A Multistate Extension of the Jolly-Seber Model: Combining adult mark-recapture data with juvenile data

by

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MSc, University of Victoria, 2014
BSc, Queen's University, 2011

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ABSTRACT

The Laskeek Bay Conservation Society has been collecting data on the East Limestone Island population of Ancient Murrelets since 1990. For the first 15 years of this decades-long study, mark-recapture data was collected annually on the adult population using one method while chicks were captured and tagged each year soon after their birth using another method. We developed a Jolly-Seber type model that integrates the adult and chick data. Using a multi-state framework, our model separates the ‘alive’ state of the JS model into several age-related states, allowing for different survival and capture parameters between states. In the Ancient Murrelet case study we found that a 6-state model with constant adult survival and capture parameters best fit the data. We determined that, since the detected chicks are rarely seen again, including these individuals in the model does not result in estimates which greatly differ from that of the standard Jolly-Seber model but in a population in which juveniles have high survival and re-capture probabilities, the MSJS model is able to reduce the bias in estimates of population parameters.

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Chapter 1
Introduction

1.1 Problem Background

Ancient Murrelets on East Limestone island have been monitored by the Laskeek Bay Conservation Society since 1990. For the first 15 years of this decades-long study, mark-recapture data were collected annually on the adult population using one method while chicks were captured and tagged each year soon after their birth using another method. Our goal is to improve upon the estimates of population abundance and survival among adults by incorporating the data collected on the chicks into a model.

1.2 Mark-recapture studies

When attempting to estimate the size of an animal population, it is often not practical nor possible to count every individual. A common technique that is used instead is to capture a subset of individuals from the population, mark them with either a tag or some other identifier, release them back into the population and then, on another occasion, capture another subset of individuals from the population, making note of any individuals who were previously marked, and putting a mark on newly captured individuals. This can be repeated across many sampling occasions, each time capturing a subset, making note of the recaptures, and marking newly captured individuals before release.

There are several variations on how a mark-recapture study can be performed. The animals may be marked with a unique identifier so each individual's capture history can be recorded throughout the study. In other cases, the animals may be marked with something which identifies the occasion of marking (batch marked), but is not unique to the individual. In this case, counts of re-captures and new-captures would be available for each sampling occasion, but not individual capture histories. The length of the study will also vary; mark-recapture studies may take place across several days, weeks, months or even years. Deciding on an appropriate model to estimate population abundance will thus depend on the data collected and the time period in which it was collected.

1.3 Closed Population Models

A closed population model is the simplest type of model used to estimate population abundance with mark-recapture data (Otis et al., 1978). With such a model, one assumes that individuals do not enter or leave the population throughout the duration of the study. Assuming that the population is closed is a major assumption. With a study occurring over a long period of time, such as the one on the adult Ancient Murrelets of East Limestone Island, the assumption of a closed population is almost certainly not valid. We thus move our attention to the exploration of models used with capture-recapture data that allow for the population to be open. That is, models that allow for births and immigration into the population.

1.4 The CJS Model

When studying a population over a long period of time, we no longer assume the population is closed. Inevitably, there will be individuals that die or permanently emigrate from the population and there will be individuals that are born or immigrate into the population. The Cormack-Jolly-Seber (CJS) model allows for the estimation of apparent survival of individuals in the population.

The CJS model was first developed by Cormack in 1964 (Cormack, 1964) and then was extended, independently, by both Jolly and Seber in 1965 (Jolly, 1965), (Seber, 1965). The development and further extensions of this model have been extremely important not only in wildlife studies but also for the advancement of statistical methodology for estimating demographic parameters in animal populations (Link & Barker, 2010). The CJS model is used when attempts are made to observe individuals from a population on T sampling occasions. This is, of course, typical of a capture-recapture study in which individuals are captured, marked with a unique identifier, and released on T sampling occasions.

The model describes two events associated with a population and the collected data; survival and capture. These events are described as Bernoulli trials wherein an individual either survives or does not survive and, assuming it survives, is either observed or is not observed. The probability of an individual surviving between occasions j and $j+1$ is denoted by ϕ_j. If an individual dies or permanently emigrates between sampling occasion j and $j+1$, we treat both of these events equally as the lack of survival, thus with probability $1-\phi_j$. On any sampling occasion an individual is either observed or not observed. Individuals that are not observed may have survived but it is possible that they did not survive and are no longer available for capture. We denote by p_j the probability of recapturing an already marked individual on sampling occasion j. The CJS model conditions on the first capture of each individual and thus only models the recaptures of the individuals that were observed at some point throughout the study. For example, in a study with T sampling occasions, the parameters are $\theta = \{p_2, p_3, ..., p_T; \phi_1, \phi_2, ..., \phi_{T-1}\}$. For an individual i that was first observed at sampling occasion j, the associated parameters are $\theta_j = \{p_{j+1}, p_{j+2}, ..., p_T; \phi_j, \phi_{j+1}, ..., \phi_{T-1}\}$.

Since the CJS model conditions on the first capture of each observed individual, it cannot be used to estimate the size of the population. If the research question is solely focused on survival estimates for the population, then the CJS model is sufficient; however, by extending this model to include the complete capture history of an individual, one could estimate many other desirable population parameters, specifically abundance.

1.5 The Jolly-Seber Model

Capture-recapture histories contain information about how marked individuals come to leave the study population (either by mortality or permanent emigration) and also about how they arrive into the population (either locally by birth or externally by immigration) (Kéry and Schaub, 2011). In order to estimate the parameters related to recruitment, the model must extend back beyond the period following the first capture (which the CJS model focusses on) and instead analyze the complete capture-histories for each marked individual. A complete capture history for T sampling occasions will consist of an ordered list of T 0's and 1's; a 0 in position j of the list means that the individual was not observed on occasion j while a 1 in position j means the individual was observed on that occasion. Information about the arrival process is contained in the zeros that appear before the first capture, as well as the first capture occasion itself. A zero before the first capture could mean that the individual was in the population and was not observed, or it could mean that the individual was not yet in the population and thus, was not able to be observed.

The Jolly-Seber (JS) model was first introduced independently by both Jolly and Seber in 1965 as an extension of the CJS model and closed population models (Kéry and Schaub, 2011). The JS model can be parameterized in a number of different ways which should all give the same estimates of population size but differ in the way recruitment is modelled. We will focus on the JS model formulated as a state-space model by Royle and Dorazio, (Royle and Dorazio, 2008), since the main model in Chapter 2 is an extended multistate JS model. The motivation for the multistate extension of the JS model comes from existing models which estimate survival and movement of a population from mark-recapture data using multistate models (Kéry and Schaub, 2011).

1.5.1 JS Model Assumptions

In all formulations of the JS model, it is assumed that unmarked animals in the population have the same probability of capture as marked animals in the population. The implication of this is that newly captured individuals are a random sample of all unmarked individuals in the population. Furthermore, the probability of being captured is the same for all individuals, both marked and unmarked, at each sampling occasion. This is referred to as the assumption of homogeneous capture. Survival is also assumed to be homogeneous in that we assume survival probabilities are the same for all individuals (marked and unmarked) between each pair of sampling occasions. These assumptions means that the JS model does not allow for heterogeneous capture or survival parameters for individuals. Additionally, it is assumed that the identifier tags are not lost, sampling occurs instantaneously, the identity of individuals is recorded without errors, and the study area is constant (Schwarz and Arnason, 1996).

1.5.2 The JS model as a State-Space Model

The observed capture histories can be described as the result of a state process and an observation process, where the observation process is dependent on the result of the state process. The possible states for an individual are 'not yet entered', 'alive' and 'permanently left the population'. The possible observed states for an individual are observed and not observed (or captured and not captured). When an individual has not yet entered the population or has permanently left the population, they cannot be observed. Only when an individual is in the state 'alive' can they be observed. It is worth noting that for an individual to be in the state 'alive', they must be in the population and available for capture. Figure 1.1, illustrates an example of the state and observation process for an individual that enters the population on occasion 3, is observed on occasions 4, 5, and 6 and then leaves the population on occasion 7.

The super-population, denoted N, represents the number of individuals that were ever alive and available for capture during the study. We assume that a fraction of the super-population is already alive and available for capture at the beginning of the study and denote this proportion by b_1. The rest of the individuals will enter the study throughout the remaining sampling occasions according to some entry probabilities which we'll denote $b_2, ..., b_T$, where b_j represents the probability that an individual is first available for capture on occasion j. These probabilities, $b_1, ..., b_T$ must sum to 1 in order to ensure that all N individuals enter the population at some point during the study. If we denote by $\mathbf{B} = (B_1, B_2, ..., B_T)$, the number of individuals that are new to the population on each occasion, then $\mathbf{B}$ can be modeled using a multinomial distribution with index N and probability vector $(b_1, b_2, ..., b_T)$.

It is very likely that some individuals in the population will never be observed. As such, the number of observed individuals n will be less than N. The matrix of complete capture histories of the observed individuals is not a complete data matrix. It is missing the all-zero capture histories for individuals in the population that are never observed. In order to have complete data matrix, we must include rows of zeros for the $N - n$ unobserved individuals in the population (Kéry and Schaub, 2012). However, as we do not know the value of the index N, this presents a challenge. In order to deal with this, we can use parameter-expanded data augmentation (Kéry and Schaub, 2011), where we set the size of some pseudo-population to M, attach $M - n$ rows of all zero capture histories to our observation matrix and let each of the M individuals transition between states 'not yet entered', 'alive' and 'permanently left

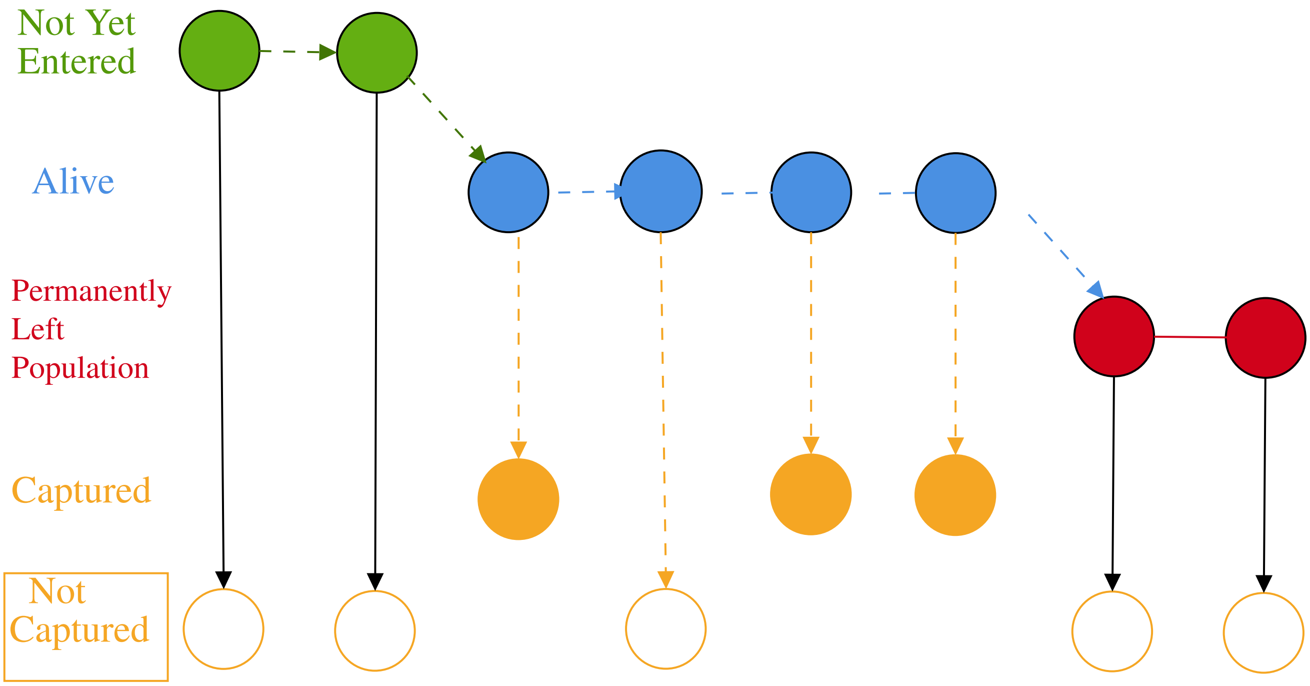

Figure 1.1: Example of the state and observation process of a marked individual with capture history X= [0, 0, 1, 0, 1, 1, 0, 0] in the Jolly-Seber model. Solid lines represent deterministic processes while dashed lines represent stochastic processes, specifically entry into the population, survival, and capture. The states ‘not yet entered’, ‘alive’ and ’permanently left the population’ are represented in green, blue and red respectively whereas the observations ‘captured’ and ’not captured’ are represented in filled and unfilled orange circles.

the population'. The selection of M must be done in a way that ensures that M is greater than N while also taking into consideration the computation time required when M is very large. Using a conservative estimation for the capture rate within the population, one could then estimate a value of N that is likely larger than the true size of the super-population. Then, M should be set to equal at least double the estimated N value so that one can be certain that $M > N$. Figure 1.2 below illustrates the observed data matrix with n rows, the complete data matrix with N rows, and the augmented data matrix with M rows.

Observed Population   True Population   Augmented Population

$$\left.\left[\begin{array}{cccc} 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 0 & 1 & 1 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \end{array}\right]\right\} n \quad \left.\left[\begin{array}{cccc} 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 0 & 1 & 1 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ \hdashline 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{array}\right]\right\} N \quad \left.\left[\begin{array}{cccc} 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 0 \\ 0 & 1 & 1 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 \\ \hdashline 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \hdashline 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{array}\right]\right\} M$$

Figure 1.2: Illustration of the observed population of size n, the true population of size N, and the augmented population of size M.

Individuals that are not a part of the super-population will remain in the state 'not yet entered' throughout the entire study while the N individuals in the super-population will enter into the state 'alive' at one of the occasions. Once an individual is in state 'alive', they can either remain in state 'alive', through survival, or move to state 'permanently left the population'. Once again, we denote survival from occasion j to $j+1$ by ϕ_j. Entry into the state 'alive' can no longer be modelled by the b_j rates described above since $\sum_{j=1}^{T} b_j = 1$ and not all of the M individuals will enter this state. Instead, we use a removal-entry parameter, denoted by γ_j, which represents the probability that an available individual in the state 'not yet entered' enters the state 'alive' on occasion j (Kéry and Schaub, 2012). The word *available* is important here; γ_j refers only to those individuals in M who have not yet entered the population before occasion j. Figure 1.3 below gives the transition diagram between states 'not yet entered', 'alive' and 'permanently left the population'. The transitions between the three states represent a Markov process since the state of an individual at time $j+1$ relies only on the previous state of the individual at time j.

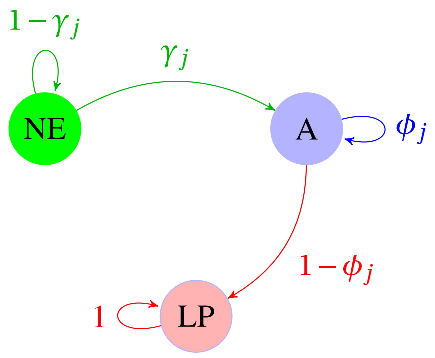

Figure 1.3: Illustration of the state transitions between states 'not yet entered' (NE), 'alive' (A), and 'permanently left the population' (LP).

The removal-entry probabilities, $\gamma_1, \gamma_2, ..., \gamma_T$, and the entry probabilities, $b_1, b_2, ..., b_T$ are not the same but they are related. The expected number of individuals that are new to the population on occasion j is the product of the number of remaining individuals in state 'not yet entered' with γ_j. That is,

$$\begin{aligned} E(B_1) &= M \cdot \gamma_1 \\ E(B_2) &= M \cdot (1-\gamma_1) \cdot \gamma_2 \\ &\;\;... \\ E(B_T) &= M \cdot (1-\gamma_1) \cdot (1-\gamma_2) \cdots (1-\gamma_{T-1}) \gamma_T. \end{aligned} \tag{1.1}$$

Then, for each sampling occasion $j \in \{1, ..., T\}$, with survival between occasions given by $\{\phi_1, \phi_2, ..., \phi_{T-1}\}$, removal-entry probabilities given by $\{\gamma_1, \gamma_2, ..., \gamma_T\}$ and capture probabilities given by $\{p_1, p_2, ..., p_T\}$, we can represent the transition between states as well as the observation process given an individual's current state with the following probability matrices.

$$\begin{array}{r c} & \begin{array}{ccc} \text{not yet entered } (j) & \text{alive } (j) & \text{left population } (j) \end{array} \\ \begin{array}{r} \text{not yet entered } (j-1) \\ \text{alive } (j-1) \\ \text{left population } (j-1) \end{array} & \left[\begin{array}{ccc} 1-\gamma_j & \gamma_j & 0 \\ 0 & \phi_{j-1} & 1-\phi_{j-1} \\ 0 & 0 & 1 \end{array} \right] \end{array}$$

$$\begin{array}{r|cc|}
 & \text{observed } (j) & \text{not observed } (j) \\
\text{not yet entered } (j) & 0 & 1 \\
\text{alive } (j) & p_j & 1-p_j \\
\text{left population } (j) & 0 & 1
\end{array}$$

We denote by z_{ij} the state of individual i at sampling occasion j where $z_{ij} = 0$ when individual i is not available for capture (thus in states 'not yet entered' or 'permanently left population') and $z_{ij} = 1$ when individual i is in state 'alive'. Under this notation, the likelihood becomes

$$L(\phi, \mathbf{p}, \gamma | \mathbf{X}, \mathbf{z}) = [\mathbf{X}|\mathbf{p}, \mathbf{z}]\,[\mathbf{z}|\phi, \gamma], \tag{1.2}$$

where $[\mathbf{z}|\phi, \gamma]$ gives the state of the individual with

$$z_{i,1} \sim Bernoulli(\gamma_1)$$

modelling the state of individual i on the first sampling occasion and

$$z_{i,j+1}|z_{i,j}, ..., z_{i,1} \sim Bernoulli\left(z_{i,j}\phi_j + \gamma_{j+1}\prod_{k=1}^{j}(1 - z_{i,k})\right)$$

determining the subsequent states of individual i with their state at time $j+1$ being dictated by survival (ϕ_j) if the individual has already entered the population or by removal-entry probability (γ_{j+1}) for an individual that is still in the state 'not yet entered' at time j. Then the first term of the likelihood, $[\mathbf{X}|\mathbf{p}, \mathbf{z}]$, represents the observation process, conditioned on the state process, and is given by

$$X_{i,j}|z_{i,j} \sim Bernoulli(z_{i,j} \cdot p_j).$$

1.5.3 Estimating Population Abundance with the JS model

Quantities of interest often include the size of the population at each sampling occasion, N_j, the number of individuals entering the population (fresh recruits) at each sampling occasion, B_j, and the size of the super-population, N. We use the latent state variable z to derive these abundance parameters as can be seen in equations 1.3, 1.4, and 1.5 below.

$$N_j = \sum_{i=1}^{M} z_{i,j} \tag{1.3}$$

$$B_j = \sum_{i=1}^{M} (1 - z_{i,j-1}) z_{i,j} \tag{1.4}$$

$$N = \sum_{j=1}^{T} B_j \tag{1.5}$$

1.5.4 Implementing a Bayesian Analysis of the JS model

In order to perform a Bayesian analysis of the model, we will need prior distributions for the parameters $\phi, \mathbf{p}$, and γ. For the survival and capture parameters, one could use an uninformative prior such as the uniform prior Uniform$(0,1)$, or a conjugate beta prior Beta(α, β) where α and β may be informed by some previous knowledge of survival or capture probabilities. It should be noted that the removal entry parameter γ is purely a nuisance parameter that is needed to describe the system. It does not carry any ecological meaning and, as such, should carry an uninformative prior such as the uniform distribution $U(0,1)$.

