

CHAPTER 14

The multi-state Jolly-Seber model

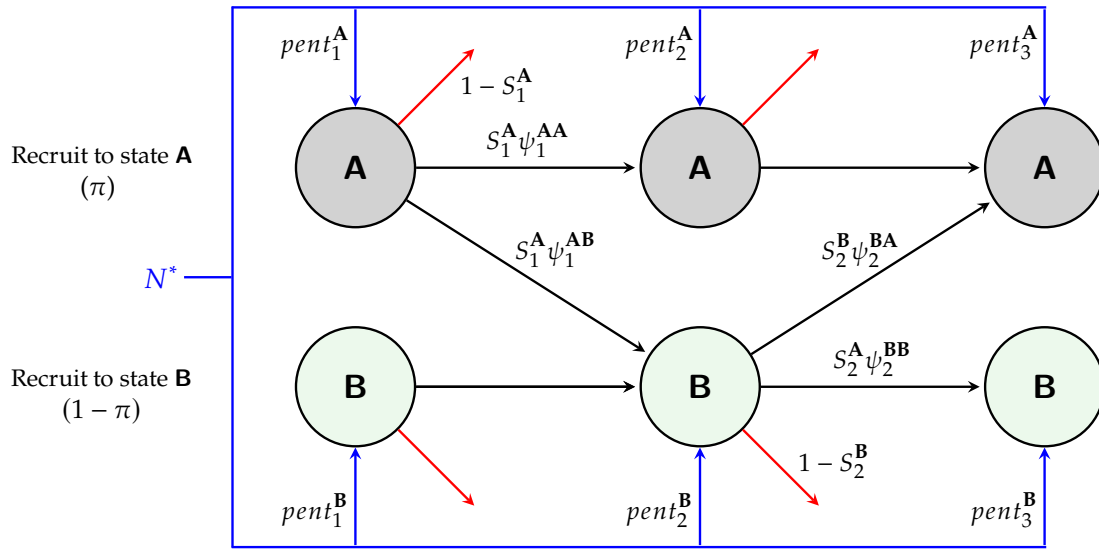
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In Chapter 10 the multi-state model was presented, conditioning on the first capture of an individual and then tracking its fate and detections through time to estimate state-specific survival probabilities and probabilities of transition among phenotypic states, locations, sub-populations, disease states, etc; all of this while accounting for state-specific detection probabilities. In Chapter 12, Jolly-Seber models were presented. Under the **POPAN** version of this model (Schwarz & Arnason 1996; Chapter 12.3.2), for each individual first detection probabilities are modeled as well as subsequent detections. Part of modeling that first detection is to also model first entry probabilities, which could represent births, immigration, or some other kind of first arrival. Other parameters estimated are total number of individuals in the population during the study, period-specific abundances, and period-specific numbers of new recruits. In this chapter we present how to implement a combination of these two model structures, a multi-state Jolly-Seber (MSJS) model (similar to Dupuis & Schwarz 2007).

14.1. Sampling protocol and model structure

The idea behind this model is illustrated in the diagram shown at the top of the next page. It represents a system with two states, **A** and **B**, modeled over three time periods. N^* individuals will enter the system over those three time periods. Arrows between states represent survival and state transitions and arrows pointing out of the system represent mortality (or permanent emigration from the system). Individuals from this superpopulation recruit to state **A** or **B** with probability π or $(1 - \pi)$, respectively. Those that will recruit to state **A** do so in sampling periods 1, 2, or 3 with probability $pent_1^A$, $pent_2^A$, and $pent_3^A$, respectively, with a similar pattern for state **B**. For each state the $pent$'s sum to 1.0.

