

WILD 502 - Multi-state models for live recaptures

(Closely follows the text on pages 454-468 of the *Williams et al.* book)

We recently reviewed *multiple age* models, which can be viewed as special cases of multi-state models. Animals change age (i.e., a state) in a deterministic manner. In other types of multi-state models, changes among states are probabilistic.

Multi-state models are a generalization of the CJS model that allow individuals to be distributed across a number of sites or phenotypic states. Thus, multi-state models consider the probabilities of transitions between or among states. Many interesting questions relate to (1) transition probabilities among states and (2) state-specific vital rates. Examples exist in evolutionary biology (trade-offs), metapopulation biology, and population & habitat management.

As a starting point for considering the transition probabilities, you need to have a basic understanding of a *Markov chain*. Here, we will consider a first-order Markov process or Markov chain. In a first-order Markov process, an animal's state at time $i+1$ depends only on its state at time i . That is, its states at earlier times do not influence the probability that it will change states between i and $i+1$. Andrei Markov was a Russian mathematician who was the first to study matrices of transition probabilities. The probabilities consider all possible combinations of transitions between or among a finite set of states.

		Time $i+1$		
		Fragmented	Intact	Sum
Time i	Fragmented	0.6	0.4	1
	Intact	0.3	0.7	1

		Time $i+1$			
		A	B	C	Sum
Time i	A	0.7	0.2	0.1	1
	B	0.6	0.3	0.1	1
	C	0.7	0.2	0.1	1

As with other data types you've encountered in the course, you estimate the parameters based on Model structure and the number of animals with each of the observable capture histories, e.g., 3 occasions and 2 states for animals Released from state 2 on occasion 1: x_{222} , x_{221} , x_{220} , x_{212} , x_{211} , x_{210} , x_{202} , x_{201} , x_{200} .

Be sure that you review and understand Table 17.17 (page 456) and Figure 17.3 (page 457) of *Williams et al.*

TABLE 17.17 Multistate m_{ij}^z -Array Representation for Data Resulting from a Four-Period Capture-Recapture Study on a Population with Three States^a

Release period i	State of release r	Number released	Period of first recapture j (state of recaptures)								
			2			3			4		
			1	2	3	1	2	3	1	2	3
1	1	R_1^1	m_{11}^{11}	m_{12}^{11}	m_{13}^{11}	m_{11}^{21}	m_{12}^{21}	m_{13}^{21}	m_{11}^{31}	m_{12}^{31}	m_{13}^{31}
1	2	R_1^2	m_{11}^{12}	m_{12}^{12}	m_{13}^{12}	m_{11}^{22}	m_{12}^{22}	m_{13}^{22}	m_{11}^{32}	m_{12}^{32}	m_{13}^{32}
1	3	R_1^3	m_{11}^{13}	m_{12}^{13}	m_{13}^{13}	m_{11}^{23}	m_{12}^{23}	m_{13}^{23}	m_{11}^{33}	m_{12}^{33}	m_{13}^{33}
2	1	R_2^1				m_{11}^{21}	m_{12}^{21}	m_{13}^{21}	m_{11}^{31}	m_{12}^{31}	m_{13}^{31}
2	2	R_2^2				m_{11}^{22}	m_{12}^{22}	m_{13}^{22}	m_{11}^{32}	m_{12}^{32}	m_{13}^{32}
2	3	R_2^3				m_{11}^{23}	m_{12}^{23}	m_{13}^{23}	m_{11}^{33}	m_{12}^{33}	m_{13}^{33}
3	1	R_3^1							m_{11}^{31}	m_{12}^{31}	m_{13}^{31}
3	2	R_3^2							m_{11}^{32}	m_{12}^{32}	m_{13}^{32}
3	3	R_3^3							m_{11}^{33}	m_{12}^{33}	m_{13}^{33}

^a R_i^z denotes the number of animals in state z that are released at time i ; m_{ij}^z denotes the number of members of R_i^z that are next captured at time j and found to be in state z at that time.

