Fast and flexible Bayesian Jolly Seber models and application to populations with

transients

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Abstract

1. Jolly Seber (JS) models are an appealing class of capture-recapture models for

modeling open populations because they allow for inferences about an array of

population parameters, including abundance, survival, and recruitment. Multiple

formulations of JS models have been developed and include both maximum

likelihood and Bayesian approaches. Bayesian approaches offer greater flexibility;

however, they are often extremely slow when applied to moderate to large

populations because the latent states of all observed individuals, as well as any

potential unobserved individuals (parameter-expanded data augmentation), must be

simulated at each time step.

2. JS model implementations can be sped up dramatically through marginalization,

whereby the conditional likelihoods of states are tracked for unique capture histories,

rather than the simulated states of all individuals. Here we describe a marginalized

implementation of a multistate JS model and compare its performance to that of an

implementation using simulated discrete states. We fit models to data generated under

two scenarios, one in which no data was missing and another in which 25% of data

was randomly removed. To illustrate how marginalization can accommodate more

complex models and datasets, we describe a modified version of the model for

application to populations with transients and fit the model to simulated data and to

data collected on Kentucky Warblers (*Geothlypis formosa*) as part of the Monitoring

Avian Productivity and Survivorship (MAPS) program.

3. Both the discrete latent state and marginalized JS model implementations performed

similarly with respect to bias and coverage; however, the marginalized

implementation was roughly 1,000 times faster when no data were missing and 100

times faster when 25% of data was missing. The marginalized model accommodating

transients also converged quickly and a more complex version of the model applied to

the larger multi-site Kentucky Warbler data set yielded useful estimates of most

parameters within a reasonable time frame (hours).

4. Gains in efficiency provided by marginalization shown here should stimulate

additional study and development of this useful class of models and provide new

opportunities for real-world applications to large complex data sets.

keywords: capture-recapture; discrete latent state, Hidden Markov model,

marginalization, Monitoring Avian Productivity and Survivorship, open population,

recruitment, residency, survival, transient model.

Introduction

Open-population capture-recapture models are important tools for estimating

demographic parameters of wildlife populations (Nichols 2005). These models include two

basic classes: (1) Cormack-Jolly-Seber (CJS) models, which condition on first capture and

provide estimates of apparent survival probability (Cormack 1964); and (2) Jolly-Seber (JS)

models (Jolly 1965, Seber 1965), which are informed by entire capture histories (i.e.,

including occasions both prior to and after first capture). JS models are appealing because

they make more complete use of available data and can provide inferences on an expanded

set of demographic parameters including abundance and recruitment-related parameters. JS

models assume that marked and unmarked animals have equal capture probability, which

may limit their applicability in some situations (e.g., mark-resight studies). However, this

assumption is likely reasonable for a broad array of studies that implement the same sampling

protocol for both captures and recaptures (e.g., Robinson et al. 2009).

A variety of formulations of both CJS and JS models have been developed and include

both maximum likelihood and Bayesian approaches (Pradel 1996, Schwarz and Arnason

1996, Link and Barker 2005, Dupuis and Schwarz 2007, Schofield and Barker 2008, Royle

and Dorazio 2012, Tenan et al. 2014, Hostetter et al. 2021). Bayesian implementations offer

several advantages over maximum likelihood methods, including ability to incorporate prior

information, flexibility for handling hierarchical random effects, and relative ease with which

derived quantities and their uncertainties can be calculated. A common Bayesian approach,

known as state-space modeling or discrete latent state modeling (Royle 2008, Yackulic et al.

2020), involves simulating the state of individuals (e.g., alive/dead) and the conditional

probability of their detection based on Bernoulli or categorical models applied to a set of

observed capture histories. For JS models, the data set must be augmented to include a set of

capture histories with no detections that represent individuals never observed to allow for

modeling of both the survival and entry processes (Kéry and Schaub 2011). A drawback of

this approach, however, is that computation times using Markov Chain Monte Carlo

(MCMC) techniques can be prohibitive for many applications, particularly when the

augmented data set includes many individuals or levels of stratification (e.g., sites or spatial

strata).

Bayesian open-population models with discrete latent states can be sped up dramatically

through marginalization (Yackulic et al. 2020). Rather than tracking the state of all

individuals at each time step, these marginalized models only require tracking likelihoods of

possible states given the demographic parameters for a reduced data set of unique capture

histories and their frequencies. Yackulic et al. (2020) provide a thorough introduction to the

marginalization in Bayesian population models, as well as code and examples for CJS

models. Here we extend this work in the context of JS models. We focus on the multistate

expression of the JS model described in Royle and Dorazio (2012), which is readily adaptable

to a variety of model extensions involving additional states (Kéry and Schaub 2011). We

apply the model to simulated complete data sets and data sets with random missing data, a

common scenario in multi-site multi-collaborator data sets (e.g., Saracco et al. 2010), and

compare parameter estimates and run times between the marginalized models and discrete

latent state implementations using the popular open-source software program JAGS

(Plummer 2003).