For the survival, transition, and detection processes, in addition to state and time dependence we incorporate age (length of time since the individual has recruited to the system) in addition to time. So individuals in state **A** who have been in the system for a sampling periods to date survive with probability $S_t^{A(a)}$, and given survival, remain in state **A** with probability $\psi_t^{AA(a)}$ or transition to state **B** with probability $\psi_t^{AB(a)}$. Individuals in state **B** survive with probability $S_t^{B(a)}$ and given survival, remain in state **B** with probability $\psi_t^{BB(a)}$ or transition to state **A** with probability $\psi_t^{BA(a)}$. Finally, for those in state **A** or **B** during sampling period (t), which have been in the system for a sampling periods, the probability of detection is $p_t^{A(a)}$ or $p_t^{B(a)}$, respectively. Full age and time structure for a parameter would be overparameterized, but this general structure at least allows for restrictive models that incorporate both effects (e.g., survival as a general function of time period and a linear function of time since arrival).



Rather than having N^* as a parameter in the model (i.e., in the model likelihood), we instead condition on those individuals n^* that are detected at least once during the study, with probability p^* , which is a function of all the model parameters listed above.

There are two principal contexts in which this model could be useful. The first is the case where time periods represent seasons or years, and therefore the interpretations of the parameters are as stated, where S denotes survival, $pent$ denotes some kind of recruitment, and N represents annual abundance. The second context is where data are collected across time periods within a season of interest (e.g., at migratory stopover areas, at multiple sea turtle nesting beaches), so that N^* refers to the total number of individuals that used the multiple sites in that season, π is the probability that, e.g., for that season a sea turtle will deposit her first clutch of eggs at beach A; $pent_t^A$ refers to the probability an individual that will deposit that first clutch during sampling period (t), $S_t^{A(a)}$ is the probability that a female that has deposited a clutch at beach A during sampling period (t), and has deposited a previous clutches that season, persists in the system to deposit another clutch during sampling period ($t + 1$), and $\psi_t^{AB(a)}$ is the probability that next clutch will be deposited at beach B. This scenario is an extension of the within-season sampling and modeling described in the multi-state open robust design model (Chapter 16; Kendall *et al.* 2019).

14.1.1. Data

The data structure for this model is identical to the multi-state model of Chapter 10. For each of K sampling periods detections are denoted by a state-specific code (e.g., A, B) and non-detections by a '0'. So, example detection histories for the 2-state, 3-period study might be 'A0B', '0BB', etc. The model structure for these two example histories is shown in the table at the top of the next page.

The expression for p^* is based on summing the probabilities of being detected for the first time in each time period. It gets complex quickly with more time periods and benefits from the use of matrix multiplication. Below is the case for just two time periods:

$$p^* = [\pi \cdot pent_1^A p_1^A + (1 - \pi) pent_1^B p_1^B] + [\pi \{pent_1^A (1 - p_1^A) S_1^A (\psi_1^{AA} p_2^A + \psi_1^{AB} p_2^B) + pent_2^A p_2^A\} + (1 - \pi) \{pent_1^B (1 - p_1^B) S_1^B (\psi_1^{BA} p_2^A + \psi_1^{BB} p_2^B) + pent_2^B p_2^B\}]$$

history	probability expression
A0B	$\left(\pi(pent_1^A) p_1^{A(1)} [\psi_1^{AA(1)} (1 - p_2^{A(2)}) S_2^{A(2)} \psi_2^{AB(2)} + \psi_1^{AB(1)} (1 - p_2^{B(2)}) S_2^{B(2)} \psi_2^{BB(2)}] p_3^{B(3)} \right) / p^*$
0BB	$\left([\pi(pent_1^A) (1 - p_1^{A(1)}) S_1^{A(1)} \psi_1^{AB(1)} + (1 - \pi) pent_1^B (1 - p_1^{B(1)}) S_1^{B(1)} \psi_1^{BB(1)}] p_2^{B(2)} S_2^{B(2)} \psi_2^{BB(2)} p_3^{B(3)} \right. \\ \left. + (1 - \pi) pent_2^B p_2^{B(1)} S_2^{B(1)} \psi_2^{BB(1)} p_3^{B(2)} \right) / p^*$

14.1.2. Estimation

Under this multinomial model we can use maximum likelihood to estimate most parameters of the model. However, as with the Jolly-Seber model, there is confounding of parameters at the beginning and end of the times series. Detection probabilities for time periods 1 and K cannot be estimated without constraints. Estimation of detection probability relies on marked individuals and therefore parameter p_1^s for state s cannot be estimated. In addition, p_K^s is confounded with S_{K-1}^s and ψ_{K-1}^{rs} . In addition, as with the Jolly-Seber model, it's assumed that unmarked and previously marked individuals have the same capture probability.