Combining the priors with the above-described likelihood, a Bayesian analysis of this model can be implemented in R (R Core Team, 2021) using software packages such as RJAGS or Nimble. Included in Appendix B is the RJAGS code for the implementation of the JS model.

In Chapter 2, we extend the JS model to include several, age-related states, detailing the stochastic process that dictates transition between states as well as the likelihood of the model and the Bayesian implementation of the model. In Chapter 3 we perform a simulation study investigating the performance of both the JS model and the extended multi-state model and in Chapter 4, we fit our extended model on the Ancient Murrelet adult mark-recapture and chick capture data. Finally, in Chapter 5 we discuss our conclusions as well as possible extensions to the research.

Chapter 2

Multistate Jolly-Seber Model Extension

We now consider how to extend the JS model in order to incorporate the data collected on the chicks. The standard JS model assumes that all individuals that are 'alive' on one occasion have the same probability of surviving to the next occasion. This assumption of homogeneous survival means that the model does not distinguish between classes of individuals which have different rates of survival. However it is often the case that juveniles and adults have differing survival rates. This means that the transition from the state 'alive' to the state 'permanently left the population' would differ according to the age of an individual in the 'alive' state.

Another difficulty is that the standard JS model assumes that all individuals that are 'alive' on one occasion have the same probability of being captured on that occasion. This assumption of homogenous capture means that the model doesn't allow for cases where different classes of individuals are captured using different methods, as the homogeneous capture assumption would be violated. In the case of the Ancient Murrelets of East Limestone Island, the capture method of newly-born juveniles differs from that of an adult. Furthermore, in this particular example, chicks leave the population area soon after birth and do not return to the island until several sampling occasions later. Both of these scenarios result in capture rates which differ from adults.

In order to incorporate the chick data with the adult mark-recapture data, the 'alive' state will need to be split into multiple age-dependent states. We thus extend the state-space formulation of the JS model to a multistate model that allows for multiple age-related states. This is to provide additional entry information as well as to improve upon the JS estimates of both the population size and survival rates. It also allows for the incorporation of data collected on a certain age state; for example, marking individuals right after birth, where the capture method is different from that used for adults.

The number of alive states will depend on the population of study as well as the data available. The idea is to break up the 'alive' state into disjoint, ordered age categories that cover the entire population where an individual who survives between occasions will move into the next, older, 'alive' state. This process repeats until the individual either moves into the 'permanently left the population' state or moves into the oldest adult 'alive' state, where it will remain until moving into the ‘permanently left the population’ state. Recall that when an individual permanently leaves the population, this either means that the individual has emmigrated to another population or has died. The decision of what age to set for the adult ‘alive’ state should be based on when one expects the survival and capture rates to stabilize for individuals of that age and older. In our example, with the Ancient Murrelets of East Limestone Island, chicks have a much lower chance of survival than the adults and they are not expected to return to the island until they are 2 or 3 years of age (Gaston, 1990). This gives us reason to believe that the survival and capture rates for chicks, 1 year old juveniles, and adults that are 2 years of age and older, will differ between age-classes. With this example, there is reason to break up the ‘alive’ state into 3 states; in which S_2 represents newly-born chicks, S_3 represents 1-year old juveniles, and S_4 represents adults, 2 years of age and older. It must also be possible to observe the state of the individual upon capture. If this is not possible, then there must be a justifiable method for determining the state of an individual upon capture. For example, with the Ancient Murrelets, it is known that newly born individuals leave the population and almost always return only when they are 2 years or older, thus newly captured individuals that are not chicks, can be assumed to be in the adult state. In this example, we would expect the capture probability of those in the 1 year old state, S_3, to be near zero.

2.1 Model Notation

The multistate extension of the JS model includes survival, capture, and removal-entry parameters as well as a latent state variable (though partially observed) and observed capture histories. We describe the notation for these parameters and variables in Table 2.1 below.

2.2 Model Assumptions

This model assumes individuals within the same state share the same survival and capture probability. We also assume that individuals in juvenile alive states will have state-dependent survival and capture probability but that these will be constant with respect to time. This means that we assume, for example, that the probability of transitioning from S_2 to S_3 (which occurs as the result of survival) will be $\phi_{juv,1}$ at any sampling occasion. This assumption is made in order to simplify the model; however, a more general model allows for time-varying juvenile parameters. This is discussed further in Section 2.4.4. Finally, as removal entry probabilities represent the proportion of individuals who are currently in state S_1 that are expected to either remain in state S_1, or transition into states S_2 or S_{k-1} on occasion j, these probabilities must be time-dependent. To better understand the transitions between states $S_1, ..., S_k$, see Figure 2.1 below. Finally, as with the JS model, it is assumed that tags are not lost, sampling occurs instantaneously, the identity of individuals is recorded without errors,

Table 2.1: The notation used in the multistate extension of the Jolly-Seber model.

Type	**Name**	**Notation**	**Description**
Complete Data	Capture History Matrix	$\mathbf{X} = \begin{bmatrix} \mathbf{X}^{obs} \\ \mathbf{0} \end{bmatrix}$	where X_{ij} indicates whether or not individual i was observed on occasion j.
Latent Variable	States & State-Matrix	$\mathbf{S} = \{S_1, S_2, ..., S_{k-1}, S_k\}$ & $\mathbf{Z} = [z_{i,j}]$	where $z_{i,j} \in \mathbf{S}$ gives the state of individual i at time j with S_1 = 'Not yet in population' and $S_2, ..., S_{k-1}$ = are the alive states broken into age-categories and S_k = 'permanently left the population'
Parameters	Juvenile Survival	$\phi_{juv} = \{\phi_{juv,1}, ..., \phi_{juv,k-3}\}$	Constant one-occasion survival probabilities for states $S_2, S_3, ..., S_{k-2}$.
	Adult Survival	$\phi_{ad} = \{\phi_1, \phi_2, ..., \phi_{T-1}\}$	Time dependent survival probabilities for individuals in the oldest alive state S_{k-1}.
	Juvenile Capture	$\mathbf{p}_{juv} = \{p_{juv,1}, ..., p_{juv,k-3}\}$	Constant capture probability for states $S_2, S_3, ..., S_{k-2}$.
	Adult Capture	$\mathbf{p}_{ad} = \{p_1, p_2, ..., p_T\}$	Time dependent capture probabilities for individuals in the oldest alive state S_{k-1}.
	Removal-Entry	$\gamma = \begin{bmatrix} \gamma_{1,1} & \gamma_{1,2} & \gamma_{1,3} \\ \gamma_{2,1} & \gamma_{2,2} & \gamma_{2,3} \\ ... & ... & ... \\ \gamma_{T,1} & \gamma_{T,2} & \gamma_{T,3} \end{bmatrix}$, where $\gamma_{t,1} + \gamma_{t,2} + \gamma_{t,3} = 1$	Time-dependent removal entry probabilities, where $\gamma_{j,1}$ is the probability of remaining in state S_1 at time j, $\gamma_{j,2}$ is the probability of being born into the population, in state S_2, at time j, and $\gamma_{j,3}$ is the probability of immigrating into the population as an adult, in state S_{k-1} at time j
Derived Parameters	Occasion-based population	$\mathbf{N} = \{N_1, N_2, ..., N_T\}$	where N_j gives the total number of individuals in the 'alive' states $S_2, ..., S_{k-1}$ on occasion j.
	Super Population	N	the total number of individuals ever alive during the entire study.
	New Entrants	$B_1, ..., B_T$	the number of individuals new to one of the 'alive' states on each occasion.

captured and recaptured individuals are a random sample from the study population and the study area is constant (Schwarz and Arnason, 1996).

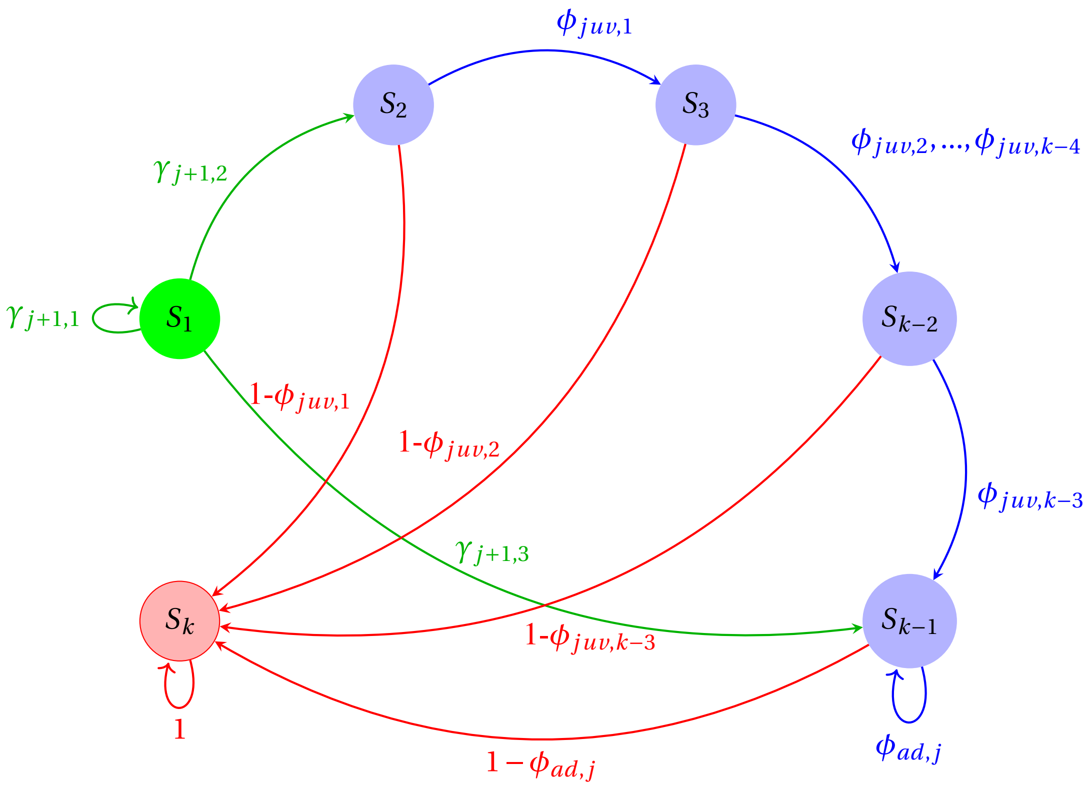

Figure 2.1: Illustration of the transitions between states $S_1, S_2, ..., S_k$ between times j and $j+1$, where S_1 is the 'not yet entered' state represented in green, $S_2, ..., S_{k-2}$ are the 'alive juvenile' states represented in blue, S_{k-1} is the 'alive adult' state also represented in blue, and S_k is the 'permanently left the population' state represented in red.

2.3 The Complete Data Likelihood

The observed capture histories in the matrix $\mathbf{X}^{obs}$ only contain rows for individuals who were observed at least once in the study. Assuming that there are juveniles and adults in the population who are never observed, which is highly likely, the complete data matrix $\mathbf{X}$ will contain the rows of $\mathbf{X}^{obs}$ as well as all-zero rows for each of the non-observed individuals that are in the super-population. Thus, the matrix $\mathbf{X}$ will have a total of N rows. Of course, we do not know the size of the super-population and thus do not know the correct number of all-zero rows to include in the complete data matrix. As was done with that state-space formulation of the JS model (Kéry and Schaub, 2012), we will once again augment the n rows of the observed data matrix with $M-n$ all-zero rows where $M > N$ represents the size of some pseudo-population from which individuals can enter into the population, in state S_2

or S_{k-1}, on occasion j with probabilities $\gamma_{j,2}$ and $\gamma_{j,3}$. Once again, we select M so that it is approximately twice as large as our expected super population size based on conservative estimates of the capture probabilities. Individuals that are not part of the super-population will remain in state S_1 for all T sampling occasions with probability $\prod_{j=1}^{T} \gamma_{j,1}$.

Using the state-transition diagram from Figure 2.1 we are able to compute the probability of an individual moving between states. Then, given the state of an individual, we can compute the probabilities associated with the observation process which simply contains the states 'observed' and 'not observed'. Thus for each sampling occasion $j \in \{1, \cdots, T\}$, we can represent the transitions between states as well as the observation process given an individual's current state with the following probability matrices.

$$P_{state} = \begin{array}{c|ccccccc|} & S_1(j) & S_2(j) & S_3(j) & ... & S_{k-2}(j) & S_{k-1}(j) & S_k(j) \\ S_1(j-1) & \gamma_{j,1} & \gamma_{j,2} & 0 & ... & 0 & \gamma_{j,3} & 0 \\ S_2(j-1) & 0 & 0 & \phi_{juv,1} & ... & 0 & 0 & 1-\phi_{juv,1} \\ S_3(j-1) & 0 & 0 & 0 & ... & 0 & 0 & 1-\phi_{juv,2} \\ ... & ... & ... & ... & ... & ... & ... & ... \\ S_{k-2}(j-1) & 0 & 0 & 0 & ... & 0 & \phi_{juv,k-3} & 1-\phi_{juv,k-2} \\ S_{k-1}(j-1) & 0 & 0 & 0 & ... & 0 & \phi_{ad,j-1} & 1-\phi_{ad,j-1} \\ S_k(j-1) & 0 & 0 & 0 & ... & 0 & 0 & 1 \end{array}$$

$$P_{obs} = \begin{array}{c|cc|} & \text{observed } (j) & \text{not observed } (j) \\ S_1(j) & 0 & 1 \\ S_2(j) & p_{juv,1} & 1-p_{juv,1} \\ S_3(j) & p_{juv,2} & 1-p_{juv,2} \\ ... & ... & ... \\ S_{k-2}(j) & p_{juv,k-3} & 1-p_{juv,k-3} \\ S_{k-1}(j) & p_{ad,j} & 1-p_{ad,j} \\ S_k(j) & 0 & 1 \end{array}$$

Considering the state matrix $\mathbf{Z}$, where z_{ij} is the state of individual i at sampling occasion j, then the likelihood is

$$L(\phi_{ad}, \phi_{juv}, \mathbf{p}_{ad}, \mathbf{p}_{juv}, \gamma \mid \mathbf{X}, \mathbf{Z}) = [\mathbf{X} \mid \mathbf{p}_{ad}, \mathbf{p}_{juv}, \mathbf{Z}][\mathbf{Z} \mid \phi_{ad}, \phi_{juv}, \gamma], \tag{2.1}$$

where $[\mathbf{Z} \mid \phi_{ad}, \phi_{juv}, \gamma]$ gives the state of the individual with

$$z_{i,1} \sim \text{Cat}(\mathbf{S}, \gamma)$$

the initial state of individual i as a categorical random variable with sample space $\mathbf{S} = \{S_1, S_2, S_3, ..., S_{k-2}, S_{k-1}, S_k\}$ and associated probabilities $\{\gamma_{1,1}, \gamma_{1,2}, 0, ..., 0, \gamma_{1,3}, 0\}$. Then, subsequent states are conditional on the previous state. For example, if the state of individual i at time $j-1$ is S_t for some $S_t \in \mathbf{S}$, $t \in 1, \cdots, k$ then,

$$z_{i,j}|z_{i,j-1} \sim \text{Cat}\left(\mathbf{S}, P_{state,t,\cdot}\right)$$

the state of individual i at time j is a categorical random variable with sample space $\mathbf{S}$ and associated probabilities given by the t-th row of the P_{state} matrix. As for the first term of the likelihood, $[\mathbf{X} \mid \mathbf{p}_{ad}, \mathbf{p}_{juv}, \mathbf{Z}]$, this represents the observation process and it conditions on the state process. Thus, supposing individual i is in state S_{t+1} at time j, then

$$X_{i,j}|z_{i,j} \sim \text{Bernoulli}(P_{obs,(t+1),1}),$$

where $P_{obs,(t+1),1}$ is the probability in the first column and $(t+1)$-st row of the P_{obs} matrix.

2.3.1 Estimating Population Abundance with the MSJS model

The occasion-based population abundance parameter, N_j, gives the number of individuals in any of the 'alive' states at time j. That is, individuals in states $S_2, ..., S_{k-1}$. We may also wish to estimate the occasion-based abundance of a particular age-state, such as the adult 'alive' state S_{k-1} or the newly-born juvenile state S_2. We will denote these parameters by $N_{\text{Adult},j}$ and $N_{\text{Juv},j}$ respectively. We are also able to derive the occasion-based new entrants parameter, B_j representing the number of individuals that are new to one of the 'alive' states on occasion j. We could similarly derive new-entrants parameters for specific age-states such as the new entrant adults, $B_{\text{Adult},j}$. Finally, we can derive the super-population parameter for all 'alive' states, denoted by N, or for any specific alive states, for example N_{Adult}. We use the latent state variable $z \in \{S_1, S_2, ..., S_{k-1}, S_k\}$ to derive these abundance parameters. In the equations 2.2-2.6 below, we derive N_j, $N_{\text{Adult},j}$, $N_{\text{Juv},j}$, $B_{\text{Adult},j}$ and N_{Adult}. All other derived parameters can be formed in a similar manner. The function $I_{z_{i,j}}(S_t)$ is an indicator function whereby $I_{z_{i,j}}(S_t) = 1$ if $z_{i,j} = S_t$ and $I_{z_{i,j}}(S_t) = 0$ otherwise.

$$N_j = \sum_{i=1}^{M} \left(\sum_{t=2}^{k-1} I_{z_{i,j}}(S_t) \right) \tag{2.2}$$

$$N_{\text{Adult},j} = \sum_{i=1}^{M} I_{z_{i,j}}(S_{k-1}) \tag{2.3}$$

$$N_{\text{Juv},j} = \sum_{i=1}^{M} I_{z_{i,j}}(S_2) \tag{2.4}$$

$$B_{\text{Adult},j} = \sum_{i=1}^{M} (1 - I_{z_{i,j}}(S_{k-1})) I_{z_{i,j}}(S_{k-1}) \tag{2.5}$$

$$N_{\text{Adult}} = \sum_{j=1}^{T} B_{\text{Adult},j} \tag{2.6}$$

2.4 Implementing a Bayesian Analysis of the model

2.4.1 Augmenting a Dummy-First Occasion

Traditionally, multistate models condition on the first capture which means there is no way to estimate the initial removal-entry parameters, $\gamma_{1,1}, \gamma_{1,2}$, and $\gamma_{1,3}$, (Kéry and Schaub, 2012). In order to get around this, we can augment the state matrix, **Z** with a leading column of 1's which starts all M individuals in state S_1, the 'not yet entered' state. In turn, we must also add a leading column of 0's to our complete capture history matrix **X**, as one cannot be observed while in state S_1. The augmentation of a dummy first occasion allows us to estimate N_1, the number of individuals already in the population on the first sampling occasion. This means that the first row of the γ matrix, $(\gamma_{1,1}, \gamma_{1,2}, 0, ...0, \gamma_{1,3}, 0)$, will represent the removal entry probabilities for the state transitions from the dummy occasion to the first sampling occasion.