We also describe an extension of the basic marginalized multistate JS model to

accommodate situations where not all sampled individuals are part of the resident

populations. This model variant can both improve inferences about survival, recruitment, and

population size, as well as allow estimation of residency probability and proportions of

residents in populations (or, conversely, transience probability and proportions of transients),

which may also often be of ecological interest (Wilson et al. 2018, Genovart and Pradel 2019,

Oro and Doak 2020). Accounting for negative bias in survival estimates due to transiency,

and estimation of residency or transiency probabilities, has been treated within the context of

CJS models (Pradel et al. 1997, Nott and DeSante 2002, Hines et al. 2003, Royle and Dorazio

2008, Saracco et al. 2010). However, transiency or residency probability estimates from these

models only apply to newly marked individuals and so may not be representative of the larger

population because they depend, to some extent, on the proportions of previously marked

individuals still alive and available for capture (Hines et al. 2003). Estimation of parameters

related to the dynamics of resident and transient individuals within seasons has been

developed within an 'open robust design' framework (Ruiz-Gutierrez et al. 2016); however,

these models require additional data and model complication that may be unnecessary if

primary interest is on between season dynamics. Treatment of these parameters in the JS

context represents an important advance because it allows for disentangling of season-

specific observation (first capture) and state (residency) processes within a simpler multi-

season open population model.

We apply this 'transient JS' model to simulated data as well as to regional data from a

migratory bird species, Kentucky Warbler (*Geothlypis formosa*), from bird-banding stations

operated as part of the Monitoring Avian Productivity and Survivorship (MAPS) program

(DeSante et al. 2004) in the Central Hardwoods Bird Conservation Region of the United

States (Sauer et al. 2003).

Materials and Methods

Multistate Jolly Seber models: structure and data

Both the discrete latent state and multistate JS model assume a "superpopulation" (*sensu*

Schwarz and Arnason 1996), N_{super} , representing the number of individuals ever alive in the

population. Membership in N_{super} is determined as a function of parameters describing the

entry process and an augmented data set consisting of *M* individuals, including all those

observed during the study, as well as any unobserved individuals that could have been

members of the superpopulation. While the number of unobserved individuals to include in

the augmented data set is somewhat arbitrary, the choice is not innocuous, particularly when

using a discrete latent state implementation – too many and run times will be unnecessarily

increased, too few and parameter estimates may be biased.

Following Kéry and Schaub (2011) and Royle and Dorazio (2012), we model the entry

process in terms of a removal entry probability, γ, which represents the probability of entry

for a member of M conditional on not having previously entered (see Appendix S1 for an

alternative parameterization). Once entered, the probability of remaining alive and in the

population is determined by a survival parameter, ϕ. We can represent the latent state of the

$i = 1, ..., M$ individuals across $t = 0, ..., T$ time periods with a matrix, $\mathbf{S}$, with entries, $s_{i,t}$ that

can take values of: $1 =$ not yet entered into the population, $2 =$ alive and in the population,

and $3 =$ dead. The number of time periods, T, includes all observed sampling occasions as

well as a dummy occasion at $t = 0$ to allow modeling of initial entry into the population. All

$s_{i,0}$ are set equal to 1 to indicate that none have entered prior to the first observed time period

at $t = 1$. The hidden Markov process determining $s_{i,t}$ can be represented with an array, $\mathbf{\Omega}$,

with individual entries $\omega_{j,k,t}$ representing probabilities of transitioning from latent state j

(rows) in time t to latent state k (columns) in time $t + 1$:

141
$$\omega_{j,k,t} = \begin{pmatrix} 1 - \gamma_t & \gamma_t & 0 \\ 0 & \phi_t & 1 - \phi_t \\ 0 & 0 & 1 \end{pmatrix}.$$

The data informing the latent states consist of a set of observed and unobserved (i.e.,

augmented) capture histories and, for the discrete latent state model, can be represented with

a $M \times T$ matrix, $\mathbf{Y}$, with entries $y_{i,t}$. For the marginalized model, the $y_{i,t}$ are summarized to a

more compact matrix, $\mathbf{YS}$, with entries $ys_{m,t}$ that represent $m = 1, ..., MS$ unique capture

histories over the T years. The data informing the marginalized model are then the $ys_{m,t}$ and

their observed frequencies. The entries of $\mathbf{Y}$ and $\mathbf{YS}$ can take values of 1 (captured) or 2s (not

captured). For computational purposes, we set all $y_{i,0} = 2$ and $ys_{m,0} = 2$ for the initial

dummy capture occasion. These capture histories are linked to latent states by a second array,