14.1.3. Derived Parameters

There are a number of derived parameters from **MARK** for the MSJS model, whose variance is developed via the Delta method (Appendix B).

- **Total abundance**

The first is the total number of individuals that are in the system at some time during the study, N^* . The value is not of interest in many cases, especially for a multi-year study. However, this model can be applied to an open multi-state process within a season, such as sea turtles arriving at and moving among various nesting beaches, where N^* refers to the total number of nesters. Regardless, the derivation of this estimator is

$$\hat{N}^* = \frac{n^*}{\hat{p}^*},$$

where n^* is the total number of individuals detected during the study.

- **State-specific, period-specific abundance**

Method 1

Like total abundance, when all states are observable abundance for each state (s) in sampling period (t) can be derived by inflating the count based on detection probability,

$$\hat{N}_t^s = \frac{n_t^s}{\hat{p}_t^s},$$

With total abundance for period (t) derived from the sum over all M states

$$\hat{N}_t = \sum_{s=1}^M \hat{N}_t^s.$$

Method 2

An alternative approach is to derive period- and state-specific abundance from total abundance and then the dynamics of the system thereafter. The general expression is in terms of matrix multiplication (Kendall *et al.*, in prep) but an example would be (ignoring age-dependence for simplicity):

$$\hat{N}_2^B = \hat{N}^* \left[\hat{\pi} \widehat{pent}_1^A \hat{S}_1^A \hat{\psi}_1^{AB} + (1 - \hat{\pi}) \left\{ \widehat{pent}_1^B \hat{S}_1^B \hat{\psi}_1^{BB} + \widehat{pent}_2^B \right\} \right].$$

This approach is useful where there are unobservable states, and therefore Method 1 is not an option.

- **Phenology parameters**

Three additional derived parameters are computed which are most meaningful for the case where the data are collected within a given season. These are expected period of first ingress to the system, expected period of last egress from the system, and expected time of residence in the system. To explain the derivation of these parameters we'll use the simple case of three sampling periods and two states **A** and **B**.

Expected Ingress and Egress Periods

Expected period of arrival to the system (a) would be an average weighted by the probability of first arrival, in either state:

$$a = 1 \cdot (\pi pent_1^A + (1 - \pi) pent_1^B) + 2 \cdot (\pi pent_2^A + (1 - \pi) pent_2^B) + 3 \cdot (\pi pent_3^A + (1 - \pi) pent_3^B).$$

Expected departure period g (meaning, departure immediately after sampling period g) involves a more complicated weighted average accounting for arrival and then departure – for example the case of two time periods:

$$\begin{aligned} g = & 1 \cdot [\pi pent_1^A (1 - S_1^A) + (1 - \pi) pent_1^B (1 - S_1^B)] \\ & + 2 \cdot [\pi \{pent_1^A S_1^A (\psi_1^{AA} (1 - S_2^A) + \psi_1^{AB} (1 - S_2^B)) + pent_2^A (1 - S_2^A)\} \\ & + (1 - \pi) \{pent_1^B S_1^B (\psi_1^{BA} (1 - S_2^A) + \psi_1^{BB} (1 - S_2^B)) + pent_2^B (1 - S_2^B)\}]. \end{aligned}$$

- **Expected Residence Time**

There are two approaches to estimating the expected number of time periods an individual spends in residence in the system (e.g., in either or both states).