2.4.2 Partially Observed States

The state of individuals who are observed while in state S_2, right after birth, is known. If these individuals are seen again, this allows us to determine the state of these individuals between the occasion of their birth and the last time they were observed. We also know that these individuals were in state S_1 on every occasion before their birth. For individuals who are not observed on the occasion of their birth, we can determine their state upon their first capture but we do not know the state of these individuals before their first capture or after their last capture. We are, however, able to determine their state on all occasions between their first and last capture. Thus, the latent state matrix **Z** is partially observed.

2.4.3 Priors for the Parameters

We need prior distributions for the parameters ϕ_{ad}, ϕ_{juv}, $\mathbf{p}_{ad}$, $\mathbf{p}_{juv}$, and γ. For the both the adult and juvenile survival and capture parameters, we use a uniform prior distribution, Uniform$(0,1)$ if we have no previous information about the population and we use a Beta(α,β) prior when there is prior information about these parameters. For the removal-entry matrix γ, whose rows must each sum to 1, we choose a Dirichlet$(\boldsymbol{\delta})$ prior for each row of the matrix with $\boldsymbol{\delta} = \{1,1,...,1\}$.

2.4.4 Possible Modifications of the Model

There are many possible modifications that can be made to this model. For starters, if the sampling occasions are relatively close together, one might expect certain consecutive 'alive' states to share common parameters between those states. For example, juveniles in states S_3 and S_4 could share the same survival and capture probabilities. Such a modification is relatively straightforward, one need only hold such parameters constant in the model. That is, for example, setting $\phi_{juv,2} = \phi_{juv,3}$ and $p_{juv,2} = p_{juv,3}$. Conversely, if the sampling occasions are far apart, perhaps spanning various seasons, the juvenile survival and capture rates for each state may vary with time. Then, for $(k-3)$ juvenile 'alive' states, and T sampling occasions, there would now be $(k-3) \times (T-1)$ survival parameters, and $(k-3) \times T$ capture parameters. Similarly, if there is cause to expect survival and/or capture to remain constant across some or all of the T sampling occasions, then this can be defined accordingly in the model. When using time-varying parameters, such as time-varying adult survival $\phi_{\text{Ad},j}$, the tail-end parameter $\phi_{\text{Ad},T-1}$ is weakly identifiable as there is less information in the data with which to estimate this parameter. Additionally, the juvenile survival rates $\phi_{\text{Juv},1}, \ldots, \phi_{\text{Juv},k-3}$ are not individually identifiable as we do not expect to see individuals while in the juvenile states $S_3, \ldots, S_{k-2}$. What we are able to estimate using the model, it the $(k-3)$-occasion survival rate for juveniles who survive to be in the adult alive state S_{k-1}.

Chapter 3
Simulation Study

3.1 Simulation Scenarios

In order to compare the multistate model extension with the original formulation of the Jolly-Seber model, we performed a simulation study with $T = 7$ capture occasions, $k = 5$ possible states including the 'not yet entered' state S_1, two juvenile states, S_2 and S_3, the adult 'alive' state S_4, and the 'permanently left the population' state, S_5. We assumed that the juvenile survival and capture probabilities are constant across all time-periods but vary between states. Thus the multi-state model includes parameters $(\phi_{\text{juv},1}, \phi_{\text{juv},2})$ and $(p_{\text{juv},1}, p_{\text{juv},2})$ as well as time-dependent survival and capture parameters for the adults in state S_4. Figure 3.1 below gives the state-transition diagram for a $k = 5$ state model with time-varying adult parameters and constant juvenile parameters. For simplicity, we drop the ad subscript and denote the adult parameters by $(\phi_1, ..., \phi_6)$ and $(p_1, ..., p_7)$. The multistate model extension also includes removal-entry parameters from state S_1 into states S_1, S_2 and S_4 for each sampling occasion. Thus, for each occasion j, the multistate model includes removal-entry parameters $\gamma_{j,1}, \gamma_{j,2}$, and $\gamma_{j,3}$. For ease of remembering, we will denote $\gamma_{j,2}$ in this chapter by $\gamma_{\text{Birth},j}$ as it represents the rate at which juveniles in the population leave state S_1 by being born into the population at time j. Similarly, we will denote $\gamma_{j,3}$ by $\gamma_{\text{Ad},j}$ as it represents the rate at which adults in the population leave state S_1 by immigrating into the population as an adult at time j.

We simulated the data in two parts; adults, in state S_4, and newly-born juveniles, in state S_2. Parameter values for the simulation scenarios are provided in Table 3.1. The juvenile survival rates were always set lower than that of the adults, motivated by the Ancient Murrelet case study. In all scenarios, we set the probability of observing a juvenile in state S_3 to 0. This is meant to represent the gap in detection that occurs in the Ancient Murrelet population, where chicks leave the island soon after birth and typically do not return until the year before they are of breeding age (Gaston, 2011). Similarly, the probability of entering the population in state S_3 is 0, as we assume juveniles do not immigrate to the island before reaching the adult state S_4. When simulating the juveniles, we use a random multinomial variable with equal entry probabilities for each occasion to determine how many juveniles

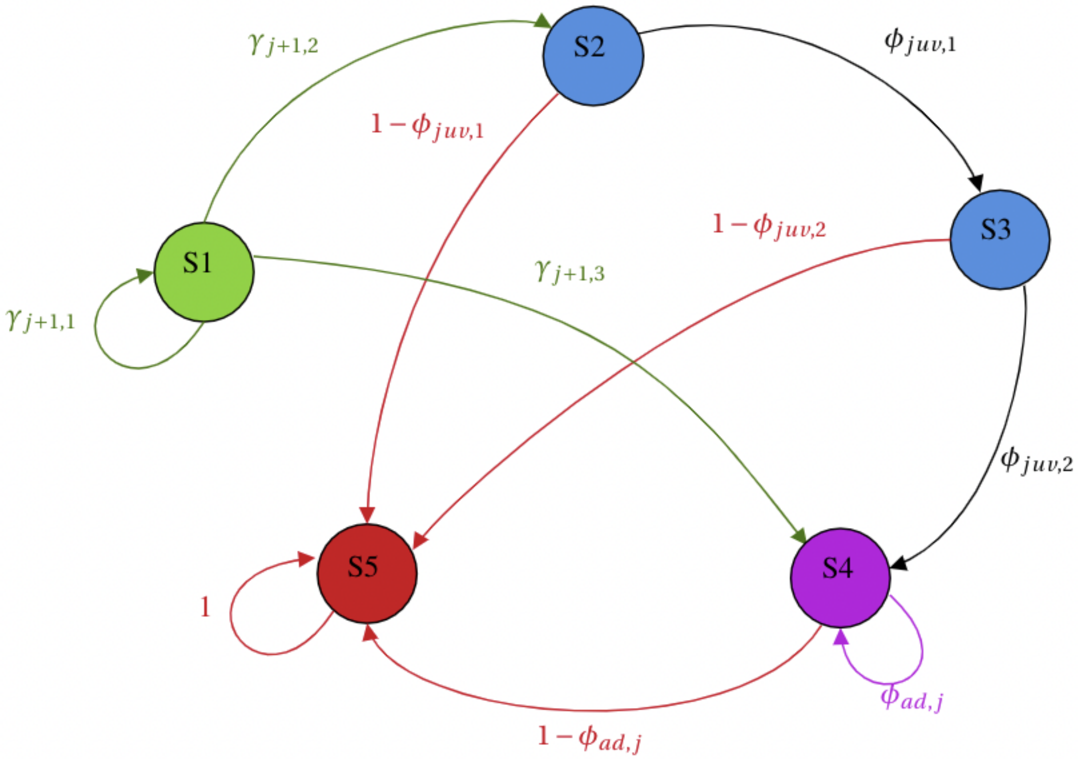

Figure 3.1: Illustration of the transitions between states S_1, S_2, S_3, S_4 and S_5 between times j and $j+1$, where S_1 is the 'not yet entered' state represented in green, S_2 and S_3 are the 'alive juvenile' states represented in blue, S_4 is the 'alive adult' state represented in purple, and S_5 is the 'permanently left the population' state represented in red.

are born into the population on each sampling occasion. Then, for an individual born into the population on occasion t, we use the juvenile survival probabilities to determine the state of this individual on occasions $t+1$ and $t+2$ along with the juvenile capture probabilities to determine the observation process of the individual on occasions t and $t+1$, with juvenile capture probability on occasion $t+1$ always set to 0. On occasion $t+2$, if the individual survived, it has entered the adult 'alive' state, S_4, and, as such, subsequent survival and capture is determined according to the adult survival and capture parameters. For the multistate extension of the JS model, entry into the population can be easily tracked as we know from the simulation the number of adults 'born' into the population each year as well as the number of new-born juveniles. With this model, a juvenile born into the population on occasion j, which survives for two occasions and thus becomes an adult on occasion $j+2$, does not contribute to the number of adults entering the population at time $j+2$. Conversely, the Jolly-Seber model only models the adult population, thus in order to track the number of adults entering the population each year, we include surviving juveniles who are moving into state S_4 for the first time. It is necessary to track the number of individuals that are new to the population on each occasion, which was determined by a multinomial random variable, in order to determine the true values of the removal-entry parameters.

In total, we considered 14 different scenarios; each with a total of 1000 simulated adults and 1000 simulated births entering the population throughout 7 sampling occasions. For each scenario, 100 data sets were generated using the same combination of parameters. The reason for choosing to simulate 100 data sets was in consideration of the significant computation time and memory required to fit the simulated data to the MSJS model. Figure 3.1 below illustrates the 14 simulation scenarios used in the study. Note that the motivation behind the parameter values in scenarios 13 and 14 comes from the estimates of adult survival and capture parameters for the Ancient Murrelet population of East Limestone Island.

We fit both the JS model and the MSJS model to the data in order to compare the effect of including the additional juvenile states. Due to the different capture and survival rates for juveniles in states S_2 and S_3, it is not possible to incorporate the birth data into the JS model. As such, the super-population that the JS model is estimating, will be the total number of individuals in the adult 'alive' state that are ever available for capture during the study. The MSJS model is able to estimate the same adult super-population, but it is also able to estimate the super-population of individuals who ever make it into state S_3 or S_4, which we will refer to as the juvenile super-population, as well as the total number of individuals that were ever in any of the 'alive' states, S_2, S_3, or S_4, which we will refer to as the total super-population. For the same reason, the JS model is able to estimate occasion-based removal-entry probabilities for adults, while the MSJS model is able to estimate occasion-based removal-entry probabilities for adults and for newly-born juveniles. Thus, comparisons can be made on each model's ability to accurately estimate the parameters $(\gamma_{\text{Ad},1},...\gamma_{\text{Ad},7})$, $(\phi_1,\cdots,\phi_6)$, $N_{\text{Adult},1},\cdots,N_{\text{Adult},7}$, and N_{Adult}, where N_{Adult} represents the size of the adult super-population. In addition, the MSJS model is also able to estimate the parameters associated with the juvenile population. This includes $(\gamma_{\text{Birth},1}, \cdots, \gamma_{\text{Birth},7})$, $(\phi_{juv,1} \cdot \phi_{juv,2})$, $N_{\text{Juv},1}, \cdots, N_{\text{Juv},7}$ and N_{Juv} and $N_1, \cdots N_7$, N, where $N_{\text{Juv},j}$ is the number of individuals on occasion j that are in one of states S_3 or $S4$ and N_{Juv} is the total number of individuals throughout the entire study that are ever in at least one of states S_3 or S_4. The reason for multiplying the juvenile survival parameters is that capture probability for individuals in state S_3 is 0, so the MSJS model will not be able to accurately estimate the distinct survival of each juvenile state, but it will be able to determine the two-period survival from state S_2 to state S_4. It is also worth noting that both models provide estimates of capture parameters but, as these are not the main focus of our estimation problem, we omit them from the subsequent comparison analysis.

Table 3.1: Parameter values for the 14 simulation scenarios with 1000 simulated adults and 1000 simulated newborn juveniles.

Scenario	$\phi_{\text{juv},1}$	$\phi_{\text{juv},2}$	ϕ	$p_{\text{juv},1}$	$p_{\text{juv},2}$	p
1	0.5	0.7	0.9	0.95	0	0.9
2	0.5	0.7	0.9	0.95	0	0.5
3	0.5	0.7	0.9	0.95	0	0.2
4	0.5	0.7	0.9	0.5	0	0.9
5	0.5	0.7	0.9	0.5	0	0.5
6	0.5	0.7	0.9	0.5	0	0.2
7	0.3	0.4	0.5	0.95	0	0.9
8	0.3	0.4	0.5	0.95	0	0.5
9	0.3	0.4	0.5	0.95	0	0.2
10	0.3	0.4	0.5	0.5	0	0.9
11	0.3	0.4	0.5	0.5	0	0.5
12	0.3	0.4	0.5	0.5	0	0.2
13	0.3	0.5	0.6	0.95	0	0.35
14	0.3	0.5	0.6	0.5	0	0.35

3.2 Simulation Results

3.2.1 Convergence

For each of the 14 scenarios and for each of the 100 simulated data sets, we fit both the MSJS and JS models to the data running 3 chains for 20000 iterations and removing a burn-in of 5000, resulting in a total of 15000 posterior samples for each parameter in the models. For each chain, initial parameter values were taken as a random draw from their prior distributions, resulting in dispersed initial values. In order to confirm that the samplers had converged, we used the method of Gelman and Rubin (1992) which compares the between-chain and within-chain variability for each parameter using several independent sequences with starting points sampled from an over-dispersed distribution. The quantity used to determine convergence, denoted by $\hat{R}$, is the quotient of the standard deviation of the pooled sample of all 3 chains (the between-chain variability) with the average of the standard deviations of each chain (the within-chain variability). As the number of iterations approaches infinity, $\hat{R}$ should approach 1 (Gelman and Rubin, 1992). Thus, for a given parameter, if $\hat{R}$ is near 1, this is evidence that the chains have converged together but it does not guarantee convergence to the posterior distribution. Conversly, if $\hat{R}$ is not near 1, then we know that the samplers have not converged (Brooks and Gelman, 1998). Using the gelman.diag function in R, we were able to compute $\hat{R}$ for each parameter of interest. Since $\hat{R} < 1.05$ in all replicates, we have evidence to support the convergence of the samplers.

3.2.2 Comparison of Relative and Absolute Bias

For each parameter, θ, we used the corresponding posterior median as a point-estimate, $\hat{\theta}$. Then, for each population size estimate, we computed the associated relative bias where, Relative Bias $= (\hat{\theta}-\theta)/\theta$ for some parameter θ. For the capture, survival, and removal-entry parameter estimates, we determined the associated absolute bias where, Absolute Bias $= |\hat{\theta}-\theta|$. We computed absolute bias for the probability parameters as they all fall between 0 and 1 and, as such, there is no need to scale the bias. As some of the true probability parameter values are quite small, dividing by the true parameter value can result in a misleading relative-bias. For each scenario described in Table 3.1, we compared the distributions of the relative and absolute biases of the common parameters for both the JS and MSJS models.

The estimation of the population parameters had varying rates of success between scenarios. The adult super-population parameter was estimated with very low relative bias in scenarios 1-6, and with higher relative bias in scenarios 7-14. The distributions of relative and absolute bias for all scenarios not included in this chapter are included in Appendix A. This suggests that lower adult survival results in a higher level of bias in the estimation of this parameter. In all scenarios, the adult super-population parameter tended to be over-estimated by both the JS and MSJS models. For the occasion-based population size parameters, $N_1, \cdots, N_7$, there were again varying results. In almost every scenario and for both models, the middle occasions $N_2, \cdots, N_6$ were estimated with lower relative bias than that of the initial and final occasions N_1 and N_7. This is to be expected as the identifiability of the first and last parameters is much weaker than that of the middle parameters. The estimation of the middle population size parameters had lowest relative bias for both models in scenarios 1, 2, 4, 5, 7, and 10 while the MSJS model produced estimates with lower relative bias than that of the JS model in scenarios 2, 3, 5, 6, and 7. This suggests that the occasion-based population size parameters are most accurately estimated when adult capture rates are high. It is difficult to comment succinctly on the over-estimation and under-estimation of these occasion-based population parameters as this trait differed by scenario and occasion.

That being said, both models did the same thing in this respect. That is, for a given scenario and occasion, say j, either both models would under-estimate N_j, both would over-estimate N_j, or both of the relative-bias distributions would be centered around 0, thus both over and under estimating the parameter. The absolute bias of the estimates of adult removal-entry parameters was quite small in all scenarios. The MSJS model had lower absolute bias for entry-removal parameters in scenarios 1-5, 7 and 10, whereas the JS model had lower absolute bias for these parameters in scenarios 13 and 14. In the remaining scenarios, both models performed similarly well. This suggests that when adult survival is less than 0.9 while at the same time adult capture is low, the MSJS model will struggle to estimate entry-removal parameters at the same level of accuracy as the JS model but when adult survival is high and/or adult capture probabilities are medium to high, the MSJS model is able to estimate removal-entry with low bias. Finally, the results of the estimation of the occasion-based adult survival parameters is best described by considering the estimation of parameters $\phi_1, \cdots, \phi_5$ separately from the estimation of ϕ_6. The first 5 survival parameters were estimated with low absolute bias by both models in scenarios 1, 2, 4, 5, 7, and 10, while in scenarios 9 and 12, both models estimated these parameters with high absolute bias. This suggests that when adult capture is low, the estimation of survival is impacted. The absolute bias for the parameter ϕ_6 was consistently higher than that of the other survival parameters which likely results from the fact that there are no further occasions on which to observe individuals. The MSJS model was able to estimate this tail-end survival parameter with lower absolute bias than that of the JS model in scenarios 2, 3, 5, 6, 7, and 10 while the JS model was able to estimate it with lower absolute bias in scenarios 1, 4, 8, 9, 12, 13, and 14. Figures 3.2, 3.3 and 3.4 below illustrate the distributions of relative bias and absolute bias for each model and each common parameter for simulation scenarios 2, 7, and 14. We show scenarios 2 and 7 in order to illustrate two scenarios in which the MSJS model performs well and we show scenario 14 as it is the scenario which most closely resembles that of the Ancient Murrelet's of East Limestone Island.