P, with entries $\rho_{j,o,t}$ indexed by latent state j (rows), observed state o (columns), and period

of observation t (not counting the dummy capture occasion), with time-specific capture

probabilities represented by p_t:

$$\rho_{j,o,t} = \begin{pmatrix} 0 & 1 \\ p_t & 1 - p_t \\ 0 & 1 \end{pmatrix}.$$

The principal difference between the discrete latent state and marginalized JS model

implementations is the definition of the likelihoods. In the discrete latent state model, the true

latent state is simulated for each individual and occasion for all $t > 0$ based on a categorical

model, $s_{i,t} \sim Cat\left(\omega_{z[i,t-1],1:3,t-1}\right)$. The likelihood is then determined based on a categorical

model of the observations conditional on the latent state, $y_{i,t} \sim Cat\left(\rho_{s[i,t],1:2,t}\right)$.

The likelihood for the marginalized JS model is defined in terms of an array, **Z**, which

tracks capture history likelihoods conditional on the demographic parameters. Its dimensions

are defined (in order) by unique capture histories, $t = 0, \dots, T$ sampling occasions (again,

including the dummy occasion at $t = 0$), and $s = 1{:}3$ states. Each entry, $\zeta_{m,t,s}$ is the

likelihood that an individual with capture history m was in state s at time t conditional on the

observed capture history through time t and values of the process and observation parameters.

As in the discrete latent state model, no individuals have entered the population at $t = 0$.

Thus, we set $\zeta_{m,0,1} = 1$ and $\zeta_{m,0,2:3} = 0$ so that all individuals are available prior to the study.

For each subsequent time step, $\zeta_{m,t,s}$ is determined by first taking the inner product of

$\zeta_{m,t-1,1:3}$ and the column vector taken from s^{th} column of the state transition matrix and then

multiplying this quantity by the probability of the observed state given the state s (i.e.,

$\zeta_{m,t,s} = \langle \zeta_{m,t-1,1:3} , \; \omega_{1:3,s,t-1} \rangle \times \rho_{s,o[m,t],t}$. For example, at the first true capture period ($t =$

1), the observation probability for capture histories with capture at that time period (i.e.,

$y_{m,1} = 1$) would be calculated as $\zeta_{m,1,1} = \zeta_{m,0,1} \omega_{1,1,0} \rho_{1,1,1} = 1 \times (1 - \gamma_0) \times 0 = 0$ for

individuals that did not enter (i.e., $s = 1$); $\zeta_{m,1,2} = \zeta_{m,0,1} \omega_{1,2,0} \rho_{2,1,1} = 1 \times \gamma_0 \times p_1 = \gamma_0 p_1$

for individuals that entered (i.e., $s = 2$); and $\zeta_{m,1,3} = \zeta_{m,0,1}\omega_{1,3,0}\rho_{2,1,1} = 1 \times 0 \times 0 = 0$ for

dead individuals (i.e., $s = 3$). Thus, the only possible transition for individuals captured at the

first true capture occasion is entry into the population.

The likelihood of each capture history is determined by summing the likelihoods of all

possible states, s, after the final capture occasion, $\sum_{s=1}^{3} \zeta_{m,T,s}$, weighted by the frequency of

the mth capture history. In BUGS language, as implemented in popular software programs

such as WinBUGS (Lunn et al. 2000), OpenBUGS (Lunn et al. 2009), JAGS (Plummer

2003), and NIMBLE (de Valpine et al. 2017), a modified version of the "ones trick" can be

used to update the posterior with these values. See Yackulic et al. (2020) and Appendix S1

for detail; Yackulic et al. (2020) also provide the appropriate approach to updating the

posterior using the program Stan (Carpenter et al. 2017).

For both the discrete latent state and marginalized models, unconditional time-specific

entry probabilities from the superpopulation to the population, b_t are derived as a function of

the entry probabilities conditional on not having previously entered, c_t, where $c_0 = \gamma_0$ and

$c_t = \gamma_t \prod_{j=0}^{t-1}(1 - \gamma_j)$ for $t \geq 1$, and the inclusion probability (i.e., probability of being a

member of the superpopulation), ψ (Kéry and Schaub 2011): $b_t = c_t/\psi$. In discrete latent

state models, secondary parameters (i.e., derived quantities) can be calculated directly from

the modeled latent states. For example, time-specific numbers of newly entered individuals

(i.e., newborns or immigrants), B_t, can be derived by counting the $z_{i,t} = 2|z_{i,t-1} = 1$, and

total time-specific abundance, N_t, can be calculated by counting the $z_{i,t} = 2$ for each sample

of the posterior distribution.