Method 1

The first is easily derived once a and g are estimated, and is essentially the difference between the two:

$$(g_i + 1) - a_i.$$

Method 2

The second is applicable only where persistence probability $S_i^{s(a)}$ is independent of state and time, and only dependent on the number of periods since first arrival. As in Kendall *et al.* (2019) expected residence time for a three-period study would be:

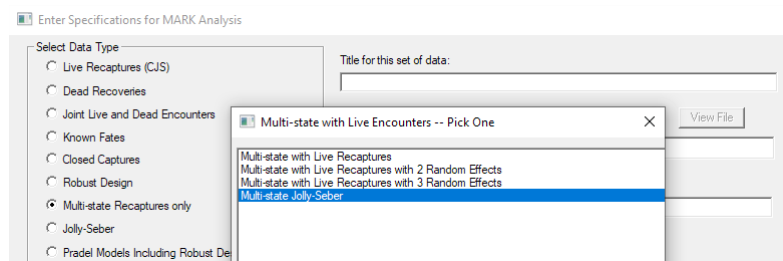
$$[1 \times (1 - S_i^{(0)})] + [2 \times (S_i^{(0)})(1 - S_i^{(1)})] + [3 \times (S_i^{(0)})(S_i^{(1)})].$$

14.2. Implementation of the MSJS model in MARK

To demonstrate implementation of the model we'll use the example of a fish species that exist in two different creeks (**N** and **T**). It's suspected that there is some movement between creeks from year to year, and interest is in annual abundance for each creek, as well as survival and movement. A sample of the data (the complete encounter history data are contained in **fish_stream.inp**) over seven years is

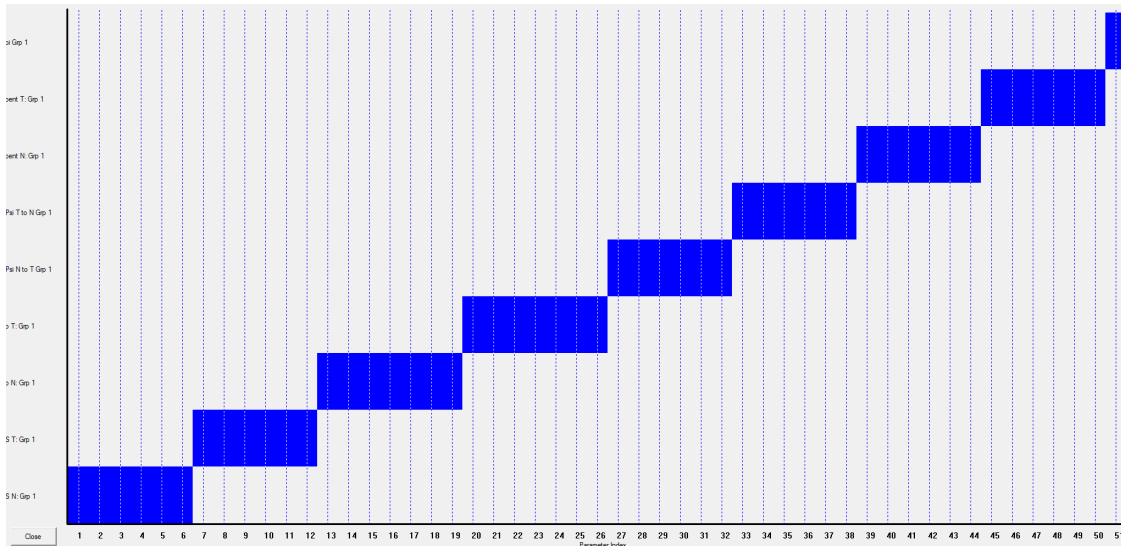
```
0T00000 1;
0T00N00 1;
0T00000 1;
0T0T000 1;
0N00000 1;
0T00000 1;
0T00000 1;
0TT0000 1;
```

In **MARK**, the MSJS model is listed with the other multi-state models:



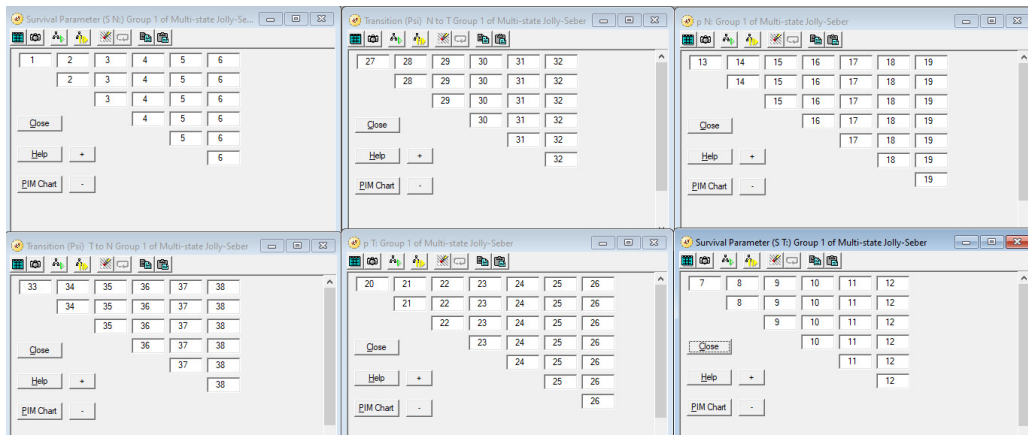
The specification screen for the MSJS model is identical to the MS model (chapter 10):

Looking at the PIM chart for this 2-state, 7-period analysis (below), you can see the various PIMs for this model.



Consistent with the parameter description above there are two PIMs, one for each state, for survival (S), detection (p), state transitions (ψ), and recruitment or ingress ($pent$). Notice also from the chart the number of parameters in each PIM, given there are 7 sampling occasions. For p there are 7 columns, one for each occasion. For S and ψ there are 6 columns, one for each time interval. For $pent$ there are also 6 columns, although there are 7 $pent$'s, one for each time period. Because $pent$'s apply to each individual in the superpopulation, which must enter the system some time during the study, the $pent$'s for each state must sum to 1.0. Therefore there are 6 $pent$'s explicitly estimated, with the 7th not listed, computed by subtracting the sum of the estimated parameters from 1. **MARK** permits you to choose either the first or last $pent$ by subtraction. More about that below. The final parameter π is a single parameter in the case of two states (one flip of the coin to determine which state an individual will eventually recruit to). With $s > 2$ states there would be $(s - 1)$ columns in the π PIM, and as in the case of $pent$, one would be derived by subtraction.

You can see below that the PIMs for ψ , p , and S are triangular rather than a single row like the **POPAN** model from Chapter 12 (because the **POPAN** model only permits time variation on parameters).



This is to allow for age in the parameters. Unlike the PIMs of the multi-state model from Chapter 10, the rows of the PIM are not based on the time since first capture, but the time since entering the system. This entry could be due to birth or immigration. For a within-year study for a migratory species, entry could be due to arrival to the study area (e.g., to breed).

With this model, like with the multi-state model, you can specify which state transition probabilities (which have to add to 1.0) you compute by subtraction of the others from 1. At the top of the screen you would select '**PIM | Change PIM Definitions**', which will lead you to the screen:

You can also designate whether the first or last *pent* for each state is computed by subtraction. After making your choice(s) for which transitions to compute by subtraction, when you click on OK the screen below will appear, and there you choose which *pent* will be computed by subtraction:

Before running a model make sure the link functions for each parameter are appropriate. There are a number of options for most parameters (e.g., Sin, Logit). For those parameters whose values must sum to ≤ 1 you will need to use the '**Mlogit**' link (see Chapters 10, 12, and 16). Below is an example set of link functions for model '**{S(c*.), p(c*.), psiTN(c*.), pent(c*t), pi}**' for the fish example. Since $\sum_{t=1}^K pent_t^N = 1.0$ and $\sum_{t=1}^K pent_t^T = 1.0$, there are separate Mlogit links for each set.

Running model '**{S(c*.), p(c*.), psiTN(c*.), pent(c*t), pi}**', the real estimates of the model parameters for the fish example are shown at the top of the next page. In this case movement is rare from creek $T \rightarrow N$ but apparently does not occur in creek N , and approximately 46% of individuals recruit to creek N .

