animal is not encountered.” This vindicates the practice of confounding the events v_1 to v_s with the states e_1 to e_s , respectively; it is only for event v_{s+1} that there is uncertainty. If p_i is the probability of encountering an animal in state i ,

$$B_t = \begin{pmatrix} p_1 & 0 & \dots & 0 \\ 0 & p_2 & \dots & 0 \\ & & \ddots & \\ 1 - p_1 & \dots & 1 - p_s & 1 \end{pmatrix}_t.$$

The initial event distribution matrix B_t^0 is obtained by replacing the p 's with 1 (the last column of B_t^0 is unused as the corresponding state dead cannot be encountered). Finally, $\pi_t = (\pi_1, \dots, \pi_s, 0)_t$ with a final 0 because, again due to the conditioning on the time of first encounter, the state dead is impossible as an initial state. The likelihood of this multievent model factorizes into two parts involving different parameters. The first part involves only the π_i 's, and the second part is exactly the likelihood of the AS model. As they have no parameters in common, each part can be maximized separately. The maximum likelihood estimates (MLEs) for the π_i 's are simply the proportions observed for the first time in each state at each occasion. The MLEs for the other parameters are those of the AS model.

3.2 A Simple Model for Studying Breeding Propensity

The study of transitions between the states breeder (B) and nonbreeder (NB) is a topic of major interest to biologists. A common situation is that where some animals are observed in breeding activity, and can thus be assigned to the state breeder with certainty, while the status of others remains elusive and is recorded as unknown. There are three states

in this model, $E = \{B, NB, \dagger\}$ and three possible events, $\Omega = \{\text{seen breeding (code 1), seen but status unknown (code 2), not seen (code 0)}\}$. The parameters of the model are, with obvious notations,

$$\Phi_t = \begin{pmatrix} \phi_{B,B} & \phi_{B,NB} & 1 - \phi_{B,B} - \phi_{B,NB} \\ \phi_{NB,B} & \phi_{NB,NB} & 1 - \phi_{NB,B} - \phi_{NB,NB} \\ 0 & 0 & 1 \end{pmatrix}_t,$$

$$B_t = \begin{pmatrix} p_{1|B} & 0 & 0 \\ p_{2|B} & p_{NB} & 0 \\ 1 - p_{1|B} - p_{2|B} & 1 - p_{NB} & 1 \end{pmatrix}_t,$$

$$\pi_t = (\pi_1, \pi_2, 0)_t.$$

$$\Phi_t = \begin{pmatrix} \phi_{CCC} & \phi_{CCD} & 0 & 0 & 1 - \phi_{CCC} - \phi_{CCD} & 0 & 0 \\ 0 & 0 & \phi_{CDC} & \phi_{CDD} & 0 & 1 - \phi_{CDC} - \phi_{CDD} & 0 \\ \phi_{DCC} & \phi_{DCD} & 0 & 0 & 1 - \phi_{DCC} - \phi_{DCD} & 0 & 0 \\ 0 & 0 & \phi_{DDC} & \phi_{DDD} & 0 & 1 - \phi_{DDC} - \phi_{DDD} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}_t,$$

The probability of encounter of a breeder is $p_{1|B} + p_{2|B}$ because a breeder can be encountered and recognized to be a breeder (code 1, probability $p_{1|B}$) or encountered with its status remaining unknown (code 2, probability $p_{2|B}$). The model can be reparameterized to exhibit the probability β that an encountered breeder is encountered in breeding activity. Then, $p_{1|B} = p_B \times \beta$ and $p_{2|B} = p_B \times (1 - \beta)$. It is then possible to write the initial-event distribution matrix B_t^0 as

$$B_t^0 = \begin{pmatrix} \beta & 0 & 0 \\ 1 - \beta & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}_t.$$

This formulation also makes it possible to constrain breeders and nonbreeders to share the same probabilities of encounter ($p_{NB} = p_B$). This model can easily be refined to account for more or less reliable clues about breeding activity. For instance, a bird seen bringing food back to a colony is a strong, although maybe not conclusive, indication that it is feeding young. Presence at a breeding colony is another indication of that animal breeding. However, the two clues may not carry the same level of evidence and are perhaps better treated as two separate events for which the conditional probabilities of occurrence given the underlying state may differ substantially.