Alternatively, secondary parameters can be derived as functions of primary (i.e.,

modeled) parameters, other secondary parameters, and/or the input data; and this approach

can be applied to either model type. For example, numbers of new entrants can be estimated

as $B_t = c_t M$, and the superpopulation size, N_{super}, can then be derived as $\sum_{t=0}^{T-1} B_t$ (Schwarz

and Arnason 1996). Time-specific abundance can be estimated as $N_1 = B_0$ for the initial

sampling period and $N_t = B_{t-1} + \phi_t N_{t-1}$ for $t > 1$, or alternatively could be estimated with

the canonical estimator, $N_t = n_t / p_t$, where the n_t represents a count of the number of

individuals observed alive at time t (i.e., summing the frequencies of all $y_{i,t} = 1$ or $ys_{m,t} =$

1). Other quantities of interest that can be derived include population growth rate, $\lambda_t =$

N_{t+1}/N_t, and per capita entry rate, $f_t = B_t/N_t$ (or, alternatively, $f_t = \lambda_t - \phi_t$; Pradel 1996,

Link and Barker 2005). Additional methods for deriving secondary parameters from

marginalized models are also possible. For example, annual abundance can be derived by

simulating latent states from reconstituted individual capture histories (i.e., converting **YS**

back to **Y**) and summing them in a manner analogous to what is described above for the

discrete latent state models (see Appendix S2 for detail).

Marginalized multistate Jolly Seber model with transients

Capture-recapture studies often include individuals that are sampled but are not resident

in the local population. These transient individuals have been defined in the context of CJS

models as individuals having zero probability of being alive and available for capture

following initial capture (Pradel et al. 1997). In the JS context, however, transients can be

defined more generally as individuals appearing only once and never returning to the

sampling area. Thus, interpretation of transience and residency probabilities in the JS context

is more ecologically relevant because it refers to the larger population, not just the population

of newly marked individuals. We can accommodate transiency in the multistate JS model by

adding a state that allows for entry as either a resident or a transient, such that there are now

four possible states, including: 1 = not yet entered; 2 = alive resident; 3 = alive transient; and

4 = dead. Distinguishing between the two alive states requires an extra parameter π, denoting

the probability of being a resident. Thus, individual entries in the transition and capture

probability arrays become:

$$\omega_{j,k,t} = \begin{pmatrix} 1 - \gamma_t & \gamma_t \pi & \gamma_t(1 - \pi) & 0 \\ 0 & \phi_t & 0 & 1 - \phi_t \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix} \text{ and } \rho_{j,o,t} = \begin{pmatrix} 0 & 1 \\ p_t & 1 - p_t \\ p_t & 1 - p_t \\ 0 & 1 \end{pmatrix}.$$

The residency probability parameter, π, is estimated in the marginalized multistate

transient JS model based on $N_i^R \sim Bin(\pi, FR_i)$, where N_i^R is the number of residents

represented by unique capture history i. In some cases, the residency state can be partially

observed. For example, within a 'robust design' sampling framework (Pollock et al. 1990),

whereby multiple secondary sampling occasions are completed within each primary sampling

occasion, individuals observed on multiple secondary sampling occasions during the primary

sampling occasion in which they were marked can be used as an indicator of residency (Nott

and DeSante 2002, Hines et al. 2003). To accommodate this scenario, and following logic

developed for the discrete latent state version of a transient CJS model (Saracco et al. 2010),

we can define an observation model for residency as: $r_i \sim Bin(\kappa, N_i^R)$, where r_i is the

number of observed residents for capture history i, κ is the probability of observing

residency, and N_i^R is the true number of residents for capture history i. Note that in contrast to

the CJS scenario, where residency observation and state probabilities are specific to years of

first capture and allow for temporal modeling, here both κ and π are time-constant.

Nevertheless, we can derive numbers of transients and residents entering the population at

each time step as $B_t^{tr} = c_t * (1 - \pi) * M$ and $B_t^{res} = c_t * \pi * M$, respectively. For transients,

the number of entries is equivalent to the number of transients in the population at any time

step; i.e., $B_t^{tr} = N_t^{tr}$. At $t = 1$, the total number of residents is also the same as the number

of resident entries, $N_1^R = B_1^R$; the number of residents can be derived as $N_t^R = B_t^R + \phi_t *$

N_{t-1}^R for subsequent time steps. The proportion of residents at any given time can then be

derived as $prop(res)_t = N_t^R / (N_t^R + N_t^{tr})$.