In addition to computing relative bias for each population parameter estimate and absolute bias for each probability parameter estimate, we also sought to understand both the accuracy and precision of these estimates by computing the relative mean squared error, MSE, for each parameter, in each scenario, for each model. The relative MSE is found by dividing the standard MSE by the true value of the parameter. Also, in each scenario, for each of the 100 simulation runs, we computed 95% credible intervals for each parameter and determined the proportion of credible intervals that contained the true value of the parameter. In all scenarios and for both models, the MSE for the removal-entry parameters was quite small and the coverage of the credible intervals was quite high. However, since the true value of the removal-entry parameters is often very small, the relative MSE can sometimes appear to be large. For the survival parameters, $\phi_1, \cdots \phi_5$, the relative MSE was small and similar for both models in most scenarios. For the last-occasion survival parameter, ϕ_6, the MSJS model is able to estimate this parameter with lower relative MSE in scenarios 2, 3, 6, 7 and

10 which suggests that the MSJS model is able to outperform the JS model in the estimation of this tail-end parameter when capture rates are medium to low or when capture is high and survival is medium. The coverage of the credible intervals for the survival parameters is good (near 95%) in all scenarios and for both models. Finally, considering the population size parameters, coverage of the credible intervals for parameters $N_1, \cdots N_7$ is good in all scenarios. The coverage of the credible intervals for the super-population parameter N, however, is not as consistent. In scenarios 1-6, the coverage probability for N is high for both models (above 93%) whereas, in scenarios 8, 9, 11, 12, 13 and 14 the coverage probability for this parameter drops slightly to the mid to high 80%'s. The worst coverage probabilities occur in scenario 7, where only 60% of the credible intervals for both models contain the true value of N, and scenario 10, where the coverage probability is 54% for the MSJS model and 45% for the JS model. The relative MSE for the occasion-based population size parameters is similar in most scenarios with the tail-end parameter, N_7, being estimated with lower relative MSE by the MSJS model in scenarios 2, 3, 6, 7, 9 and 10. Tables 3.2, 3.3, and 3.4 show the relative MSE values and 95% CI coverage for scenarios 2, 7, and 14 which are the same scenarios for which we showed the graphs of the distributions of relative and absolute bias. The tables for the remaining scenarios are included in Appendix A.

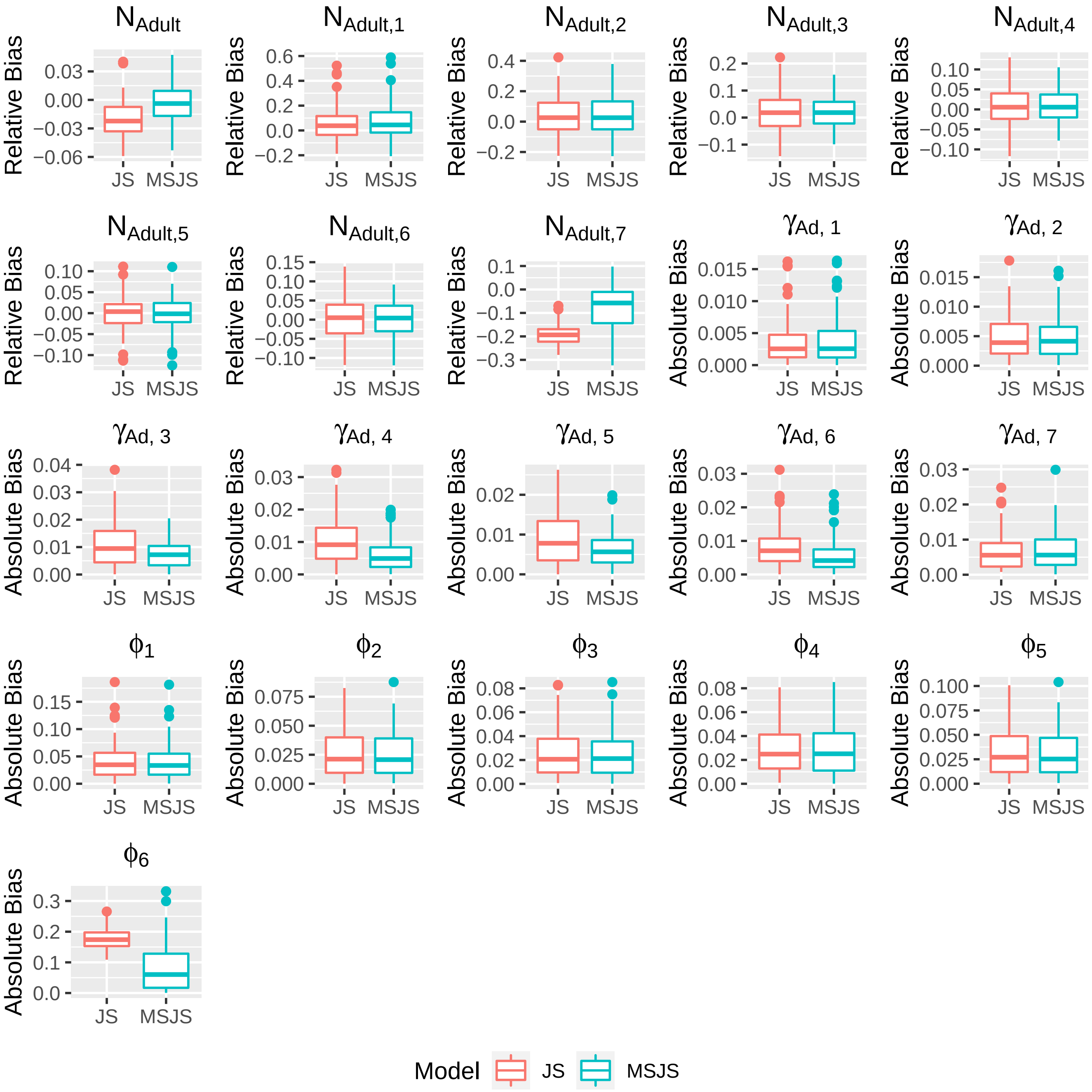

Figure 3.2: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 2).

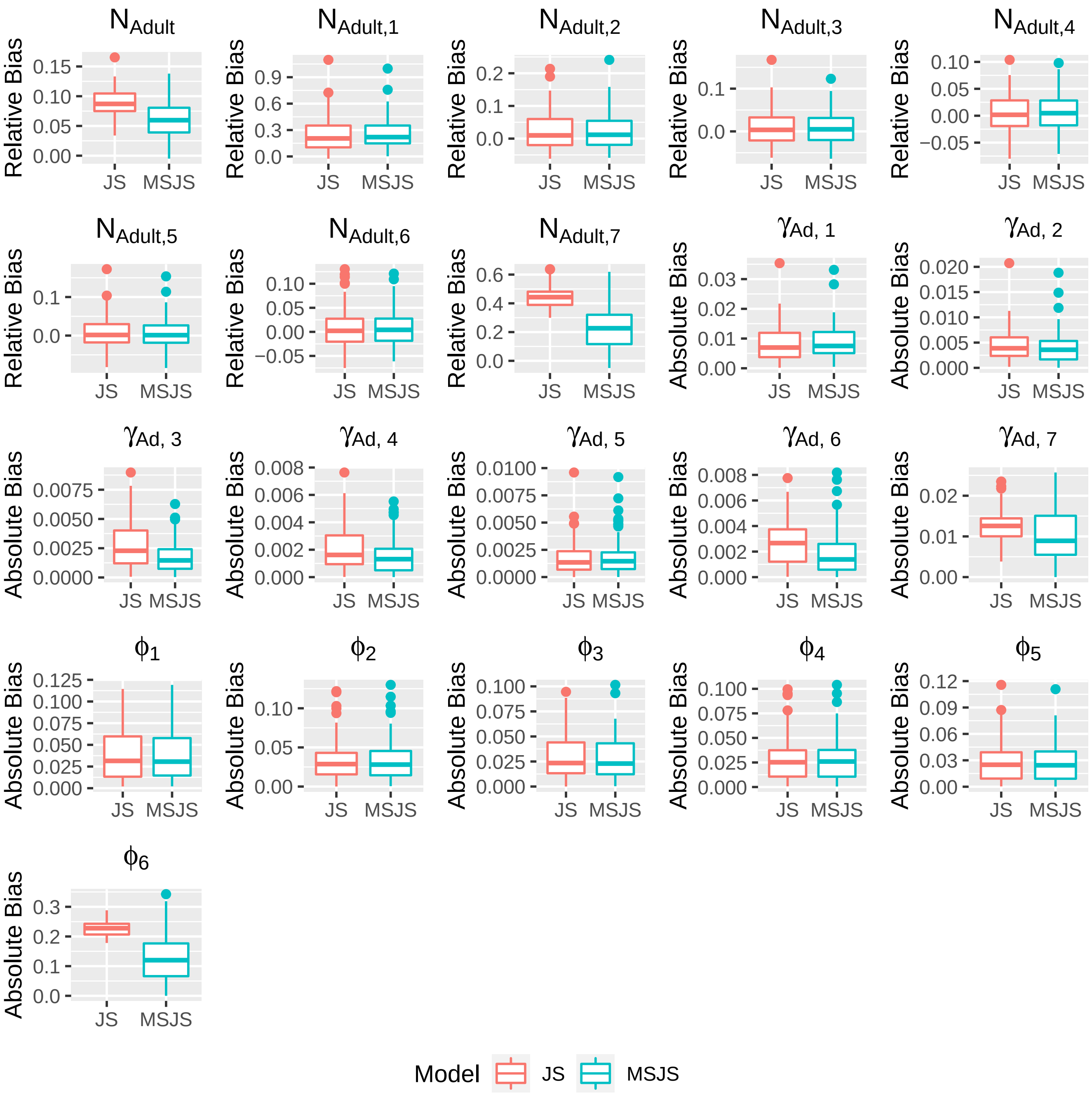

Figure 3.3: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 7).

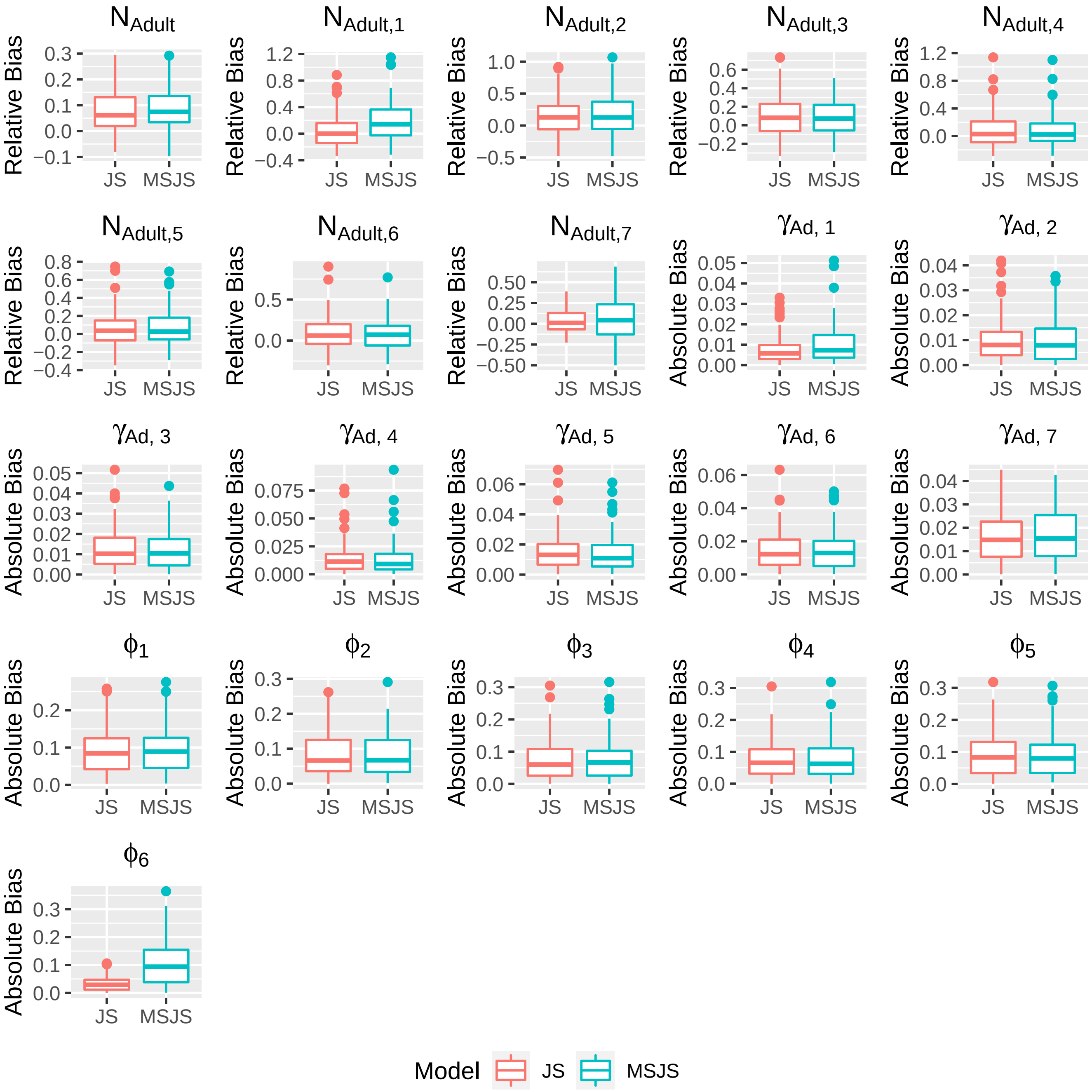

Figure 3.4: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\boldsymbol{\phi_{juv}} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 14).

Table 3.2: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 2). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.03	0.02	1.00	1.00	0	0
N_2	0.02	0.02	0.94	0.94	0.02	0.02
N_3	0.00	0.01	0.96	0.96	0.02	0.02
N_4	0.00	0.00	0.97	0.94	0.02	0.02
N_5	0.00	0.00	0.95	0.96	0.02	0.02
N_6	0.00	0.00	0.98	0.97	0.01	0.02
N_7	0.01	0.04	0.95	1.00	0.02	0
N	0.00	0.00	0.99	1.00	0.01	0
$\gamma_{\text{Ad},1}$	0.03	0.02	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.03	0.04	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.07	0.04	0.97	0.97	0.02	0.02
$\gamma_{\text{Ad},4}$	0.04	0.05	0.94	0.94	0.02	0.02
$\gamma_{\text{Ad},5}$	0.04	0.03	0.98	0.96	0.01	0.02
$\gamma_{\text{Ad},6}$	0.03	0.02	0.96	0.97	0.02	0.02
$\gamma_{\text{Ad},7}$	0.03	0.06	0.97	0.95	0.02	0.02
ϕ_1	0.00	0.00	0.97	0.97	0.02	0.02
ϕ_2	0.00	0.00	0.98	0.99	0.01	0.01
ϕ_3	0.00	0.00	0.96	0.95	0.02	0.02
ϕ_4	0.00	0.00	0.97	0.98	0.02	0.01
ϕ_5	0.00	0.00	0.97	0.95	0.02	0.02
ϕ_6	0.02	0.04	0.97	1.00	0.02	0

Table 3.3: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 7). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.10	0.10	0.98	0.98	0.01	0.01
N_2	0.00	0.00	0.94	0.94	0.02	0.02
N_3	0.00	0.00	0.98	0.98	0.01	0.01
N_4	0.00	0.00	0.95	0.96	0.02	0.02
N_5	0.00	0.00	0.94	0.95	0.02	0.02
N_6	0.00	0.00	0.93	0.94	0.03	0.02
N_7	0.08	0.20	0.96	1.00	0.02	0
N	0.00	0.01	0.60	0.58	0.05	0.05
$\gamma_{\text{Ad},1}$	0.10	0.11	0.99	0.98	0.01	0.01
$\gamma_{\text{Ad},2}$	0.03	0.03	1.00	0.99	0	0.01
$\gamma_{\text{Ad},3}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},4}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},5}$	0.00	0.00	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},6}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},7}$	0.08	0.20	0.99	0.99	0.01	0.01
ϕ_1	0.01	0.01	0.91	0.91	0.03	0.03
ϕ_2	0.01	0.01	0.94	0.94	0.02	0.02
ϕ_3	0.00	0.00	0.97	0.97	0.02	0.02
ϕ_4	0.01	0.01	0.94	0.93	0.02	0.03
ϕ_5	0.01	0.01	0.91	0.93	0.03	0.03
ϕ_6	0.09	0.21	0.93	0.94	0.03	0.02

Table 3.4: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\boldsymbol{\phi_{juv}} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 14). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.12	0.06	1.00	1.00	0	0
N_2	0.13	0.10	0.95	0.96	0.02	0.02
N_3	0.04	0.06	0.95	0.95	0.02	0.02
N_4	0.06	0.06	0.91	0.93	0.03	0.03
N_5	0.04	0.04	0.93	0.94	0.03	0.02
N_6	0.04	0.05	0.94	0.95	0.02	0.02
N_7	0.07	0.02	1.00	1.00	0	0
N	0.01	0.01	0.89	0.94	0.03	0.02
$\gamma_{\text{Ad},1}$	0.12	0.06	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.11	0.14	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.14	0.13	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},4}$	0.21	0.19	0.94	0.95	0.02	0.02
$\gamma_{\text{Ad},5}$	0.14	0.17	0.97	0.95	0.02	0.02
$\gamma_{\text{Ad},6}$	0.11	0.15	0.98	0.96	0.01	0.02
$\gamma_{\text{Ad},7}$	0.12	0.09	0.97	1.00	0.02	0
ϕ_1	0.04	0.04	0.98	0.99	0.01	0.01
ϕ_2	0.03	0.03	0.99	0.98	0.01	0.01
ϕ_3	0.02	0.02	0.96	0.96	0.02	0.02
ϕ_4	0.03	0.03	0.94	0.94	0.02	0.02
ϕ_5	0.03	0.04	0.94	0.96	0.02	0.02
ϕ_6	0.05	0.00	0.99	1.00	0.01	0

For the question of which model performs best, there does not seem to be one definitive answer. In many scenarios and for many parameters, both models performed very well. However, the MSJS model is able to incorporate all of the simulated data whereas the JS is not which means that the MSJS model better represents the data. For this reason, the MSJS model is also able to estimate parameters associated with the juvenile population which is an advantage over the JS model. There are many other advantages to the MSJS model; for example, the MSJS model allows for the distinction of capture, survival and removal-entry rates between individuals belonging to different states. This, in turn, allows for the incorporation of mark-recapture data on newly-born individuals that is collected in a manner that is different than that collected on the adults. The MSJS model is also able to estimate the population size of not-only the adults, but of any combination of individuals in the alive states S_2, S_3, and S_4. This gives greater control in terms of defining the population of interest. Furthermore, with the MSJS model, we are able to separately estimate the rate of birth and of adult immigration as entry into the population by way of either state S_2 or S_4 as these parameters are modelled separately by $\gamma_{\text{Birth},j}$ and $\gamma_{\text{Ad},j}$. That being said, the accuracy of the estimation of the additional juvenile parameters varies between scenarios. With the exception of the first and last occasion parameters, population parameter estimates had low relative-bias in scenarios 1, 2, 7 and 10, that is, when adult capture probability is high. The two-occasion juvenile survival rate, $\phi_{juv,1} \cdot \phi_{juv,2}$, is estimated with low absolute bias in every scenario but has the lowest absolute bias in scenarios 1, 2, 7, 8, and 10 which suggests that high capture rates improve estimates of juvenile survival. Finally, the juvenile birth removal-entry probabilities, $\gamma_{\text{Birth},1}, \cdots \gamma_{\text{Birth},7}$, were estimated with lowest absolute bias in scenarios 1, 2, 3, 7, 8, 9 and 13. This implies that the accuracy of estimation of birth entry-removal probabilities relies on the birth detection rate being high. Figures 3.5 and 3.6 illustrate the distributions of relative and absolute bias for simulation scenarios 1 and 14 for the juvenile parameters. Scenario 1 is one in which birth detection is 0.95 while, in scenario 14, birth detection is 0.5. The figures illustrate the great impact of the birth detection rate on the relative and absolute bias of the estimates of the juvenile parameters. The distributions of relative and absolute bias for the remaining scenarios are included in Appendix A.