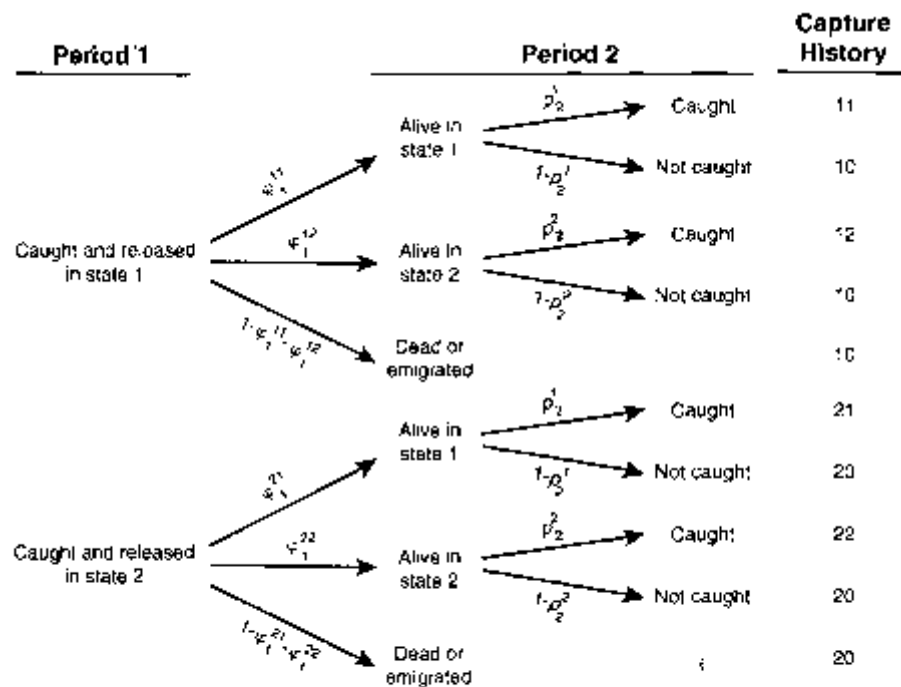
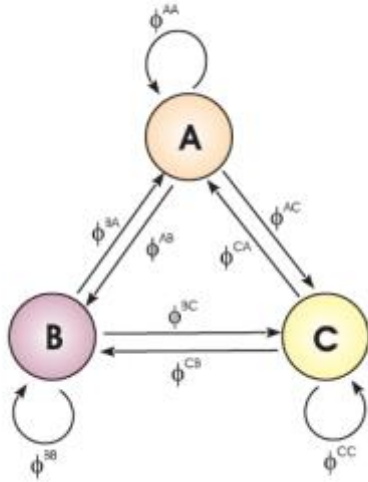


FIGURE 17.3 Tree diagram of events and associated probabilities for animals released in period 1 from both locations of a two-location, two-period study under the Amason-Schwarz multistate model.

Parameters of the multi-state are similar to those of single-state models but now ϕ and p are state-specific rates and ϕ incorporates transition probabilities.

ϕ_i^{rs} = Probability of being alive & in state s at time $i+1$ given that you were in state r at time i . It considers both survival & transition = survival-transition probability.



Pr[11020 | released at occasion 1] =

$$\phi_1^{11} \cdot p_2^1 \cdot [\phi_2^{11} \cdot (1 - p_3^1) \cdot \phi_3^{12} \cdot p_4^2 + \phi_2^{12} \cdot (1 - p_3^2) \cdot \phi_3^{22} \cdot p_4^2] \cdot (1 - \phi_4^{22} \cdot p_5^2 - \phi_4^{21} \cdot p_5^1)$$

I think you can see how 0's in the Encounter Histories create complicated probability statements! But ... you are still just considering the possible ways in which the encounter history could arise.

Often you will want to decompose the ϕ_i^{rs} into its components: S_i^r & ψ_i^{rs}

S_i^r = Probability that an animal in state r at time i survives and remains in the study population until time $i+1$. Survival depends only on your state at time i .