A critical assumption of this formulation of the transient JS model is that p_t, the

probability of capture at least once across the season, is the same for both transient and

resident individuals. This is plausible if most individuals enter the population early in the

season and we think of p_t as an initial capture probability, π as the probability of persisting

for multiple sampling periods, and κ as the probability of capturing an individual that persists

for multiple periods. Nevertheless, we acknowledge that in many cases residents and

transients will have differential exposure to capture, resulting in violations of the assumption

of equal p_t between these two groups. Accounting for these differences can be

accommodated with additional model development and data from secondary samples within

seasons (e.g., Ruiz-Gutierrez et al. 2016). For simplicity, we do not consider this additional

complication here.

Discrete v. marginalized multistate JS models: a simulation study

To compare the relative speed and efficacy of discrete latent state and marginalized JS

models, we simulated 100 capture-recapture data sets. As in Kéry and Schaub (2011), we

assumed a superpopulation size of $N_{super} = 400$ across $T - 1 = 7$ capture occasions, a

constant survival probability of $\phi = 0.70$, entry probabilities of $b_1 = 0.34$ and $b_{2...7} = 0.11$,

and a constant capture probability of $p = 0.50$. We assumed $U(0,1)$ prior distributions for

survival, ϕ, capture probability p, and entry probabilities b_t. Data sets were augmented with

500 all-ones capture histories to account for unobserved individuals for a total of M capture

histories (observed + unobserved). These individual capture histories made up the basic data

sets for the discrete latent state JS model, an $M \times T$ matrix, where T represents the number of

sampling occasions, including the dummy occasion. For the marginalized model, data sets

(including the augmented individuals) were aggregated to MS unique observed capture

histories and their frequencies.

To explore potential effects of missing data, we randomly assigned 25% of the

individual × capture occasion data generated in the simulated data sets to be missing. For the

marginalized models, capture histories were then collapsed to unique capture history × effort

(missing or not). Missing data in the two model types are handled differently. For the discrete

latent state models, missing data values are imputed with the categorical models of the state

and observation process in the same way they are for the complete data situations, which

should result in relatively little increases in model run times. However, for the marginalized

models, where state and capture probabilities are tracked with deterministic nodes, missing

data can be accommodated by setting capture probabilities to zero for missed occasions. This

requires tracking capture probabilities and conditional state likelihoods across an additional

dimension allowing for different capture probabilities among individuals sampled at different

times, which may result in relatively greater loss in efficiency. An alternative approach,

which we do not explore here but that could also have implications for model run times,

would be to define a multistate model for p_t, whereby p_t can take 'available' or 'unavailable'

states depending on whether sampling occurred (e.g., Lovich et al. 2014).

For the discrete latent state models, we derived secondary parameters as functions of the

summed latent states as in Kéry and Schaub (2011). For the marginalized models, we derived

secondary parameters as analytical functions of the primary parameters and data or other

second-order states, as described above, as a simulation study based on the primary parameter

values used here showed better credible interval coverage, faster implementation time, and

less biased parameter estimates compared to alternative methods of deriving second-order

states and secondary parameters (Appendix S2).

To assess models and data sets, we compared the ability of models to recover data

generating values, 95% credible interval coverage, credible interval widths, and model run

times. We implemented all models in JAGS (Plummer 2003) with the jagsUI package

(Kellner 2015) in R (R Core Team 2021). R code for simulating data and implementing

models is provided in the data package (Saracco and Yackulic 2023), and a detailed

description of model code is provided in Appendix S1.

Transient marginalized multistate JS models

We applied a transient marginalized multistate JS model to 100 simulated data sets using

the same parameters as the marginalized JS model above, but with the added residency

parameters set to $\pi = 0.6$ and $\kappa = 0.4$. Simulation and model details are provided in the data

package.