3.3 The Memory Model

This is the generalization of the AS model where transition probabilities from t to $t + 1$ depend on the state at time $t - 1$. In the absence of knowledge of the state occupied at $t - 1$, there is uncertainty as to which transition should apply and

the multistate framework is thus not appropriate. Brownie et al. (1993) have proposed a partial likelihood procedure based on the capture histories with at least two successive known states. The complete treatment considers that the relevant states are the pairs of successive ‘‘states.’’ To avoid confusion, let us suppose that we are dealing with geographical locations called sites. It is thus the pairs of successive sites, which are relevant. With two sites, C and D , the state set E is formed of seven states: $\{CC, CD, DC, DD, C\dagger, D\dagger, \dagger\dagger\}$, the current location coming second. The location currently observed constitutes the event: $\Omega = \{\text{seen in } C \text{ (code 1), seen in } D \text{ (code 2), not seen (code 0)}\}$. With p_C (respectively p_D) the probability of encounter of an animal currently at site C (respectively D), and ϕ_{uvw} the probability of transition from v to w for an animal previously at site u , the parameters of the model are

$$B_t = \begin{pmatrix} p_C & 0 & p_C & 0 & 0 & 0 & 0 \\ 0 & p_D & 0 & p_D & 0 & 0 & 0 \\ 1 - p_C & 1 - p_D & 1 - p_C & 1 - p_D & 1 & 1 & 1 \end{pmatrix}_t,$$

$$B_t^0 = \begin{pmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 & 1 \end{pmatrix}_t,$$

$$\pi_t = (\pi_{CC}, \pi_{CD}, \pi_{DC}, 1 - \pi_{CC} - \pi_{CD} - \pi_{DC}, 0, 0, 0)_t.$$

3.4 The JMV Model

The JMV model is another generalization of the AS model. This time, it is the encounter probability which is allowed to depend on the site occupied at $t - 1$. The solution is similar to that for the memory model in terms of states to consider. Again, assuming for clarity that we are dealing with two geographical sites, the states in the multievent formalization are $E = \{CC, CD, DC, DD, C\dagger, D\dagger, \dagger\dagger\}$, and the event set is $\Omega = \{\text{seen in } C \text{ (code 1), seen in } D \text{ (code 2), not seen (code 0)}\}$. The parameters of the model are

$$\Phi_t = \begin{pmatrix} \phi_{CC} & \phi_{CD} & 0 & 0 & 1 - \phi_{CC} - \phi_{CD} & 0 & 0 \\ 0 & 0 & \phi_{DC} & \phi_{DD} & 0 & 1 - \phi_{DC} - \phi_{DD} & 0 \\ \phi_{CC} & \phi_{CD} & 0 & 0 & 1 - \phi_{CC} - \phi_{CD} & 0 & 0 \\ 0 & 0 & \phi_{DC} & \phi_{DD} & 0 & 1 - \phi_{DC} - \phi_{DD} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}_t,$$

$$B_t = \begin{pmatrix} p_{CC} & 0 & p_{DC} & 0 & 0 & 0 & 0 \\ 0 & p_{CD} & 0 & p_{DD} & 0 & 0 & 0 \\ 1 - p_{CC} & 1 - p_{CD} & 1 - p_{DC} & 1 - p_{DD} & 1 & 1 & 1 \end{pmatrix}_t,$$

$$B_t^0 = \begin{pmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 & 1 \end{pmatrix}_t,$$

$$\boldsymbol{\pi}_t = (\pi_{CC}, \pi_{CD}, \pi_{DC}, 1 - \pi_{CC} - \pi_{CD} - \pi_{DC}, 0, 0, 0)_t.$$

It is possible to combine the memory and the JMV model.