This is appropriate for some situations, e.g., movement occurs near the end of the interval *or* most of the mortality in the interval occurs while the animal is in the previous state *or* most of the mortality in the interval is due to the previous state. Of course it will not be appropriate for all situations.

ψ_i^{rs} = Probability that an animal is in state s at time $i+1$ given that it was in state r at time i and that it survived to time $i+1$ and stayed in the study population.

Decomposition of ϕ_i^{rs} into its components S_i^r & ψ_i^{rs} is done by $\phi_i^{rs} = S_i^r \cdot \psi_i^{rs}$.

Analysis on the composite ϕ_i^{rs} or the components S_i^r & ψ_i^{rs} are equivalent and both contain the same number of parameters. Consider the survival and transition parameters to be estimated for the 1st interval of a study with 2 states:

1. $\phi_1^{11}, \phi_1^{12}, \phi_1^{22}, \phi_2^{21}$

2. $S_1^1, \psi_1^{12}, S_1^2, \psi_1^{21}$ Remember: $1 - \psi_1^{12} = \psi_1^{11}$ and $1 - \psi_1^{21} = \psi_1^{22}$

To estimate the parameters of multi-state models, you can use capture history data (Program MARK) or m_{ij} array (MSSURVIV).

MARK by default treats $\psi_i^{rr} = 1 - \sum_{s \neq r} \psi_i^{rs}$ and works with the components S_i^r & ψ_i^{rs} . But

MARK now does allow you to choose which ψ_i^{rs} to obtain by subtraction.

MSSURVIV is flexible for both of these features though a bit less user-friendly. M-SURGE also handles these models and was specifically designed for this data type. E-SURGE is even more flexible and allows for state uncertainty.

The time-dependent model described here, considered in MARK, and covered by Williams et al. is the Arnason-Schwarz model. There is also a Jolly Movement model (JMV model) that allows p_i to depend on state at time i and $i-1$.

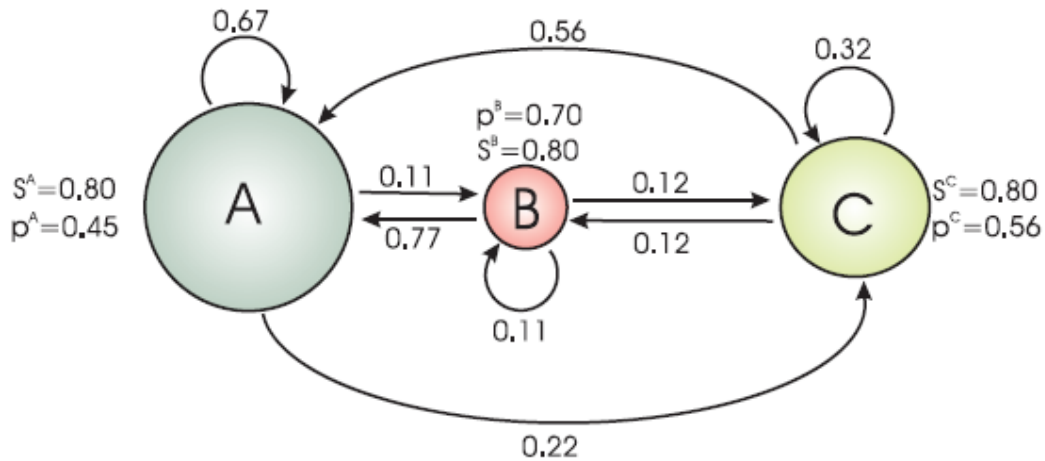
As you have seen for other data types in the course, you can develop competing models that: (1) reduce the number of parameters considered, i.e., test for state- and time-specificity in the rates; (2) use covariates, i.e., attributes of groups, age, individual characteristics. For example, when modeling the transition probabilities among sites, it is sometimes useful to consider the distance between sites (with the design matrix in MARK). This can greatly reduce the number of parameters that need to be considered and can be interesting biologically.