We applied a version of this model to capture-recapture data from 2912 adult Kentucky

Warblers (*Geothlypis formosa*) banded between 1993 and 2015 in the Central Hardwoods

Bird Conservation Region in the United States (Sauer et al. 2003) as part of the Monitoring

Avian Productivity and Survivorship (MAPS) program. These data were collected at 51

MAPS stations, which on average operated ~ 10 yrs (sd = 6) of the 23-yr time span, resulting

in ~ 42% (28058 of 66976) of the individual × year data points missing. For the analysis,

these data were summarized to yield 876 unique capture histories. We used a $Beta\big(1/(T -$

$1), 2 - t/(T - 1)\big)$ prior distribution on γ_t due to the missing data and large number of

sampling periods (Dorazio 2020). Initial attempts using $U(0,1)$ priors for γ_t with MAPS data

resulted in marginal posterior distributions on N peaking at M, regardless of how many

unobserved individuals the data set was augmented with. To allow for spatial variation in

capture probability, we modeled $p_{sta[i]}$ with a logit-linear model with intercept and a random

station effect distributed as $Norm(0, \sigma^2)$. In addition, we included annual variation in

survival by modeling ϕ_t with a logit-linear model with intercept and a random year effect

distributed as $Norm(0, \sigma^2)$. We applied standard vague priors for intercepts ($Norm(0,0.01)$)

and variances of random effects ($Unif(0,10)$).

Results

Discrete v. marginalized multistate JS models

Median estimates of the data generating parameter values were successfully recovered

for both the discrete latent state and marginalized multistate JS model implementations (Fig.

1). Credible interval coverage was close to nominal at the 95% level for most parameters and

scenarios, although it was slightly lower for the N_{super} and p parameters (Table 1; Fig. 1).

Coverage for the N_{super} and p parameters for models with missing data was especially low

(~ 80-90%). The abundance estimates, N_t and N_{super}, tended to be biased high for all

models and data scenarios. Median bias of posterior medians for the abundance parameters

was lowest for the discrete latent state model with complete data (+ 3-7%), slightly higher for

the marginalized model with complete data (+ 5-8%), and greater still for the models with

missing data (+ 6-12% for the discrete latent state model and + 7-14% for the marginalized

model). Estimates of capture probability, p, tended to be biased low and was similar between

models (median – 5% bias in posterior p medians for both models with complete data and –

6% for models with missing data). Credible interval widths were essentially identical

between the discrete and marginalized models for the entry, survival, and capture probability

parameters; however, widths were ~ 10-20% greater for derived parameters, such as N_{super}

(Table 1). The marginalized models ran much faster than the discrete latent state models,

reaching 1000 effective samples for the least converged parameter ~ 100 × (missing data

model) to 1000 × faster than the discrete latent state versions (Fig. 2).

Transient model applied to simulated data

The model converged quickly, with a median time to achieve 1000 effective samples of

the least converged parameter of 0.5 minutes. Parameter estimates were very similar to the

data generating values, suggesting that the model can provide reliable inferences about

residency probability, numbers of residents in the population, survival and recapture

probabilities under the assumption of equal p_t between residents and transients. As for the

basic model version, however, estimates of capture probability tended to be biased low and

population size high (Fig. 3). Residency probability also tended to be biased high (Fig. 3a).

Coverage of 95% credible intervals was relatively low for capture probability and

superpopulation size of residents (between 80% and 85%, Fig. 3c).

Application to MAPS data

Based on a model run with 3 MCMC chains of 40000, burn-in of 10000, and thinning

rate of 3 (for a total of 30000 saved posterior samples), the model took approximately 24

hours to run, considerably longer than our simpler simulation examples. Most parameters

converged relatively quickly with the median time to achieve 1000 effective samples of 4

hours; however, a few parameters took longer with the least converged parameter taking 3.7

days to achieve 1000 effective samples. All parameters had $\hat{R} < 1.01$, suggesting satisfactory

convergence.

Model results suggested that survival probability was relatively consistent across the

study (ϕ=0.5 [0.46, 0.54]; σ=0.09 [0, 0.3]; Fig. 4a). The derived recruitment rate was much

more variable, particularly for the first and last time intervals (Fig. 4b). However, precision

of the recruitment estimates was also lower for those intervals and likely reflect the low

number of stations operated during the first and last years of the time series (8 and 3,

respectively). Annual population change and abundance matched patterns of recruitment

(Figs. 4c, d), suggesting the importance of this demographic rate in driving population

dynamics. Residency probability, π, was estimated to be ($\pi = 0.53$ [0.44, 0.64], and the

proportion of residents in the population was relatively consistent across years, again with the

exception of first and last years (Fig. 4e).

Discussion

370   Bayesian modeling with MCMC estimation provides a flexible framework for

371 implementing capture-recapture models with latent states and complex hierarchical model

372 structures. However, because common Bayesian implementations of these models require

373 simulating discrete latent states of each individual at each time step, they can be slow to

374 converge and require long run times for moderate to large data sets (Yackulic et al. 2020).