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Real Function Parameters of {S(c*),p(c*),psiTN(.),pent(c*t),pi PIM}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:S N:	0.5384933	0.0197744	0.4995807	0.5769425
2:S T:	0.5919121	0.0285067	0.5350840	0.6463845
3:p N:	0.1685327	0.0125174	0.1454001	0.1945080
4:p T:	0.0730930	0.0087209	0.0577355	0.0921362
5:Psi N to T	0.7392710E-08	0.5714360E-05	-0.1119275E-04	0.1120754E-04
6:Psi T to N	0.0085913	0.0039296	0.0034960	0.0209567
7:pent N:	0.2516169	0.0132614	0.2265247	0.2784877
8:pent N:	0.2541529	0.0136108	0.2284089	0.2817390
9:pent N:	0.4207359E-23	0.9942147E-16	-0.1948661E-15	0.1948661E-15
10:pent N:	0.1008937	0.0108616	0.0815093	0.1242643
11:pent N:	0.1211070	0.0115416	0.1002439	0.1456094
12:pent N:	0.2464626	0.0128300	0.2221863	0.2724621
13:pent T:	0.5300078	0.0224516	0.4858833	0.5736680
14:pent T:	0.1600354E-22	0.0000000	0.1600354E-22	0.1600354E-22
15:pent T:	0.0126862	0.0226364	0.3718325E-03	0.3074117
16:pent T:	0.1303574	0.0180986	0.0987923	0.1701042
17:pent T:	0.0311927	0.0170593	0.0105365	0.0887134
18:pent T:	0.1466542	0.0166067	0.1169975	0.1822765
19:pi	0.4629684	0.0271680	0.4103377	0.5164375

Output for derived parameters is below. The first section is the estimate of N^* , the total number of individuals in the system over 7 years. In this case we don't associate any particular interpretation to this number.

Estimates of Derived Parameters

Total Abundance Estimates of {S(c*),p(c*),psiTN(.),pent(c*t),pi PIM}

Grp.	N*-hat	Standard Error	95% Confidence Interval	
			Lower	Upper
1	22382.692	1199.3522	20181.374	24890.971

The next section of the derived output contains state-specific annual estimates of abundance using method 1 described above, where $\hat{N}_t^s = n_t^s / \hat{p}_t^s$.

Abundance Estimates of {S(c*),p(c*),psiTN(.),pent(c*t),pi PIM}

Grp.	Str.	Occ.	Abundance	Standard Error	95% Confidence Interval	
					Lower	Upper
1	N	1	267.01066	44.287717	195.73805	371.98267
1	N	2	2760.2721	236.73340	2341.1885	3273.0162
1	N	3	4157.7880	273.27642	3664.0090	4738.0883
1	N	4	2261.0913	204.92974	1897.3608	2703.8370
1	N	5	2276.8652	188.50091	1942.1674	2683.9680
1	N	6	2497.0962	207.45364	2128.1210	2944.3988
1	N	7	3909.9588	312.05931	3354.0522	4581.7793
1	T	1	1792.2352	263.65711	1350.4740	2394.0270
1	T	2	7422.5372	808.23490	6011.1782	9196.2520
1	T	3	4355.7440	617.15611	3317.4798	5758.9987
1	T	4	2708.5585	347.29814	2114.5003	3485.8964
1	T	5	3156.3779	409.69251	2457.9262	4076.2783
1	T	6	2227.1898	299.35621	1718.2058	2901.0564
1	T	7	3069.7892	405.69437	2378.5686	3981.2314

The section of the output that follows contains year-specific estimates of total abundance, summed across states, with precision and confidence interval.

Summed Abundance Estimates of {S(c*),p(c*),psiTN(.),pent(c*t),pi PIM}					
Grp.	Occ.	Abundance	Standard Error	95% Confidence Interval	
				Lower	Upper
1	1	2059.2459	266.86174	1604.5187	2658.7221
1	2	10182.809	835.60255	8685.3018	11971.354
1	3	8513.5320	666.64013	7319.3920	9941.0782
1	4	4969.6498	399.86870	4250.8568	5823.0305
1	5	5433.2431	446.57164	4634.9580	6391.4444
1	6	4724.2860	359.99037	4076.0464	5491.2622
1	7	6979.7480	505.36337	6067.1253	8053.4654

Following this, state- and year-specific estimates of abundance using method 2, where abundance is derived from N^* and state dynamics, are included. In this case this method is not necessary, since fish in each state are captured.