model	description
$S^r p^s \phi^s$	general model - all groups (strata) different - constant over time
$S p^s \phi^s$	constant survival - group difference in recapture and movement
$S^r p^s \phi^s$	constant recapture - group differences in survival and movement
$S^r p^s \psi$	constant movement (inter-island all equal) - group differences in survival and recapture
$S^{quality} p^s \phi^s$	survival constrained to be a function of island quality - group differences in recapture and movement
$S^r p^{size} \psi^s$	recapture constrained as a function of island size - group differences in survival and movement
$S^r p^s \psi^{distance}$	inter-island movement a function of inter-island distance - group differences in survival and recapture
$S p^{size} \psi^{distance}$	recapture a function of island size, movement a function of inter-island distance - constant survival
$S^{quality} p^{size} \psi^{distance}$	survival a function of island quality, recapture a function of island size, and inter-island movement a function of inter-island distance

Goodness-of-Fit can now be evaluated using U-Care using extensions of what you saw under the CJS section of the course. We won't go into the details in this course.

In some situations, you cannot defend only considering that transitions follow a 1st-order Markov process. More complex models can be evaluated for this process under those circumstances. For example, you may wish to consider a 2nd-order Markov chain or memory model whereby the values of ψ_i^{rs} depend on the state at time i and $i-1$. A paper on Canada geese by Hestbeck et al. is a nice example of the use of 2nd-order models.

Multi-state methods are very important and can provide a variety of meaningful estimates.



Multinomial logit link (mlogit)

When you have >2 states, you can run into estimation problems for some of the state transitions. For example, for a scenario with states A, B, and C, imagine that you estimate $\psi(AA)$ by subtraction, i.e., $\psi(AA) = 1 - \psi(AB) - \psi(AC)$, and that estimated rates for $\psi(AB)$ and $\psi(AC)$ are 0.53 and 0.49, respectively, such that $\psi(AA)$ is estimated as -0.02, which isn't possible for the actual transition. Program MARK allows you to use the "mlogit" link function for state transitions, which prevents such a problem. The sidebar in chapter 10 of C&W on the multinomial logit link, which begins on page 10-23, provides the details of how this link function works and how to implement it in MARK. If you are doing multistate modeling, you should be aware of the potential issue and solution with state transitions being estimated as <0.

Problematic likelihood surface

As explained in chapter 10 of C&W (see page 10-40), multi-state models can have some challenging numerical estimation problems. The chapter provides information on the root of such problems and ideas on how to avoid such problems. In particular, they note that an issue that can arise for this data type is that the likelihood surface can have multiple peaks (multi-modal), which can make it difficult to find the true maximum likelihood estimates (the standard algorithm can find a local maximum, i.e., smaller peak surrounded by lower spots in the likelihood surface, rather than the global, or true, maximum). (Note if you think about minimizing the $-2\ln L$ value, you then think of trying to find the global minimum value and worry about getting stuck at local minima). Providing the model with starting values from a simpler model can help. Also, a technique called *simulated annealing*, which is slower as it requires many evaluations of the likelihood surface to arrive at final estimates, can be used. It handles the problem by periodically making random jumps to new parameter values as part of the routine. It can be a good idea to try this alternate approach before reporting final values from multi-state models.

Interesting uses of multi-state models

It is possible to use multi-state models for some common problems in studies of wild animals. Imagine a scenario where you are radio-tracking animals every week for known-fate type data, but occasionally fail to find all the animals, e.g., perhaps bad weather prevents completing a telemetry flight). One can use a multi-state model with states live and dead to model such data. The key is to realize that (1) you can fix the survival parameter (S) to 1.0, (b) you estimate survival rate using the ψ that corresponds to transitioning from the live state to the dead state, and (c) that you can fix the probability of transitioning from the dead state to the live state as 0. This approach allows for imperfect detection of animals in either live or dead states despite the use of telemetry.

The approach above can be generalized to handle multiple causes of death, e.g., natural and human-caused. Again, you can fix $S = 1.0$ and estimate the probabilities of transitioning from the live state to each of the dead states as well as the probability of remaining in the live state (i.e., your estimate of survival rate). This class of models is very flexible and powerful and well worth learning how to use well.