375 This is especially true for JS models, where observed capture histories must be augmented

376 with potentially large numbers of unobserved individuals to encompass the population of

377 interest. Here we show that through marginalization, whereby the individual capture histories

378 are aggregated to unique capture histories (or unique capture history × covariate) and their

379 frequencies, and state probabilities, rather than individual states, are tracked, parameter

380 estimates can be recovered in a fraction of the time. This gain in efficiency greatly expands

381 the potential applications for this useful class of capture-recapture model.

382   Because JS models do not condition on first capture, they require an assumption of equal

383 capture probability for captured and uncaptured individuals, which may limit their utility for

384 certain sampling scenarios (e.g., mark-resighting studies). However, whenever this

385 assumption is reasonable, these models provide an attractive alternative to CJS models,

386 because they enable inferences about an expanded suite of demographic parameters including

387 recruitment, population size, and population dynamics. As proposed in the original

388 formulations of Jolly (1965) and Seber (1965), population size can be estimated within a CJS

389 modeling context by simply dividing the number of individuals captured by the recapture

390 probability estimate (Dugger et al. 2004, McDonald et al. 2005 p. 241, see Yackulic et al.

391 2014, Appendix C for a complex application). However, this approach can lead to population

392 size estimates that suggest negative recruitment because entry parameters are not included in

393 the likelihood (Schwarz and Arnason 1996). By modeling both the recruitment and survival

394 processes, JS approaches provide a means of preventing such inconsistencies. Other options

395 that do condition on capture, yet are still able to provide inferences on recruitment through

396 modeling capture histories both forward and backward in time, offer an alternative approach

397 (Pradel 1996, Link and Barker 2005). These 'reverse-symmetry' models offer an advantage

398 over JS models in that the recruitment or population growth parameters can be included in the

399 likelihood and so modeled directly, rather than derived from the survival and population size

400 parameters (Tenan et al. 2014, Saracco et al. 2020). In addition, because they are based on

401 applying time-specific multinomial likelihoods to a compact set of sufficient statistics, they

402 too can be implemented quickly using Bayesian methods. Nevertheless, these reverse-

403 symmetry models do not allow the same level of flexibility as the multi-state JS models for

404 handling complexities such as transiency or demographic rates that depend on states that

405 change over time [e.g., age class or breeding status; Kendall et al. (2019), Hostetter et al.

406 (2021)]. Finally, while these models can provide inference about population dynamics

407 parameters, they are largely unable to inform population size (but see Tenan et al. 2019).

408   Median parameter estimates from our simulation study were very similar between the

409 discrete latent state and marginalized JS models for the set of parameter values we considered

410 in our simulations. However, both model implementations showed slight negative bias in

411 capture probability estimates and positive bias in population size estimates. These biases

412 were magnified for model runs with random missing data. We suggest that additional study is

413 needed to better understand the potential effects of missing data, including different amounts

414 and types of missing data (e.g., random v. consecutive missed years at particular sites), on

415 inferences across a range of combinations of parameter values. Understanding the

416 consequences of missing data is especially important for monitoring programs, such as

MAPS, where as much as half the sampling occasions can commonly be missed due to

stations entering and leaving the program over the years.

Credible intervals were wider for the marginalized v. discrete latent state models for the

population size and other parameters derived as deterministic functions of population size.

Nevertheless, these estimates exhibited better coverage compared to the discrete latent state

model or marginalized model with parameters derived from conditional estimates applied to

reconstituted capture histories (Appendix S2). Given the greater speed of implementation,

better coverage, and lack of bias in year-specific population size, recruitment, and population

change estimates, we suggest that this approach appears to be the most generally useful

among those considered here for implementing models and estimating derived parameters.

We described a variation of the basic marginalized multistate JS model to illustrate the

versatility of the basic modeling framework to address a common complication of many

capture-mark-recapture programs that involves the sampling of individuals that are not part

of the target population. This 'transient' version of the marginalized multistate JS model

assumes equal capture probability between residents and transients, which may be unrealistic

in many situations; however, because capture probability is informed here by between-year

recaptures, we suggest that it is unlikely to bias estimates of resident population size. Higher

resident than transient recapture probabilities would nonetheless be expected to result in

underestimates of transient populations and overestimates of the proportion of residents in

populations. Additional within-season data and model development (e.g., Ruiz Gutierrez et

al. 2016) will be required to provide a more complete understanding of resident and transient

components of populations.

The version of the transient JS model that we describe here successfully recovered

parameter values from our simulations, although the same biases in capture probability and

superpopulation estimates seen in the basic JS version were also evident in the transient

model, and there was some evidence in bias in the residency probability parameter as well.

We suggest that additional study is needed to assess how biases may change across different

combinations of parameter values.