4. A Numerical Example

Owing to its importance, I illustrate the general method with an application of the memory model to the study of transitions between wintering sites of Canada geese (see Hestbeck et al., 1991 for details of the study). The data are the same as those used in the partial likelihood approach of Brownie et al. (1993). For the sake of comparison, I have calculated, under the full likelihood of Section 3.3, the MLEs of the interannual transitions between the mid-Atlantic (M) and the Chesapeake (C) regions from bandings or resightings taking place in the years 1984–1989 (Brownie et al., 1993, Table 8). The likelihood has been directly optimized using a quasi-Newton algorithm. The parameters were maintained within range by a combination of the continuation ratio method (see, for instance, McCullagh and Nelder, 1983, p. 103–104) and logit transformations. The program is written in MATLAB (Hanselman and Littlefield, 2000). The program and a document describing the program in detail are available at <ftp://ftp.cefe.cnrs.fr/biom/Soft-CR/Memnon/>. The memory model for the Canada goose data converges in approximately 1 minute on a PC with a 1.5-GHz processor.

In Table 1, it can be seen that there is generally good agreement between the two analyses, with occasional discrepancies.

Although the precision is enhanced with the full likelihood, the increase is not great.

The encounter probabilities are relatively well estimated while the initial state probabilities appear imprecise (Table 2). The parameters relative to the first year (initial-state probabilities) and last year (encounter and initial-state probabilities) or to the first and last intervals (transition probabilities) are not estimable without additional assumptions. In particular, only the product of a last transition probability by the encounter probability at the site of arrival $(\phi_{uw})_{T-1} \times (p_w)_T$ is estimable. For the initial-state probabilities of each occasion, the situation is more complex. The sum of the estimates of the probabilities of the states sharing the same current site is always equal to the proportion among the newly encountered individuals that start from this particular site at this particular occasion. For instance, $\pi_{.C} = \pi_{CC} + \pi_{MC}$ at occasion 2 is estimated as the proportion among the individuals newly encountered at occasion 2 that are encountered at site C (Chesapeake). This suggests the following reparameterization of $\boldsymbol{\pi}_t$: $(\pi_{.C}\alpha_{CC}, \pi_{.C}(1 - \alpha_{CC}), (1 - \pi_{.C})\alpha_{CM}, (1 - \pi_{.C}) \times (1 - \alpha_{CM}), 0, 0, 0)_t$. With this new parameterization, it can be shown that the likelihood factorizes into a term involving only the $\pi_{.C}$'s and a term involving only the other parameters. The first term is the product of the $\pi_{.C}$'s and $1 - \pi_{.C}$'s occasion by occasion with each time the number of individuals starting from C or M, respectively, as exponents. It is optimized by the proportions indicated above. The α_{CC} 's and α_{CM} 's are not estimable at the first and last occasions.

5. Discussion

As well as providing a solution to the problem of uncertain states, the multievent approach presented here shows that the CR models belong to the family of hidden Markov models (HMMs) (see, for instance, MacDonald and Zucchini, 1997). More precisely, the time-dependent multievent model is a non-homogeneous nonstationary HMM. The link so established opens the way to the importation of new techniques into the field of CR. For instance, the parameters $(\Phi_t, B_t^0, B_t, \boldsymbol{\pi}_t)$ could

Table 1

Estimates of annual transition probabilities under the memory model for Canada geese wintering in the mid-Atlantic (M) and Chesapeake (C) regions (estimated standard errors in parentheses). Previous estimates obtained with a partial likelihood by Brownie et al. (1993) are given between brackets [] for comparison.

Annual interval t to $t + 1$	Transition made in t to $t + 1$	Estimated transition probability if	
		Location at $t + 1 =$ location at $t - 1$	Location at $t + 1 \neq$ location at $t - 1$
1985–1986	MM	0.59 (0.05) [0.57 (0.05)]	0.44 (0.06) [0.38 (0.07)]
	MC	0.24 (0.07) [0.22 (0.07)]	0.05 (0.03) [0.04 (0.02)]
	CM	0.30 (0.07) [0.34 (0.09)]	0.06 (0.01) [0.05 (0.01)]
	CC	0.63 (0.03) [0.66 (0.04)]	0.35 (0.07) [0.21 (0.09)]
1986–1987	MM	0.58 (0.03) [0.58 (0.04)]	0.29 (0.04) [0.31 (0.05)]
	MC	0.28 (0.03) [0.37 (0.06)]	0.07 (0.02) [0.06 (0.02)]
	CM	0.12 (0.04) [0.13 (0.04)]	0.05 (0.01) [0.03 (0.01)]
	CC	0.67 (0.03) [0.67 (0.03)]	0.51 (0.05) [0.42 (0.06)]
1987–1988	MM	0.54 (0.04) [0.54 (0.04)]	0.27 (0.05) [0.27 (0.05)]
	MC	0.28 (0.03) [0.31 (0.06)]	0.15 (0.02) [0.14 (0.02)]
	CM	0.22 (0.04) [0.22 (0.04)]	0.05 (0.01) [0.03 (0.01)]
	CC	0.59 (0.02) [0.59 (0.03)]	0.59 (0.05) [0.51 (0.06)]