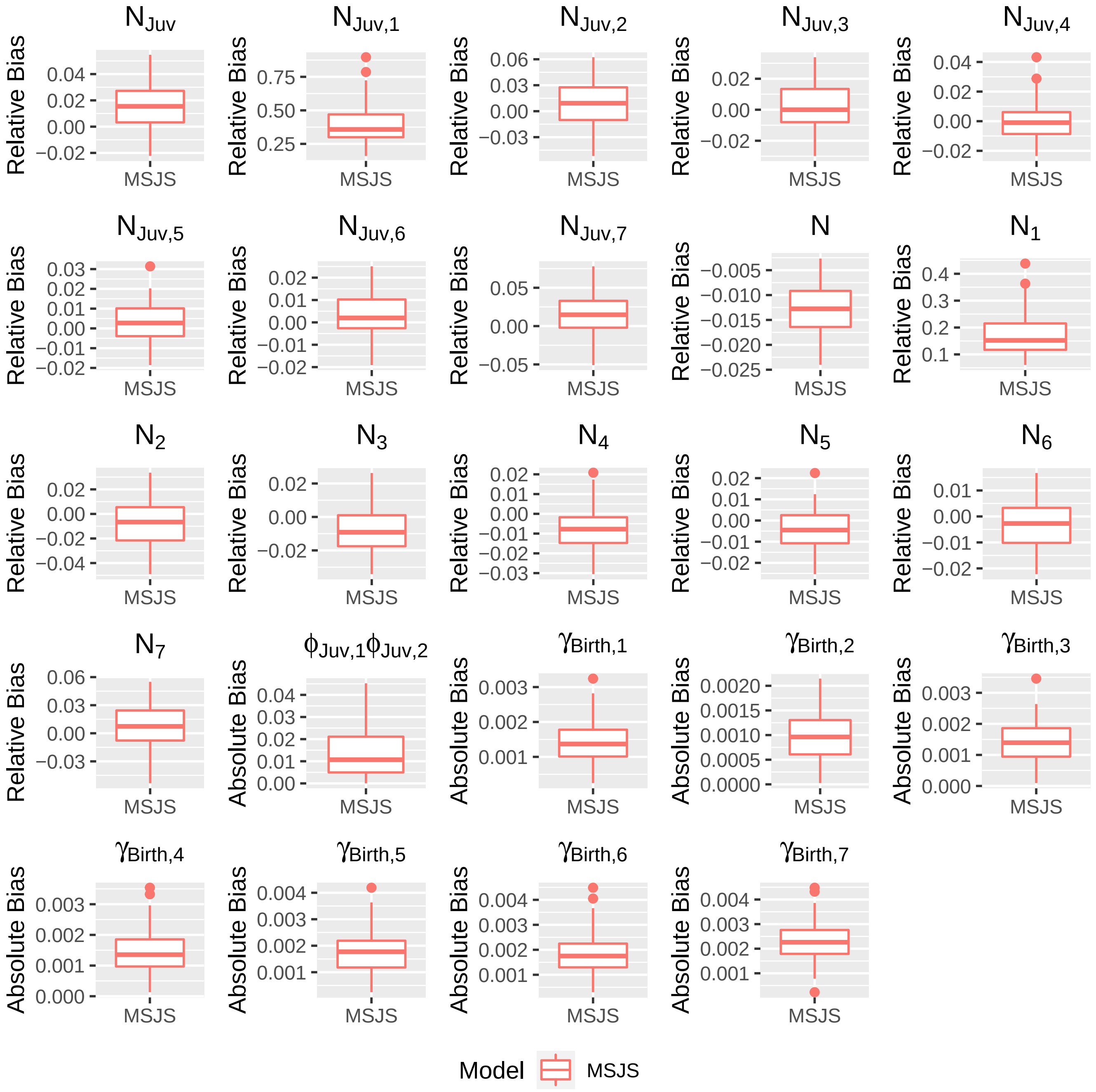

Figure 3.5: Distributions of relative and absolute bias for juvenile model parameters when the data is simulated for N= 1000 adults and N=1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 1, MSJS model).

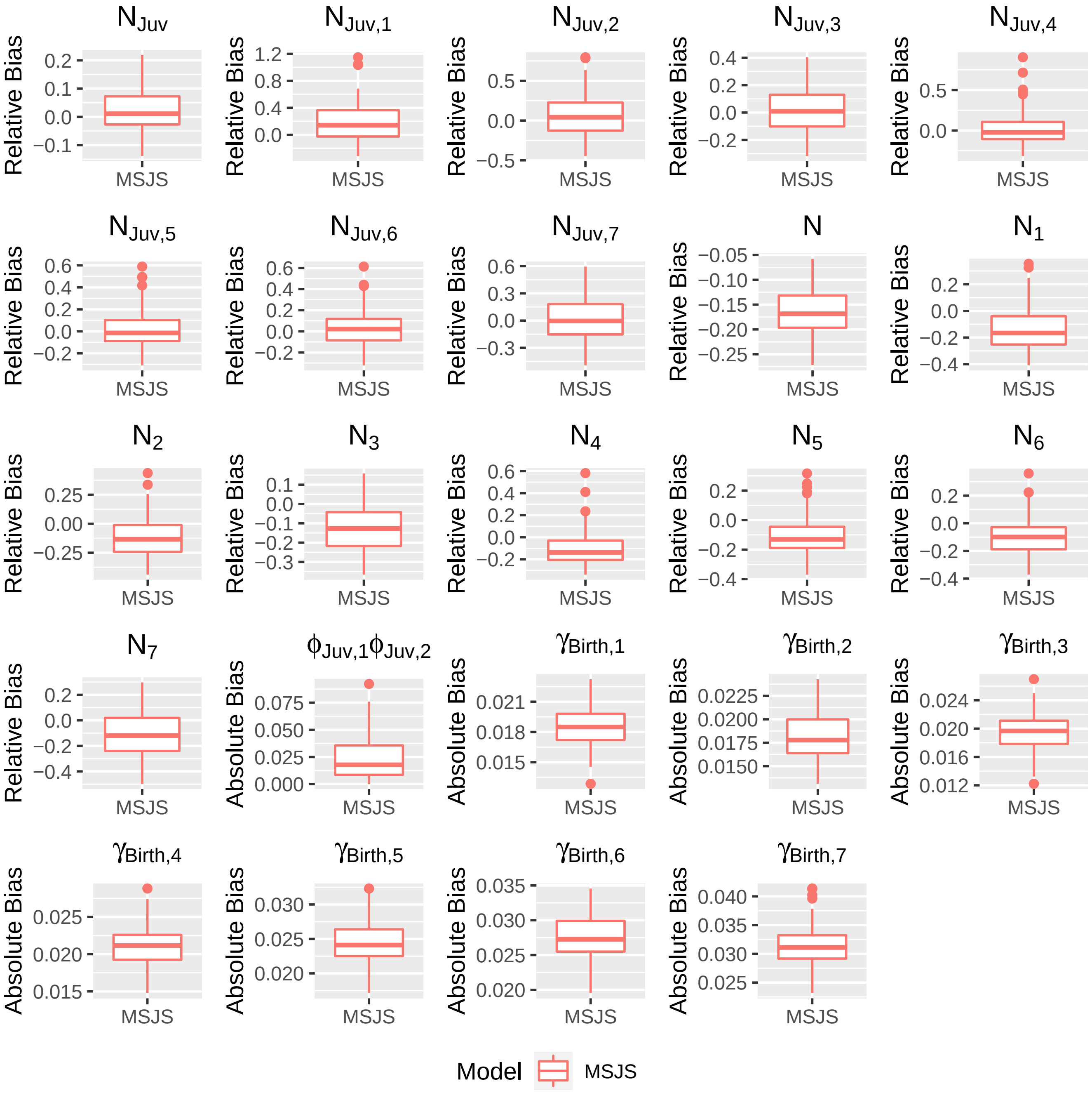

Figure 3.6: Distributions of relative and absolute bias for juvenile model parameters when the data is simulated for N= 1000 adults and N=1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\phi_{juv} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 14, MSJS model).

Chapter 4

Case Study: Ancient Murrelet Population on Limestone Island

Ancient Murrelets (*Synthliboramphus antiquus*) are burrow-nesting seabirds widespread throughout the North Pacific. Over half the world's population is thought to breed on Haida Gwaii, an archipelago off British Columbia's west coast (Gaston, 1994). In 1990, the Laskeek Bay Conservation Society (LBCS) began monitoring the Ancient Murrelet population on East Limestone Island to study the dynamic relationship between ocean and forest (Laskeek Bay, 2021). Figure 4.1 shows the location of East Limestone Island in relation to the rest of Haida Gwaii. Ancient Murrelet chicks, unlike almost all other seabird species, leave their nest at only a few days old. Led by the slope of the land as well as the moonlight and sound of the sea, they run to the ocean to join their parents (Gaston, 1990).

4.1 Data Collection

From 1990 to 2003, the LBCS tagged and released both chicks and adults. The trapping of the chicks occurred as they departed from their burrows by guiding them to banding stations close to the shore using a funnel system. There were six trapping stations that were all operated nightly throughout the chick departure period, with four funnels on the island's North Cove and two funnels on the island's Cabin Cove (see Figure 4.2). Upon capture, the chicks were banded with unique identifiers, weighed, and released to the sea as quickly as possible (usually in less than 5 minutes) (Gaston, 2013). It is estimated that the six trapping stations were able to intercept approximately 50% of the chicks departing their burrows during the study period (Gaston, 2011). After 2006, due to population decline concerns, chicks continued to be counted at the funnels but the birds were no longer banded to reduce handling time. Further, some of the funnels were no longer in use due to a blowdown that occurred on the North Cove of the island in 2010 (Laskeek Bay Conservation Society, 2021).

Between the years of 1990 and 2003, adult Ancient Murrelets were captured annually during two time periods; before the onset of incubation (beginning of April) and after the

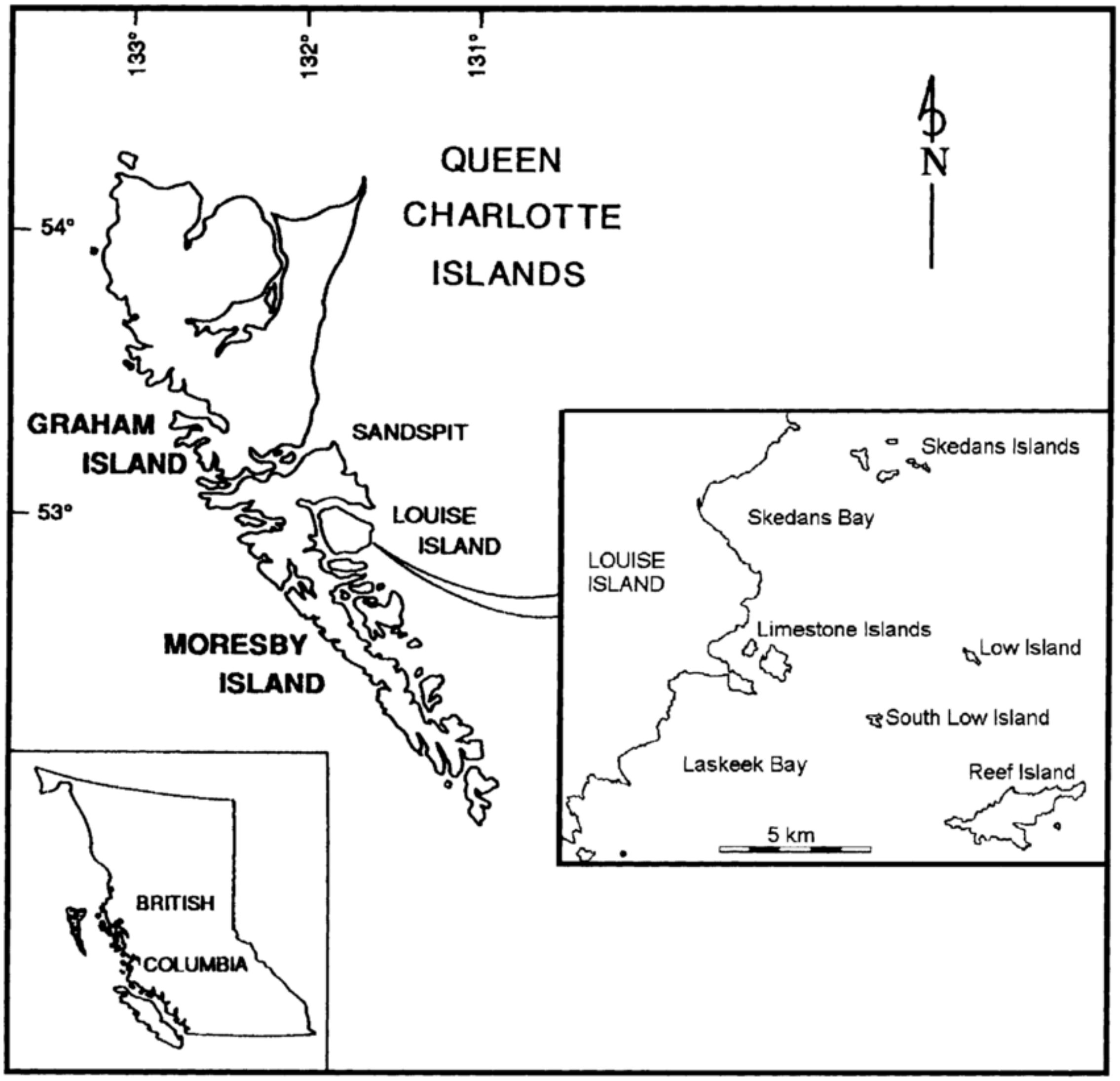

Figure 4.1: Map of Haida Gwaii showing the Limestone Islands. Image from Vila et al. (2003).

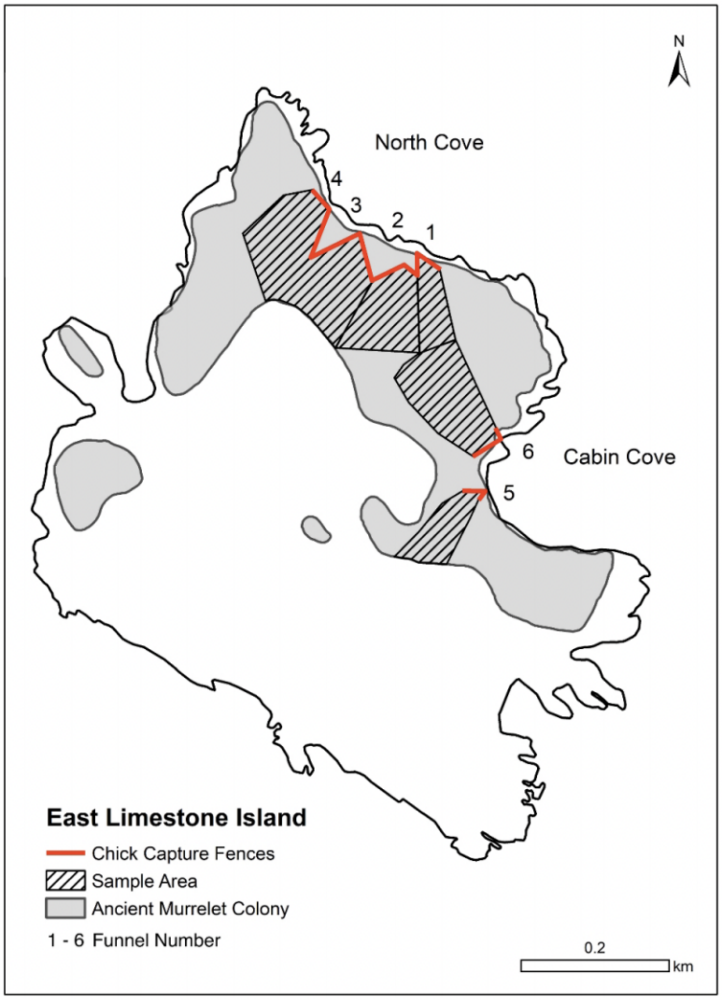

Figure 4.2: Map of East Limestone Island which illustrates the Ancient Murrelet colony, the chick capture fences and the sample area covered by each funnel. The chick trapping funnels are labelled by number with funnels 1-4 in the North Cove of the island and funnels 5-6 in Cabin Cove. Image from Parker et al. (2020).

20th of May by which time the chicks had begun departure from their burrows (Laskeek Bay Conservation Society, 2021). The method used to capture the adults changed part way through the study. From 1990 to 1994, the adults were located on the ground with a flashlight or headlamp and caught with hand-held dip nets. From 1995 to 2003, the adults were intercepted while departing from the colony using three large plastic flight nets which extended from the ground up to about 6 metres in height and were 70 metres in length (Gaston, 2011). Upon capture, the adults were banded with unique identifiers, inspected to determine the presence and size of brood patches, and then released. The size of the brood patch determines whether or not an adult is of breeding age. Birds with patches that are less than 11 mm in maximum diameter are considered to be non-breeders whereas adults with brood patches greater than 19 mm in maximum diameter are considered breeders (Gaston, 1990). Unfortunately, the size of the brood patch was not recorded for all captured individuals and, as such, this part of the data was not used in our model. Non-breeding birds are typically 2 and 3 years of age and will generally come to the colony in order to assess and select breeding sites ahead of their first nesting attempt which usually occurs at 3 or 4 years of age (Gaston, 1990).

4.2 Model Selection

Given that chicks leave the island soon after birth and are not expected to return to the island until they are 2 or 3 years of age, it seems reasonable that either a 5-state or 6-state model are good candidates for the combined Ancient Murrelet chick and adult mark-recapture data. In the case of a 5-state model, chicks are born into state S_2, leave the island and are not expected to be observed in state S_3, and, if they survive for 2 years, return to the island in the final 'alive' state, S_4. With a 6-state model, chicks are born into state S_2, leave the island and are not expected to return while in states S_3 and S_4, and, if they survive for 3 years, return to the island in state S_5. Figure 4.3 below illustrates the state-transition diagram for the 6-state model with constant juvenile parameters and time-varying adult survival. The transition diagram for the 5-state model can be found on page 19 in Chapter 3.