While our application to the MAPS Kentucky Warbler data set was much slower than

the simple simulation scenarios we considered, this was not entirely unexpected given the

larger dimensions of the data set (~ 20 x the number of rows representing unique site x

capture histories and > 3 x the number of sampling occasions compared to the simulated

transient model data sets), random effects structure for the survival and capture probability

models, and large number of missed sampling occasions. Even with the longer run time,

reasonable inferences for most parameters were obtained within a few hours, demonstrating

the potential utility of this modeling framework for more complicated real-world examples.

Ideally, study design, objectives, and characteristics of the data set at hand should dictate

possible model applications without having to consider constraints of long implementation

times. We hope that the marginalized versions of the JS model described here will stimulate

additional study and development of this useful class of models and open new potential

applications to large complex data sets.

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Conflict of Interest Statement

The authors declare no conflict of interest.

Author Contributions

J. Saracco and C. Yackulic conceived the ideas and designed methodology; J. Saracco

prepared and analysed the data and led the writing of the manuscript. Both authors

contributed critically to the drafts and gave final approval for publication.

Data Availability

R code and data needed to reproduce results are archived in the Open Science

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476
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Table 1. 95% credible interval coverage and widths [mean with (SE) below] for the discrete latent state (D), marginalized (M), discrete latent

state with 25% missing data (D.NA), and marginalized with 25% missing data (M.NA) multistate Jolly Seber models applied to 100 simulated

data sets.

	% coverage					Width			
	D	M	D.NA	M.NA		D	M	D.NA	M.NA
N_{super}	90 (3.0)	92 (2.7)	83 (3.8)	87 (3.4)		82.1 (0.9)	99.3 (0.7)	116.4 (1.7)	129 (1.3)
ϕ	94 (2.4)	94 (2.4)	92 (2.7)	91 (2.9)		0.104 (0.000)	0.104 (0.001)	0.132 (0.001)	0.132 (0.001)
b_1	98 (1.4)	98 (1.4)	97 (1.7)	98 (1.4)		0.157 (0.001)	0.157 (0.001)	0.185 (0.001)	0.185 (0.001)
b_2	97 (1.7)	97 (1.7)	97 (1.7)	97 (1.7)		0.010 (0.010)	0.010 (0.010)	0.010 (0.010)	0.010 (0.010)
b_3	96 (2.0)	96 (2.0)	98 (1.4)	97 (1.7)		0.129 (0.001)	0.129 (0.001)	0.154 (0.002)	0.155 (0.002)
b_4	94 (2.4)	94 (2.4)	96 (2.0)	97 (1.7)		0.123 (0.001)	0.124 (0.001)	0.150 (0.002)	0.150 (0.002)
b_5	95 (2.2)	95 (2.2)	96 (2.0)	96 (2.0)		0.122 (0.001)	0.122 (0.001)	0.148 (0.002)	0.148 (0.002)
b_6	95 (2.2)	95 (2.2)	97 (1.7)	97 (1.7)		0.119 (0.001)	0.119 (0.001)	0.146 (0.002)	0.146 (0.002)
b_7	95 (2.2)	95 (2.2)	96 (2.0)	96 (2.0)		0.115 (0.001)	0.115 (0.001)	0.142 (0.002)	0.142 (0.002)
p	93 (2.6)	92 (2.7)	87 (3.4)	89 (3.1)		0.139 (0.001)	0.140 (0.001)	0.183 (0.002)	0.184 (0.002)

Figure 1. Boxplots of posterior medians for adult apparent survival probability, ϕ, entry

probability, b, capture probability, p (a); annual abundance, N_t, and superpopulation

abundance, N_{super}, (b) from discrete (D) and marginalized (M) multistate Jolly Seber models

applied to 100 complete simulated data sets and 100 data sets with 25% missing data. Data-

generating values are indicated with red lines.

Figure 2. Boxplot of the time required to reach 1000 effective samples of the least converged

parameter for discrete (D) and marginalized (M) multistate Jolly Seber models applied to 100

complete simulated data sets and to the same 100 data sets but with 25% of the data randomly

missing.

Figure 3. Boxplots of posterior medians for adult apparent survival probability, residency

probability, entry probability, capture probability (a), and superpopulation size of resident

individuals (b) from a marginalized multistate transient Jolly Seber model applied to 100

simulated data sets. Data-generating values are indicated with red lines. Mean 95% credible

interval coverage of model parameters is shown in (c).

Figure 4. Medians $\pm$ 95% credible intervals for annual demographic parameters estimated

for Kentucky warblers banded in the Central Hardwoods Bird Conservation Region as part of

the Monitoring Avian Productivity and Survivorship (MAPS) program.