Table 2

Estimates of encounter and initial-state probabilities under the memory model for Canada geese wintering in the mid-Atlantic (M) and Chesapeake (C) regions (estimated standard errors in parentheses)

Encounter probabilities				
Site	1985	1986	1987	1988
M	0.67 (0.05)	0.48 (0.03)	0.52 (0.02)	0.52 (0.03)
C	0.43 (0.02)	0.35 (0.01)	0.37 (0.01)	0.39 (0.01)
Initial-state probabilities				
State	1985	1986	1987	1988
MM	0.06 (0.11)	0.09 (0.05)	0.01 (0.07)	0.06 (0.04)
MC	0.06 (0.04)	0.14 (0.10)	0.10 (0.04)	0.13 (0.06)
CM	0.29 (0.12)	0.32 (0.06)	0.36 (0.08)	0.21 (0.04)
CC	0.59 (0.05)	0.45 (0.09)	0.53 (0.05)	0.60 (0.03)

be estimated using the Baum–Welch algorithm (Baum and Petrie, 1966), which is essentially an EM algorithm. However, the direct optimization of the likelihood seems preferable to Baum–Welch when it is easy to implement and works well as here (MacDonald and Zucchini, 1997, Chapter 2.7). Potentially more interesting is the determination of the most likely state trajectory with the Viterbi algorithm (Rabiner and Juang, 1993). A possible application is the estimation of the cumulative reproductive success of an animal with a particular capture history when the model for studying breeding propensity (Section 3.2) is being applied. In an HMM, it is also possible to calculate the probabilities of the final states. This may serve to determine the probability that an animal is alive by the end of the study, or the probability that an animal is a female when sex is derived from imperfect clues. In relation to the determination of sex, it may be worth noting that the use of continuous measures, such as biometrical measures, can perfectly be accommodated within the multievent framework. The only modification consists in replacing the conditional event probabilities b_{ij} 's with conditional densities.

Another remark is that the classical multistate CR analyses ignore a piece of information uncovered by the treatment of the AS model as a particular case of the time-dependent multievent model (Section 3.1), namely, that leading to the estimation of initial-state probabilities. These probabilities may prove useful. For instance, under the assumption of similar encounter probabilities of newly marked and previously marked animals, the initial-state probabilities can be rewritten so as to yield the proportions in each state in the unmarked component of the population. In turn, this may be interesting as an estimate of, say, the proportion of the population occupying each site in a multisite study, or the sex ratio when sex is to be estimated.

Another aspect is the flexibility of these models. Groups, age, and covariables can be introduced in a straightforward manner. For instance, an age structure is already naturally present due to the conditioning on the initial encounter. The two event distribution matrices of Sections 2 and 3, B_i and

B_i^0 , which coexist at the same date, do correspond to two different age classes. This can easily be generalized. The state (E) and event (Ω) sets themselves may vary by group, age, or time. The best example is probably provided by seasonal studies. For a population monitored during the breeding and the wintering seasons, the states taken into consideration may be “breeder” and “nonbreeder” during the breeding season but the particular wintering site occupied during the wintering season. As for the event sets, they will probably differ, being related to breeding activities during one season and to wintering activities during the other. An example of an age-dependent state set is in fact available in the time-dependent multievent model itself. Again due to the conditioning on the time of first encounter, the nonobservable states (including the state “dead”) are ruled out as initial states. For all practical purposes, the initial state set, E^0 , is thus a reduced state set. As a last illustration of the potential of the multievent framework, let us consider a way of dealing with the very common phenomenon of capture heterogeneity. Often capture heterogeneity can be treated by the consideration of a fixed limited number of catchability classes (see, for instance, Pledger, Pollock, and Norris, 2003). This approach can be cast within the multievent framework by treating the catchability classes as hidden frozen states with distinct probabilities of encounter. A byproduct of this formulation is that the initial-state probabilities, corrected for encounter probabilities and the proportion of marked animals in the population, produce an estimate of the proportion of each class in the population.