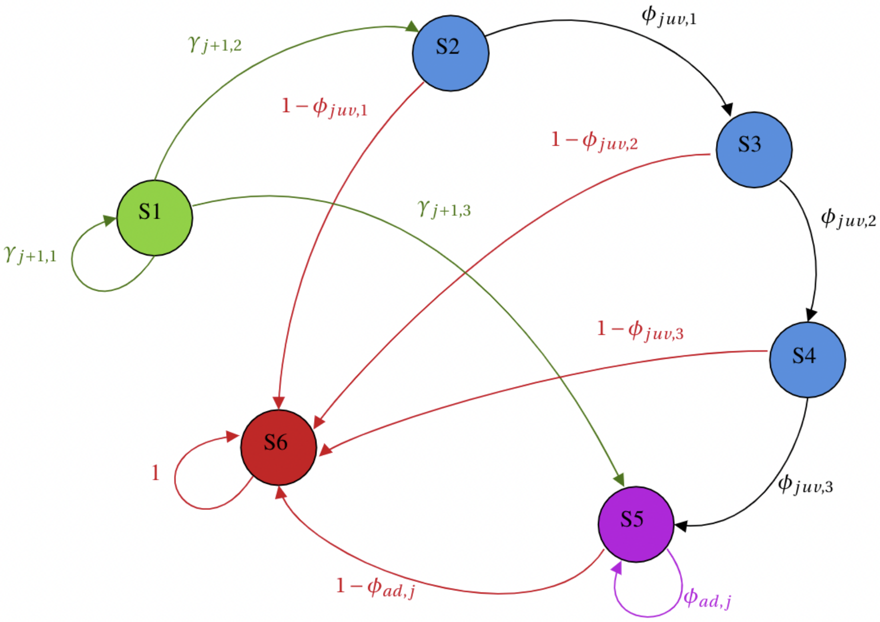

Figure 4.3: Illustration of the transitions between states S_1, S_2, S_3, S_4, S_5 and S_6 between times j and $j+1$, where S_1 is the 'not yet entered' state represented in green, S_2, S_3 and S_4 are the 'alive juvenile' states represented in blue, S_5 is the 'alive adult' state also represented in blue, and S_6 is the 'dead' state represented in red.

Since the adult Ancient Murrelets were captured using a different technique before 1995 from that used between 1995-2003, we focused on fitting the data from the later block of time in order to allow for the possibility of a model with constant rate of capture among the adults. Then, for both the 5- and 6-state models, we fit the adult capture and survival parameters to be either constant or time-varying. As mentioned in Chapter 2, for simplicity of the model, we make the assumption that the juvenile capture and survival rates are constant over time. In total we fit eight models to the data (Table 4.1). We used Uniform$(0,1)$ priors for adult capture probabilities and both adult and juvenile survival probabilities, a Dirichlet prior for removal-entry probabilities for each occasion, and, given the prior knowledge that the capture rate of chicks has been estimated to be 0.5 (Gaston, 2011), we used a Beta$(10,10)$ prior on that capture parameter, $p_{\text{Juv},1}$ as it is more heavily centered around 0.5. As there were a total of 1400 unique adults observed throughout the study, using a conservative estimate of adult capture of 0.2 leads to an estimated adult super-population of 7000. There were 4861 unique chicks observed throughout the study with an estimated chick capture rate of 0.5 leading to an estimated chick super-population of 9722. Using this information, we added 16000 rows of all-zero capture histories to the observed data matrix for a pseudo-population size, M of approximately 22000. This value of M is chosen to be safely greater than N but not so much greater as to cause significant computational lag.

We used deviance information criterion (DIC) as part of our model selection technique. However, defining a DIC measure in cases such as ours, where the models contain latent variables, is problematic and is not necessarily a reliable way to select the best model (Pooley & Marion, 2018). As such, we used DIC as a way to identify the number of states that the selected model should contain. We saw that, for both the 5-state and 6-state models, the constant survival and capture model and the time-varying survival and constant capture models yield the lowest DIC and that the DIC in these two scenarios is lower with the 6-state model. Thus we fit a 6-state model to the data. Table 4.1 details the candidate models and resulting DIC values.

Table 4.1: Parameter descriptions, number of parameters, deviance information criterion (DIC), and ΔDIC of eight candidate models fit to the combined adult and chick Ancient Murrelet data from 1995-2006. The abbreviation 'C' is used to represent 'constant' and 'V' is used to represent 'time-varying' parameters. In all models removal-entry parameters vary with time and juvenile capture and survival are constant.

Number of States	ϕ_{ad}	p_{ad}	Number of Parameters	DIC	ΔDIC
5	C	C	34	136124.8	50805.7
5	C	V	42	145612.4	60293.3
5	V	C	41	102003.7	16684.6
5	V	V	49	165414.8	80095.7
6	C	C	36	85319.1	0
6	C	V	44	199293.0	113973.9
6	V	C	43	98081.1	12762
6	V	V	51	214934.9	129615.8

In order to determine which of the four possible 6-state models best fit the data, we combined all possible models together using a method involving indicator variables which was first developed by Lynn Kuo and Bani Mallick in 1998 (Kuo and Mallick, 1998). Using this method, we set I_ϕ and I_p, to represent whether or not adult survival and adult capture are constant. Letting ϕ^* and p^* represent constant rates of survival and capture and ϕ_j^* and p_j^* represent time-varying rates of survival and capture, we can thus define adult survival, ϕ_j, and adult capture, p_j, as shown in equations 4.1 and 4.2 below, where $I_\phi = 1$ if survival is time-dependent and $I_p = 1$ if capture is time-dependent. Due to our preference for choosing a simpler model for the data, we place Bernoulli(0.05) prior distributions on both indicator variables.

$$\phi_j = (1 - I_\phi)\phi^* + I_\phi \phi_j^* \tag{4.1}$$

$$p_j = (1 - I_p)p^* + I_p p_j^* \tag{4.2}$$

In order for the above-described models to converge, the samplers needed to run for a longer time than was required in the simulation studies. For each model we augmented the observed capture histories with 16000 all-zero rows, ran 4 chains for 70000 iterations with a burn-in of 35000 resulting in 35000 posterior samples for each parameter. Again, we used the Gelman and Rubin quantity $\hat{R}$, ensuring that $\hat{R} < 1.05$ for all parameters.

4.3 The Selected Model and its Results

The resulting probabilities associated with the indicator variables are $P(I_\phi = 1) = 0.08$ and $P(I_p = 1) = 0.03$, which suggests that the 6-state model that best fits the data is the one in which adult survival and capture probabilities are both constant. In Table 4.2 below, we list the mean and median estimates for each adult parameter as well as the corresponding 95% credible interval. The removal-entry parameters are not very useful on their own, it is when they are multiplied with M that we can obtain the expected number of individuals entering the population on each occasion, as shown in equation 1.1 in Chapter 1. We will denote the number of adults that are new to the population on occasion j by B_j, where B_1 represents the number of adults that were in the population at the beginning of the study. Table 4.3 gives the expected number of adults entering the population on each occasion based on the selected model's estimates of the removal-entry parameters.

The resulting point-estimate for adult survival is 0.62 with 95% credible interval $(0.59, 0.65)$ and the point-estimate for adult capture is 0.28 with 95% credible interval $(0.25, 0.32)$. Since we do not expect to observe individuals in juvenile states, the juvenile survival parameters $\phi_{\text{Juv},1}, \phi_{\text{Juv},2}$, and $\phi_{\text{Juv},3}$ are not identifiable. Instead, we can estimate the three year survival rate $\hat{\phi}_{\text{juv},1} \cdot \hat{\phi}_{\text{juv},2} \cdot \hat{\phi}_{\text{juv},3} = 0.33 \cdot 0.29 \cdot 0.64 \approx 0.06$. This corresponds closest to scenarios 13 and 14 of the simulation study in which the data was simulated using an adult survival rate of 0.6 and an adult capture rate of 0.35. We also know, from previous research, that the chick detection rate, $p_{juv,1}$ should be approximately 0.5 (Gaston, 2011) which means that scenario 14 from the simulation study represents the Ancient Murrelet data the closest. We know from the scenario 14 simulation that the MSJS model has a slight tendency to over-estimate the occasion-based adult population parameters, as well as to over-estimate the removal-entry parameters and survival.

The expected number of new adults in the year 2000 is extremely low. Table 4.4, illustrates the number of adults captured on each occasion as well as the subset of those adults that were recaptured in that year. It is worth noting that the number of adults captured in the year 2000 is significantly lower than in any other year with many of the observed adults being previously tagged and recaptured on this occasion.

Table 4.2: Parameter estimates and credible intervals for the 6-state multistate Jolly-Seber extension model with constant adult survival and capture.

Parameter	Posterior Mean	Posterior Median	95% Credible Interval
N_1	733	730	(625, 856)
N_2	980	976	(850, 1126)
N_3	1207	1200	(1068, 1372)
N_4	997	996	(876, 1132)
N_5	833	832	(753, 924)
N_6	504	503	(440, 578)
N_7	592	590	(512, 681)
N_8	569	567	(499, 649)
N_9	413	412	(358, 479)
N	2852	2850	(2643, 3074)
$\gamma_{\text{Birth},1}$	0.03	0.03	(0.03, 0.04)
$\gamma_{\text{Birth},2}$	0.03	0.03	(0.02, 0.03)
$\gamma_{\text{Birth},3}$	0.03	0.03	(0.02, 0.04)
$\gamma_{\text{Birth},4}$	0.01	0.01	(0.01, 0.02)
$\gamma_{\text{Birth},5}$	0.01	0.01	(0.01, 0.02)
$\gamma_{\text{Birth},6}$	0	0	(0, 0)
$\gamma_{\text{Birth},7}$	0.02	0.01	(0.01, 0.02)
$\gamma_{\text{Birth},8}$	0.01	0.01	(0.01, 0.02)
$\gamma_{\text{Birth},9}$	0	0	(0, 0.01)
$\gamma_{\text{Ad},1}$	0.03	0.03	(0.03, 0.03)
$\gamma_{\text{Ad},2}$	0.04	0.04	(0.03, 0.04)
$\gamma_{\text{Ad},3}$	0.03	0.03	(0.03, 0.04)
$\gamma_{\text{Ad},4}$	0.03	0.03	(0.03, 0.03)
$\gamma_{\text{Ad},5}$	0.03	0.03	(0.02, 0.03)
$\gamma_{\text{Ad},6}$	0.03	0.03	(0.03, 0.04)
$\gamma_{\text{Ad},7}$	0.04	0.04	(0.04, 0.05)
$\gamma_{\text{Ad},8}$	0.04	0.04	(0.04, 0.05)
$\gamma_{\text{Ad},9}$	0.04	0.04	(0.04, 0.05)
p_{ad}	0.28	0.29	(0.25, 0.32)
$p_{\text{juv},1}$	0.85	0.85	(0.8, 0.91)
$p_{\text{juv},2}$	0	0	(0, 0)
$p_{\text{juv},3}$	0.16	0.15	(0.05, 0.32)
ϕ_{ad}	0.62	0.62	(0.59, 0.65)
$\phi_{\text{juv},1}$	0.33	0.11	(0.01, 0.97)
$\phi_{\text{juv},2}$	0.29	0.15	(0.01, 0.93)
$\phi_{\text{juv},3}$	0.64	0.64	(0.22, 0.98)

Table 4.3: Expected number of adults that are new to the population on each occasion as well as the corresponding 95% credible interval computed from the removal-entry parameter estimates from the 6-state MSJS model with constant adult survival and capture rates.

Year	Expected Number of New Adults	95% Credible Interval
1995	733	(615,868)
1996	540	(422, 672)
1997	591	(457, 735)
1998	251	(142, 369)
1999	214	(126, 308)
2000	5	(0, 20)
2001	258	(180, 349)
2002	187	(110, 273)
2003	42	(3, 103)

Table 4.4: The number of adults that are captured on each sampling occasion as well as the subset of these adults that are recaptured in that same occasion.

Year	1995	1996	1997	1998	1999	2000	2001	2002	2003
Total number of captured adults	209	271	368	273	254	64	182	164	141
Subset of adults that are recaptured	0	25	89	78	66	37	80	65	87

For comparison, we fit the standard JS model with constant surival and capture rates to the Ancient Murrelet data. We did not use the chick-capture data when fitting the JS model but instead used only the adult mark-recapture data. We again computed mean and median estimates for each parameter as well as 95% credible intervals. Table 4.5 below provides these values while Table 4.6 gives the expected number of adults that are new to the population on each occasion.

Table 4.5: Parameter estimates and credible intervals for the 6-state Jolly-Seber model with constant adult survival and capture.

Parameter	Posterior Mean	Posterior Median	95% Credible Interval
N_1	703	702	(614, 806)
N_2	946	946	(837, 1062)
N_3	1167	1165	(1045, 1301)
N_4	977	976	(875, 1086)
N_5	818	817	(750, 895)
N_6	483	483	(426, 548)
N_7	580	579	(506, 661)
N_8	560	559	(495, 634)
N_9	397	397	(346, 455)
N	2804	2806	(2670, 2949)
$\gamma_{\text{Ad},1}$	0.04	0.04	(0.03, 0.04)
$\gamma_{\text{Ad},2}$	0.03	0.03	(0.03, 0.04)
$\gamma_{\text{Ad},3}$	0.04	0.04	(0.03, 0.04)
$\gamma_{\text{Ad},4}$	0.02	0.02	(0.01, 0.02)
$\gamma_{\text{Ad},5}$	0.01	0.01	(0.01, 0.02)
$\gamma_{\text{Ad},6}$	0	0	(0, 0)
$\gamma_{\text{Ad},7}$	0.02	0.02	(0.01, 0.02)
$\gamma_{\text{Ad},8}$	0.01	0.01	(0.01, 0.02)
$\gamma_{\text{Ad},9}$	0	0	(0, 0.01)
p_{ad}	0.3	0.29	(0.27, 0.32)
ϕ_{ad}	0.61	0.61	(0.58, 0.64)

Table 4.6: Expected number of adults that are new to the population on each occasion as well as the corresponding 95% credible interval computed from the removal-entry parameter estimates from the standard JS model with constant adult survival and capture rates.

Year	Expected Number of New Adults	95% Credible Interval
1995	701	(668,745)
1996	676	(542, 816)
1997	738	(594, 882)
1998	345	(219, 469)
1999	290	(192, 384)
2000	7	(0, 25)
2001	341	(262, 424)
2002	245	(165, 321)
2003	51	(4, 117)

Both the MSJS and the JS models are producing similar parameter estimates for the population. This suggests that there is not enough additional information coming from the chick capture data to alter the parameter estimates. This is perhaps not entirely surprising as very few chicks are observed again after their initial capture. Table 4.7 provides the number of chicks captured on each occasion as well as the subset of those chicks that are ever captured again.

Table 4.7: The number of chicks that are captured on each sampling occasion as well as the subset of these chicks that are ever recaptured in a future sampling occasion.

Year	1995	1996	1997	1998	1999	2000	2001	2002	2003
Number of captured chicks	587	648	574	474	393	499	569	584	533
Number of observed chicks that are ever recaptured	6	8	4	3	1	2	0	0	0

There could be many reasons to explain why so few chicks are ever seen again. One reason could be that chicks have a very low 3-year survival rate, which is what the MSJS model is estimating with $\hat{\phi}_{\text{juv},1} \cdot \hat{\phi}_{\text{juv},2} \cdot \hat{\phi}_{\text{juv},3} = 0.33 \cdot 0.29 \cdot 0.64 \approx 0.06$. Another reason could be tag-loss which, for simplification purposes, our model has assumed does not occur. There is also the possibility that the chicks emigrate to another island, possibly the nearby Reef Island colony, which would be represented by chicks moving into the state ‘permanently left the population’. Regardless of the reason behind the low recapture of those individuals first observed as chicks, the result is that the chicks provide very little information about the future number of adults in the population. Given that the estimates from both models are so similar and the parameter estimates resemble a simulation scenario in which the JS model performed just as well if not better than the MSJS model, for this particular set of data, it makes sense to fit the adult data only, using the JS model, and to investigate a better way of incorporating the chick data into the MSJS model. We discuss some possible extensions of the MSJS model below.

Chapter 5
Conclusions and Further Research

5.1 Conclusions

We developed a multistate extension of the standard Jolly-Seber model, MSJS, which incorporates data collected on different age-classes of individuals in the same model. This model allows us to use unique capture and survival parameters for each class of individual. For example, with the Ancient Murrelet population of East Limestone Island, this allows us to fit both the chick capture data and the adult mark-recapture data to the same model, representing survival and capture of chicks with different parameters than the survival and capture of adults. The standard Jolly-Seber model, JS, is not able to do this as one of its underlying assumptions is that all individuals have the same probability of capture and survival on a given occasion. Thus, we can fit only the mark-recapture data collected on the adults to the JS model.

From the simulation study, we see that, in certain scenarios, the MSJS model is able to outperform the JS model. The MSJS model is able to estimate the occasion-based population size parameters, N_j, and the adult survival parameters, $\phi_{ad,j}$, with lower bias than that of the estimates produced by the JS model in scenarios in which adult survival is high while at the same time adult capture is medium to low or when adult survival is medium while at the same time adult capture is high. We also see that the MSJS model provides estimation of the removal-entry parameters, $\gamma_{\text{Ad},j}$, with lower bias than those provided by the JS model in scenarios in which adult survival is high. This suggests that when the survival of the both adults and chicks is high, the inclusion of chick data in the MSJS model provides additional information on the adult parameters. The relative MSE of the tail-end parameters, ϕ_6 and N_7, is lower for the MSJS model in scenarios in which adult survival is high while at the same time adult capture is medium to low or when adult survival is medium while at the same time adult capture is high. The MSJS model, however, does not always improve upon the results of the JS model. When both adult survival and adult capture are high, the MSJS model and the JS model perform similarly well. When adult survival is medium, either 0.5 or 0.6, and adult capture is medium to low, then the MSJS model and the JS model perform similarly well for the estimation of most parameters but the JS model estimates result in lower relative

MSE for the tail-end parameters, N_1, N_7 and ϕ_6. The MSJS model is also able to estimate population parameters regarding the juvenile population. From the simulation study, we saw that the MSJS model is able to estimate these juvenile parameters with low bias as long as the detection rate at birth is high.

The MSJS model that best fits the Ancient Murrelet data is the 6-state constant adult survival and constant adult capture probabilities model. The 6 possible states of an individual are 'not yet entered the population', 'newly born', '1 year old', '2 years old', 'adult, older than 2 years', and 'permanently left the population'. The parameter estimates that resulted from this model resembled the ones used in simulation scenario 14 and gave similar results to the JS model. We expect that the juvenile parameter estimates from the MSJS model will be biased as we know from previous research on the Ancient Murrelet population that detection at birth is around 50% (Gaston, 2011), and our detection rate was estimated to be 85%. The raw chick data show that very few individuals that are detected at birth are ever seen again. This is consistent with the suggestion that many Ancient Murrelet's disperse from their natal colony to breed (Gaston, 1990). It is thus not surprising that both the MSJS and JS models produced similar estimates as the chicks are providing very little additional information about the future population of adults.