Abundance Estimates without TSA of {S(c*.),p(c*.),psiTN(.),pent(c*t),pi PIM}						
95% Confidence Interval						
Grp.	Str.	Occ.	Abundance	Standard Error	Lower	Upper
1	N	1	267.01049	19.831702	231.41773	309.39900
1	N	2	2765.0420	205.36829	2396.4591	3203.9985
1	N	3	5019.7973	372.83599	4350.6532	5816.7012
1	N	4	1323.1853	98.277100	1146.8034	1533.2439
1	N	5	2343.7588	174.07827	2031.3334	2715.8356
1	N	6	2314.0910	171.87475	2005.6203	2681.4580
1	N	7	4082.2938	303.20469	3538.1199	4730.3669
1	T	1	1792.2375	213.83691	1423.1462	2266.7568
1	T	2	7032.1381	839.02422	5583.9477	8893.9925
1	T	3	4979.9577	594.17280	3954.3910	6298.4694
1	T	4	2585.7473	308.51280	2053.2415	3270.3591
1	T	5	3488.7066	416.24743	2770.2464	4412.3893
1	T	6	2011.1368	239.95440	1596.9656	2543.6126
1	T	7	2859.3713	341.15966	2270.5157	3616.4289

The following section contains total abundance by year, based on method 2.

Summed Abundance Estimates without TSA of {S(c*),p(c*),psiTN(.),pent(c*t),pi PIM}					
Grp.	Occ.	Abundance	Standard Error	95% Confidence Interval	
				Lower	Upper
1	1	2059.2480	214.65324	1683.2955	2528.9713
1	2	9797.1801	862.76879	8261.7491	11656.372
1	3	9999.7550	699.83942	8731.5957	11481.729
1	4	3908.9326	323.30708	3330.4740	4602.0452
1	5	5832.4654	450.35737	5022.2454	6792.8271
1	6	4325.2277	294.44171	3790.6770	4947.6005
1	7	6941.6651	455.26008	6113.1803	7901.7379

The final section of output (shown at the top of the next page) includes estimates for expected ingress (arrival for within season model) period, expected egress (departure for within season model) period, and expected residence time in the system for methods 1 and 2 listed above. Again, these parameters could be of interest for a cross-year study, but are more likely to be of interest in examining phenology and duration of study area use for a given season.

Expected Ingress, Egress, and Residence Times 1&2 {S(c*.),p(c*.),psiTN(.),pent(c*t),pi PIM}				
Grp.	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1	3.6450309	0.0628476	3.5218495	3.7682122
1	4.5600156	0.0535610	4.4550360	4.6649952
1	1.9149848	0.0637151	1.7901032	2.0398663
1	2.1383658	0.0843105	1.9731172	2.3036143

14.3. Summary

The MSJS model in **MARK** should provide a flexible framework for modeling ingress, survival, state transitions, and abundance in a variety of contexts. This includes populations and metapopulations monitored across years, and well as within-year arrival, use, state transitions, and departure for species that use a study area seasonally.

14.4. References

- Dupuis, J. A., and Schwarz, C. J. (2007) A Bayesian approach to the multi-state Jolly-Seber capture-recapture model. *Biometrics*, **63**, 1015-1022.
- Kendall, W. L., Stapleton, S., White, G. C., Richardson, J. I., Pearson, K. N., and Mason, P. (2019) A multi-state open robust design: population dynamics, reproductive effort, and phenology of sea turtles from tagging data. *Ecological Monographs*, **89**, e01329.
- Schwarz, C. J., and Arnason, A. N. (1996) A general methodology for the analysis of capture-recapture populations in open populations. *Biometrics*, **52**, 860-873.