The multievent models are thus easy to design and to fit. However, they have potentially many parameters and identifiability is an issue. For instance, in Section 4, the parameters of the memory model at the first and last time steps were not estimable. It is unclear whether the number of events should be limited in relation to the number of states. Formal tools have been developed for the study of redundancy in multinomial models (Catchpole and Morgan, 1997). Their application to multistate models relied on the product multinomial structure embodied in the m -array summarization of the data (Gimenez, Choquet, and Lebreton, 2003). This summarization does not carry over to the multievent models. Thus, only the multinomial distribution of animals over the different encounter histories remains available for an application of the general method. In practice, this may prove prohibitively difficult due to the high number of potential encounter histories. It may thus be that we are, at least temporarily, back to the study of individual models one at a time. The question of the assessment of fit, which has received a specific treatment only recently for multistate models (Pradel, Wintrebert, and Gimenez, 2003), is another open issue.

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REFERENCES

- Arnason, A. N. (1972). Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* **13**, 97–113.
- Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology* **15**, 1–8.
- Baum, L. E. and Petrie, T. (1966). Statistical inference for probabilistic functions of finite state Markov chains. *Annals of Mathematical Statistics* **37**, 1554–1563.
- Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H., and Hestbeck, J. (1993). Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* **49**, 1173–1187.
- Catchpole, E. A. and Morgan, B. J. T. (1997). Detecting parameter redundancy. *Biometrika* **84**, 187–196.
- Dupuis, J. A. (1995). Bayesian estimation of movement and survival probabilities from capture–recapture data. *Biometrika* **82**, 761–772.
- Fujiwara, M. and Caswell, H. (2002). Estimating population projection matrices from multi-stage mark-recapture data. *Ecology* **83**, 3257–3265.
- Gimenez, O., Choquet, R., and Lebreton, J.-D. (2003). Parameter redundancy in multistate capture–recapture models. *Biometrical Journal* **45**, 704–722.
- Hanselman, D. and Littlefield, B. R. (2000). *Mastering MATLAB 6*. Englewood Cliffs, New Jersey: Prentice Hall.
- Hestbeck, J. B., Nichols, J. D., and Malecki, R. A. (1991). Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* **72**, 523–533.
- Kendall, W. L., Hines, J. E., and Nichols, J. D. (2003). Adjusting multistate capture–recapture models for misclassification bias: Manatee breeding proportions. *Ecology* **84**, 1058–1066.
- Lebreton, J.-D. (1995). The future of population dynamic studies using marked individuals: A statistician’s perspective. *Journal of Applied Statistics* **22**, 1009–1030.
- Lebreton, J.-D. and Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics* **29**, 353–369.
- Lebreton, J.-D., Alméras, T., and Pradel, R. (1999). Competing events, mixture of information and multistrata recapture models. *Bird Study* **46**, 39–46.
- MacDonald, I. L. and Zucchini, W. (1997). *Hidden Markov and Other Models for Discrete-Valued Time Series*. London: Chapman and Hall.
- McCullagh, P. and Nelder, J. A. (1983). *Generalized Linear Models. Monographs on Statistics and Applied Probability*. London: Chapman and Hall.
- Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L., and Link, W. A. (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology* **75**, 2052–2065.
- Pledger, S., Pollock, K. H., and Norris, J. L. (2003). Open capture–recapture models with heterogeneity: I. Cormack–Jolly–Seber model. *Biometrics* **59**, 786–794.
- Pradel, R., Wintrebert, C., and Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason–Schwarz multisite capture–recapture model. *Biometrics* **59**, 43–53.
- Rabiner, L. R. and Juang, B.-H. (1993). *Fundamentals of Speech Recognition*. Englewood Cliffs, New Jersey: Prentice Hall.
- Schwarz, C. J. and Seber, G. A. (1999). Estimating animal abundance: Review III. *Statistical Science* **14**, 427–456.

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