The selected model resulted in a posterior-mean-estimate for the constant adult capture rate of 0.28 with 95% credible interval $(0.25, 0.32)$ and a posterior-mean-estimate for the constant adult survival rate of 0.62 with 95% credible interval $(0.59, 0.65)$. This is in line with previous research where the survival rate of adult Ancient Murrelet's was estimated using two rates; survival in the year following first capture and survival in each subsequent year. Survival analyses were carried out using mark-recapture methods implemented in the software M-SURGE 1.7 (Gaston, 2011). This resulted in an estimate of 0.43 ± 0.02 SE for survival in the year following the first capture and an estimate of 0.73 ± 0.01 SE for survival in each of the subsequent years (Gaston, 2011).

In a previous study, an N-mixture model, using the annual Ancient Murrelet chick counts, was used to estimate the annual number of adult breeding pairs on East Limestone Island (Parker et al, 2020). The annual population estimates provided by this model were substantially higher than the estimates of the adult population size given by both the MSJS and JS models. For example, in 1995, the MSJS model estimates the adult population size as 733 birds and the JS model estimates the adult population size as 701 birds while the N-mixture model gave an estimate of 901 breeding pairs of adults, thus 1802 breeding adults. Also, in 1995, the Canadian Wildlife Service (CWS) used mean burrow density across transects and mean occupancy rate for the colony to estimate the population of breeding adults on the island (Lemon, 2007). This study resulted in an estimated 1270 breeding pairs, or 2540 breeding adults. Some of the difference between the MSJS model estimates and the N-mixture model estimates can be accounted for in the data as the chick counts for some years were higher than the number of chicks that were marked. The N-mixture model used chick count data to determine estimates for the adult population while the MSJS model uses adult and chick mark-recapture data to estimate the adult population. However, as the chicks are rarely seen again, this does not account for much of the difference in the adult population size estimates. The drastic difference in estimates is likely due to the fact that the sample of Ancient Murrelet adults represented in the adult mark-recapture data used in both the MSJS and JS models is not representative of the full population of Ancient Murrelets on East Limestone Island. There is an important distinction between the biological population and the sample population. The biological population of interest is the adult population of Ancient Murrelet's on East Limestone Island whereas the sample population is the set of adult Ancient Murrelet's whose flight paths intersect with the nets used for capture. The capturing of adults was done using three nets that were placed in the same three locations each year; the North Cove, Spring Valley, and Cabin Cove. As can be seen in Figure 5.1, the three nets do not cover most of the East coast of the island and thus are never able to capture adults whose flight paths do not intersect with the nets. Ancient Murrelet's are very likely to return to the same burrow each year (Gaston, 1994) and, as such, the adults with burrows that are not part of the covered flight-paths, are not a part of the population that the MSJS and JS models are estimating. The MSJS and the JS models are providing estimates of some subset of the population of adult Ancient Murrelet's on East Limestone Island.

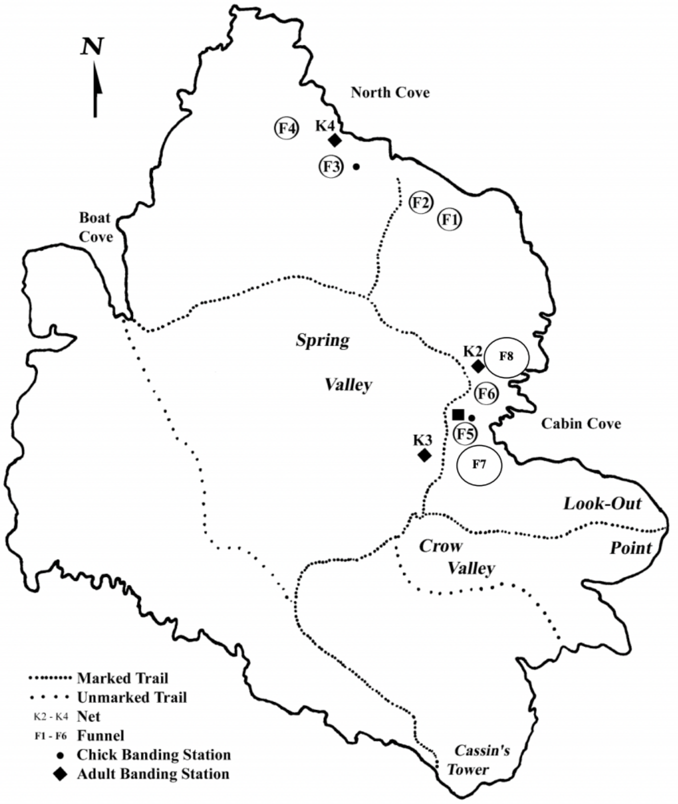

Figure 5.1: Map of East Limestone Island identifying the location of the three nets, $K2$, $K3$, and $K4$, placed in the North Cove, Spring Valley and Cabin Cove. Image from Laskeek Bay Conservation Society (2013).

5.2 Possible Model Extensions and Further Research

The results of the case-study in Chapter 4 motivate research into other possible extensions of the model which might find a more useful way to incorporate the data provided by the chicks. Instead of considering the impact of the number chicks on future population sizes, it might be more useful to instead model the relationship between the number of chicks observed on occasion j and the adult population on the same occasion j. This relationship has previously been considered. A statistical model estimating population abundance using counts from an auxiliary population and N-mixture models was created using Ancient Murrelet's on East Limestone Island as a case study (Parker et al, 2020). In this study, the available chick-count data was combined with known clutch size to estimate the total number of breeding pairs. A further extension of the MSJS model could thus involve informing a lower bound on the number of adults on a given occasion using the chick count from that year. We could also extend our model by including chick count data from 2004 up until current years as the

Laskeek Bay Conservation Society still performs a chick count each year.

The probabilities of adult and juvenile survival within an animal population are likely not independent of one another. As such, the MSJS model (which involves both of these parameters) might be able to better estimate juvenile survival parameters if they are expressed in terms of their relationship to adult survival. For example, perhaps the relationship between juvenile and adult survival could be expressed as the relationship; $\mathrm{logit}(\phi_{\mathrm{Ad},j}) = \beta_0 + \beta_1 j$ and $\mathrm{logit}(\phi_{\mathrm{juv},j}) = \beta_0 + \beta_1 j + \beta_2$. Further research could involve investigating if such a relationship exists and then representing it in the MSJS model.

The last possible extension of the MSJS which we will discuss would involve splitting up each of the annual adult-sampling occasions into two separate occasions as the adult Ancient Murrelt's of East Limestone Island were actually captured on two sampling occasions; at the beginning of April and toward the end of May. Since individual adults were available for capture on both occasions, we could fit a robust design model, assuming closure within each year, as a way to obtain independent estimates of capture probability for each year. We could also extend the model to include the data from 1990 to 1994, when the method used to capture adults was different. If we are able to estimate the capture probability independently for each year, then the impact of the difference in capture method would be represented in the estimates of capture probabilities in those years.

Appendix A
Simulation Study Distributions and Tables

A.1 Distributions of Relative and Absolute Bias for Common Model Parameters

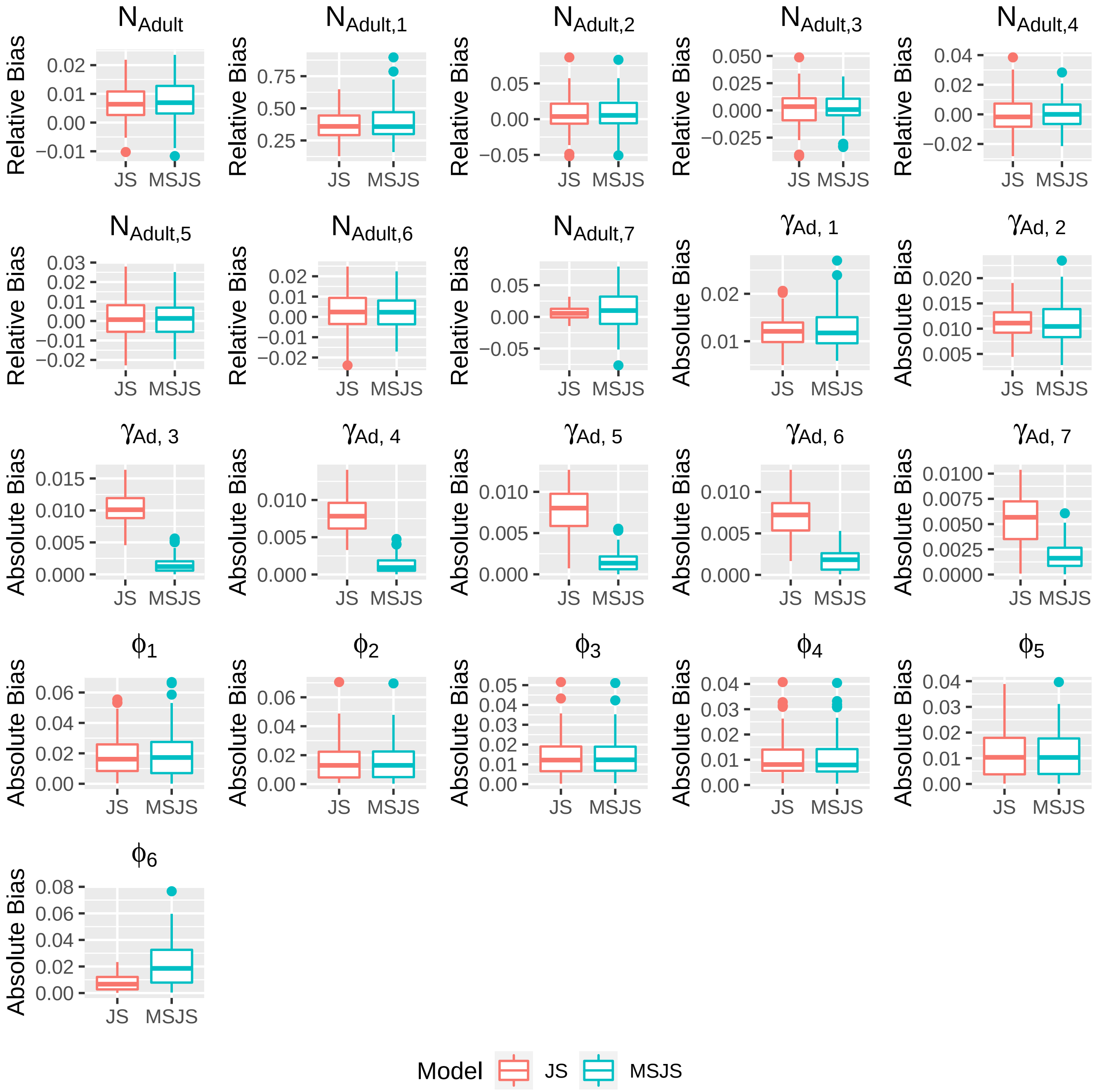

Figure A.1: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 1).

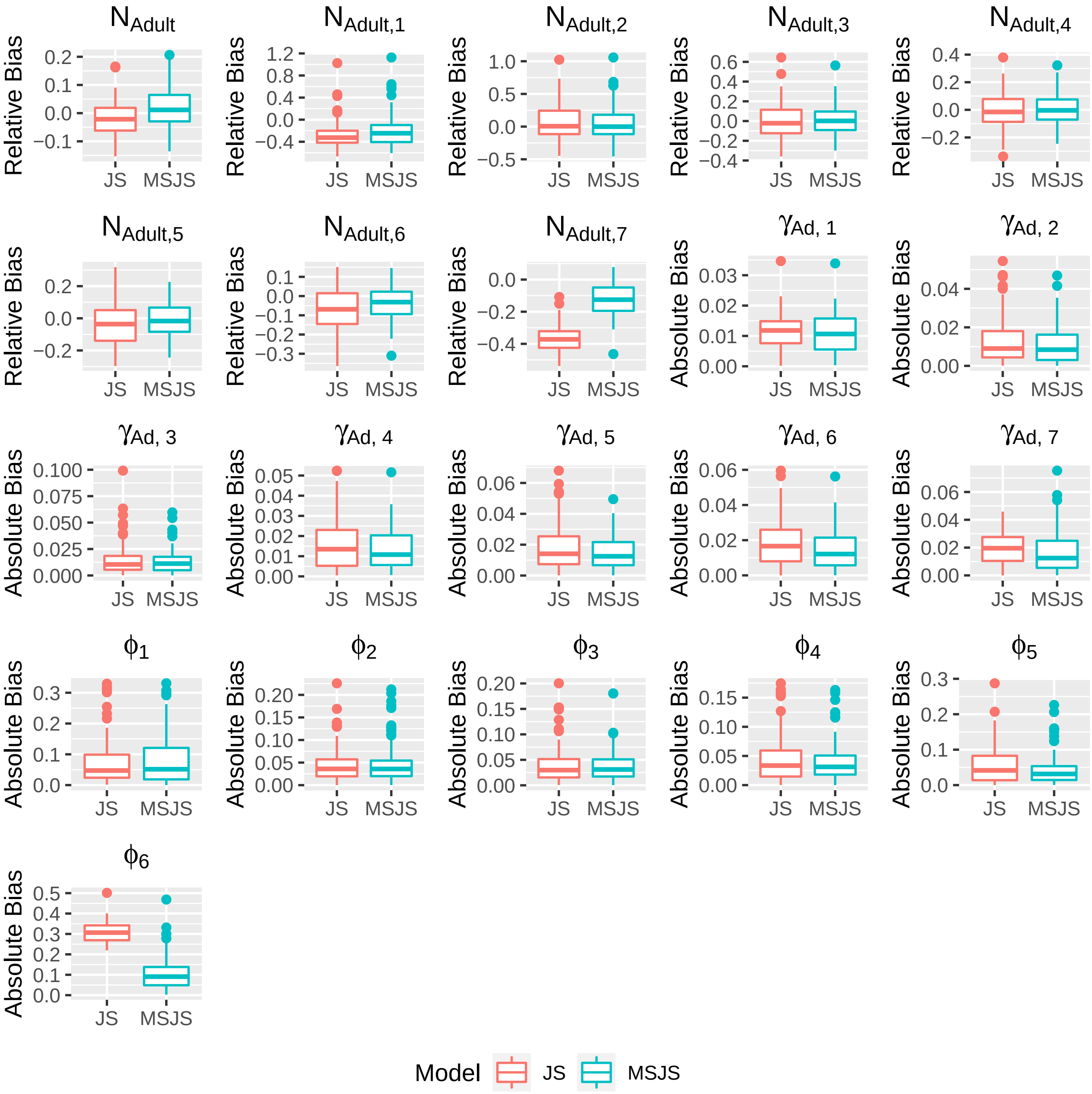

Figure A.2: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 3).

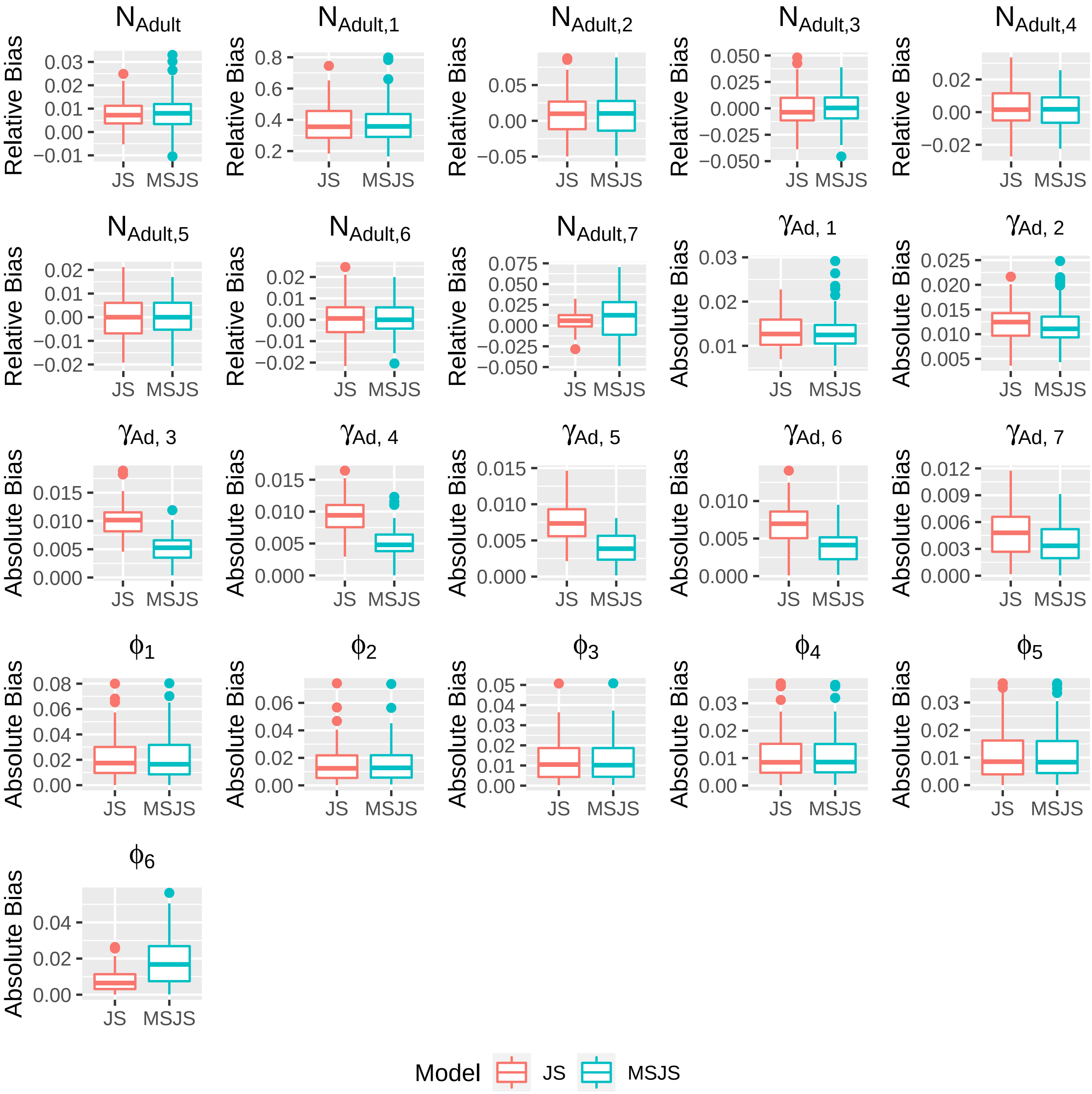

Figure A.3: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 4).

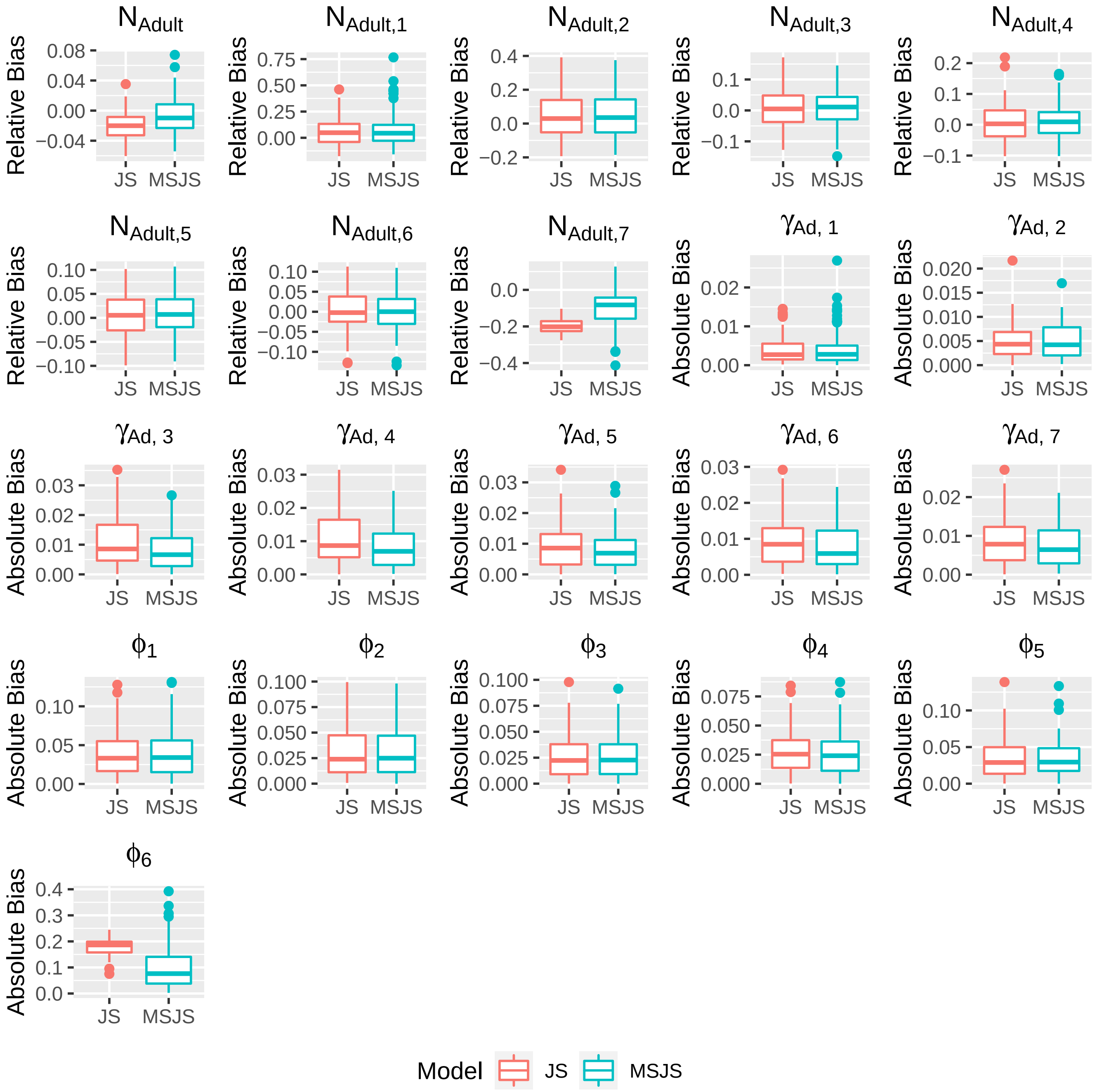

Figure A.4: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 5).

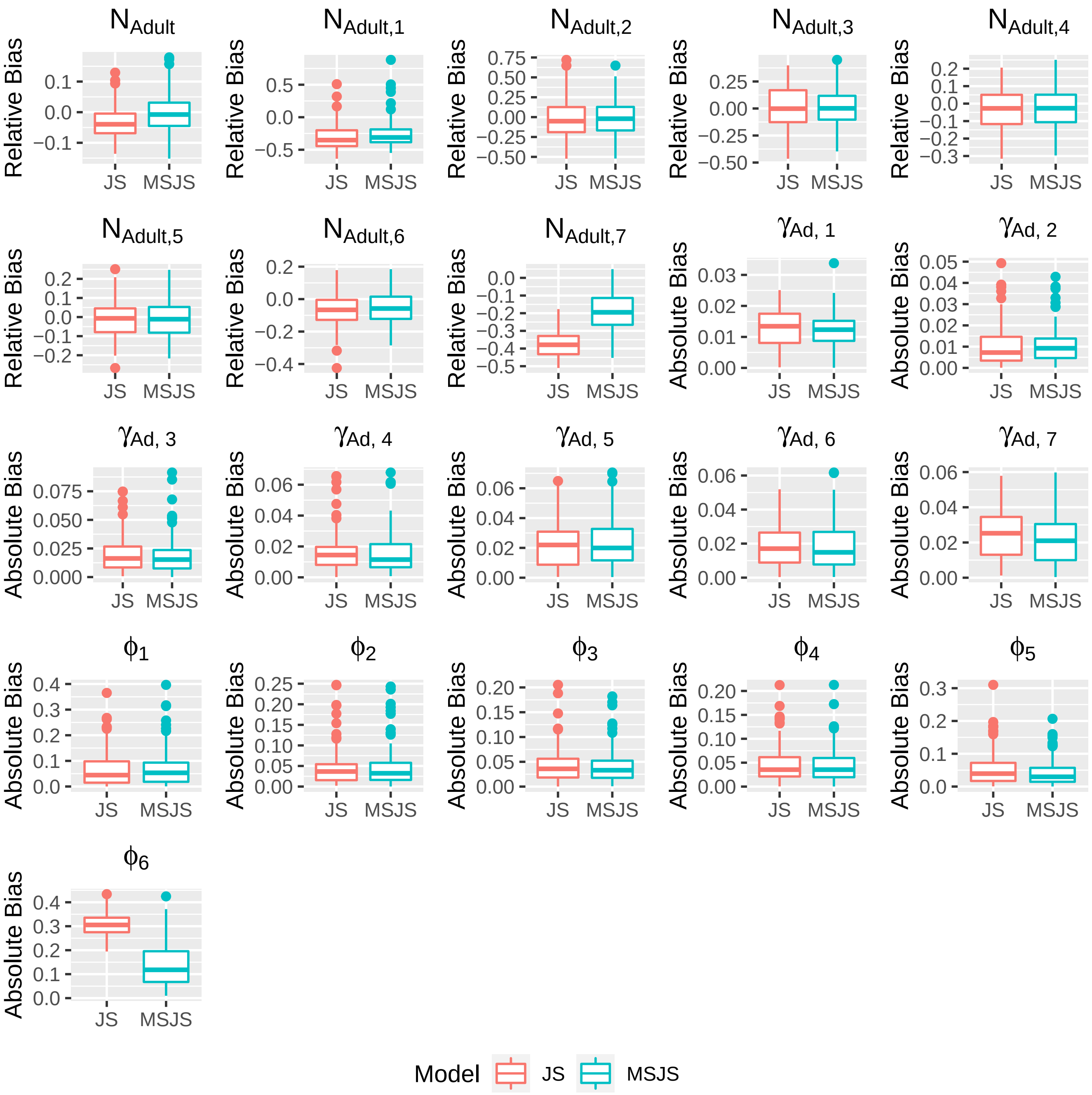

Figure A.5: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 6).

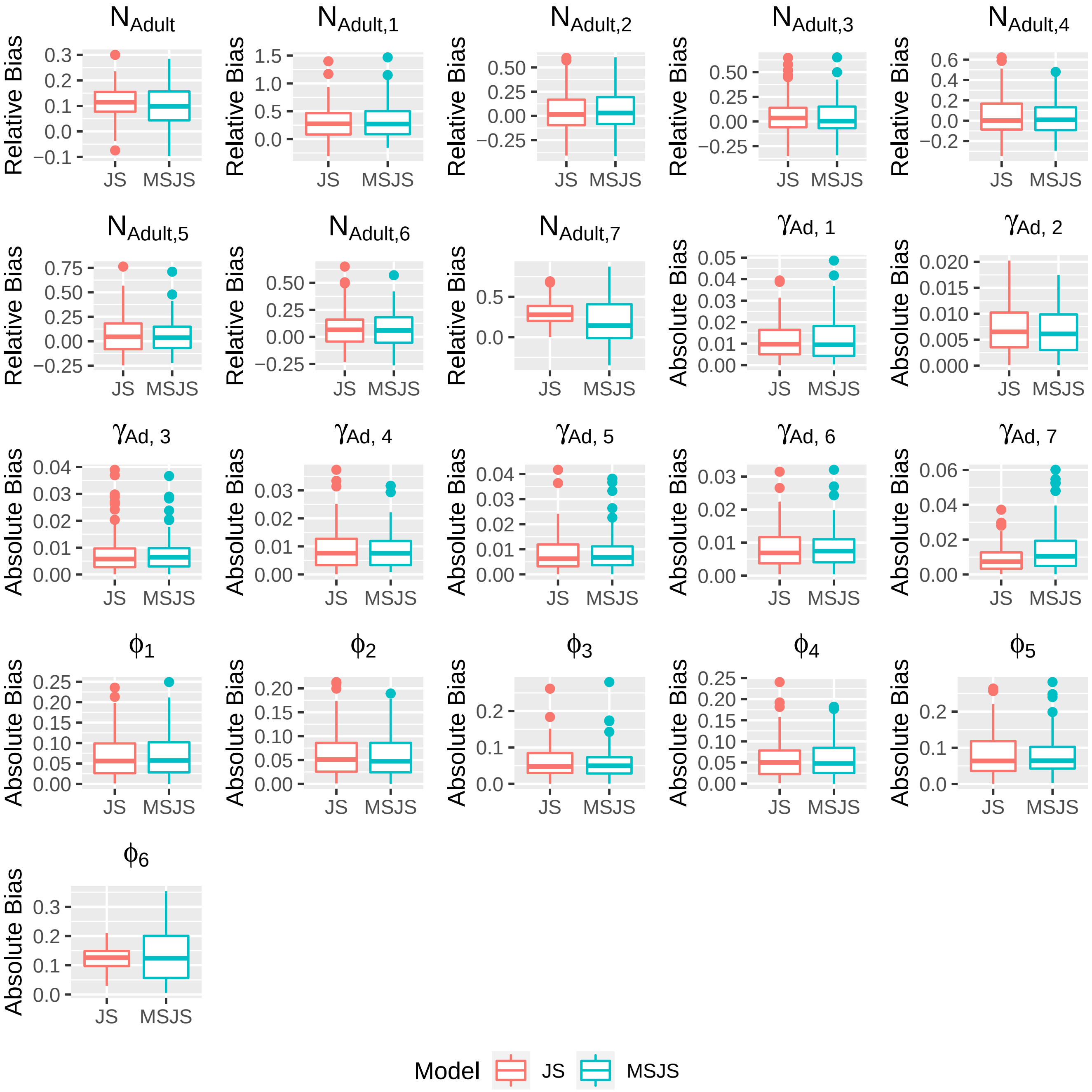

Figure A.6: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 8).

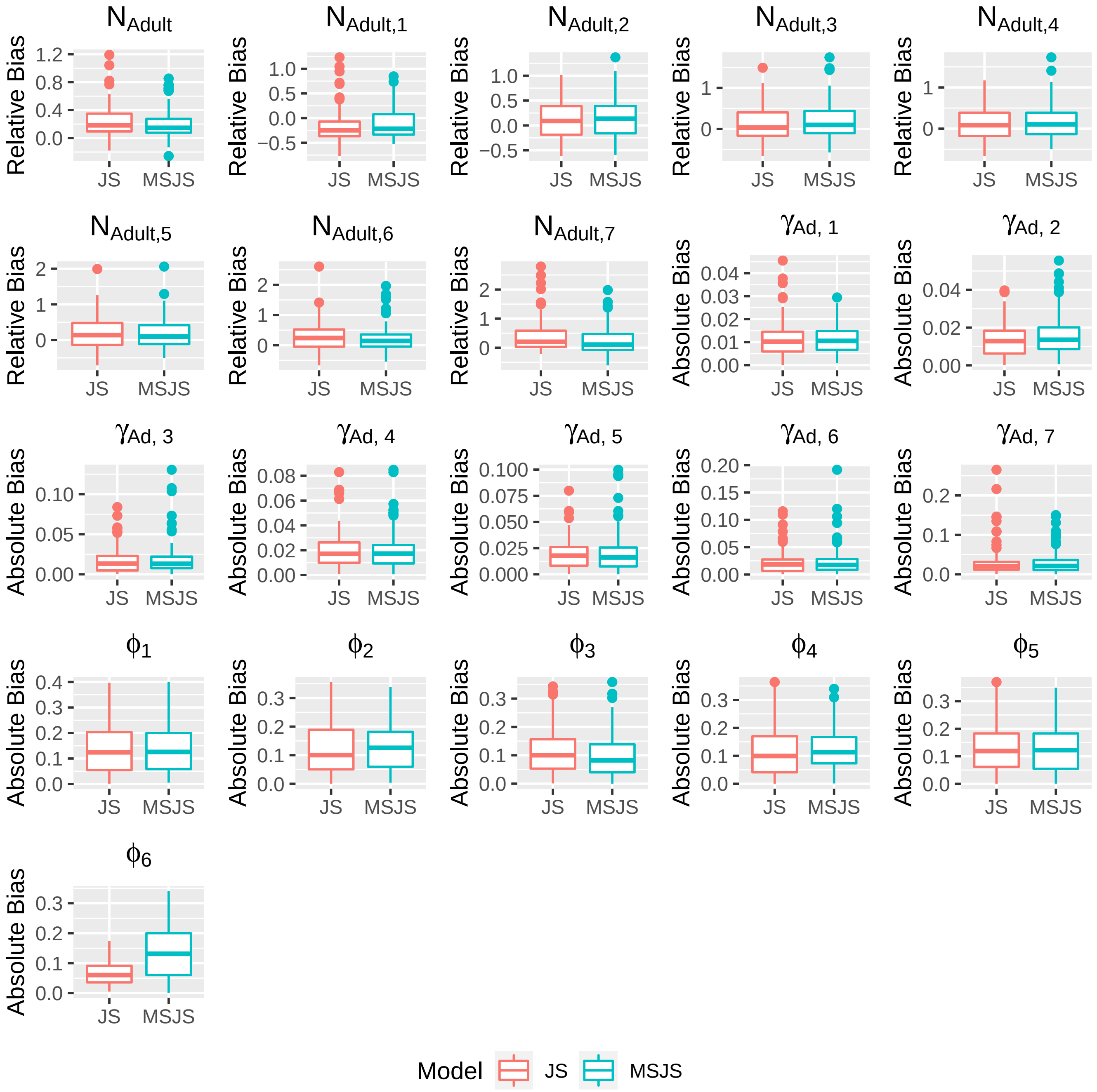

Figure A.7: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 9).

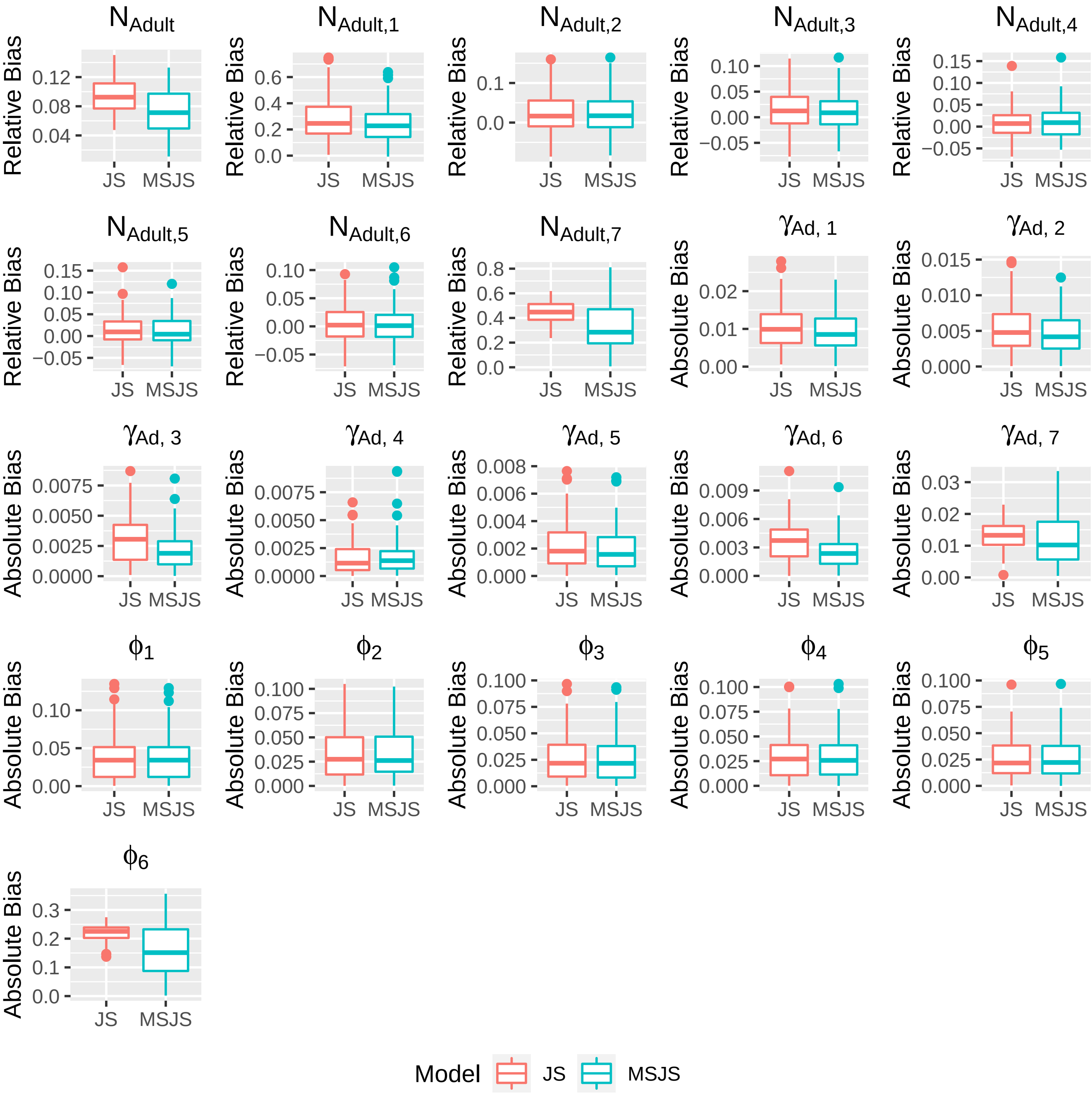

Figure A.8: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 10).

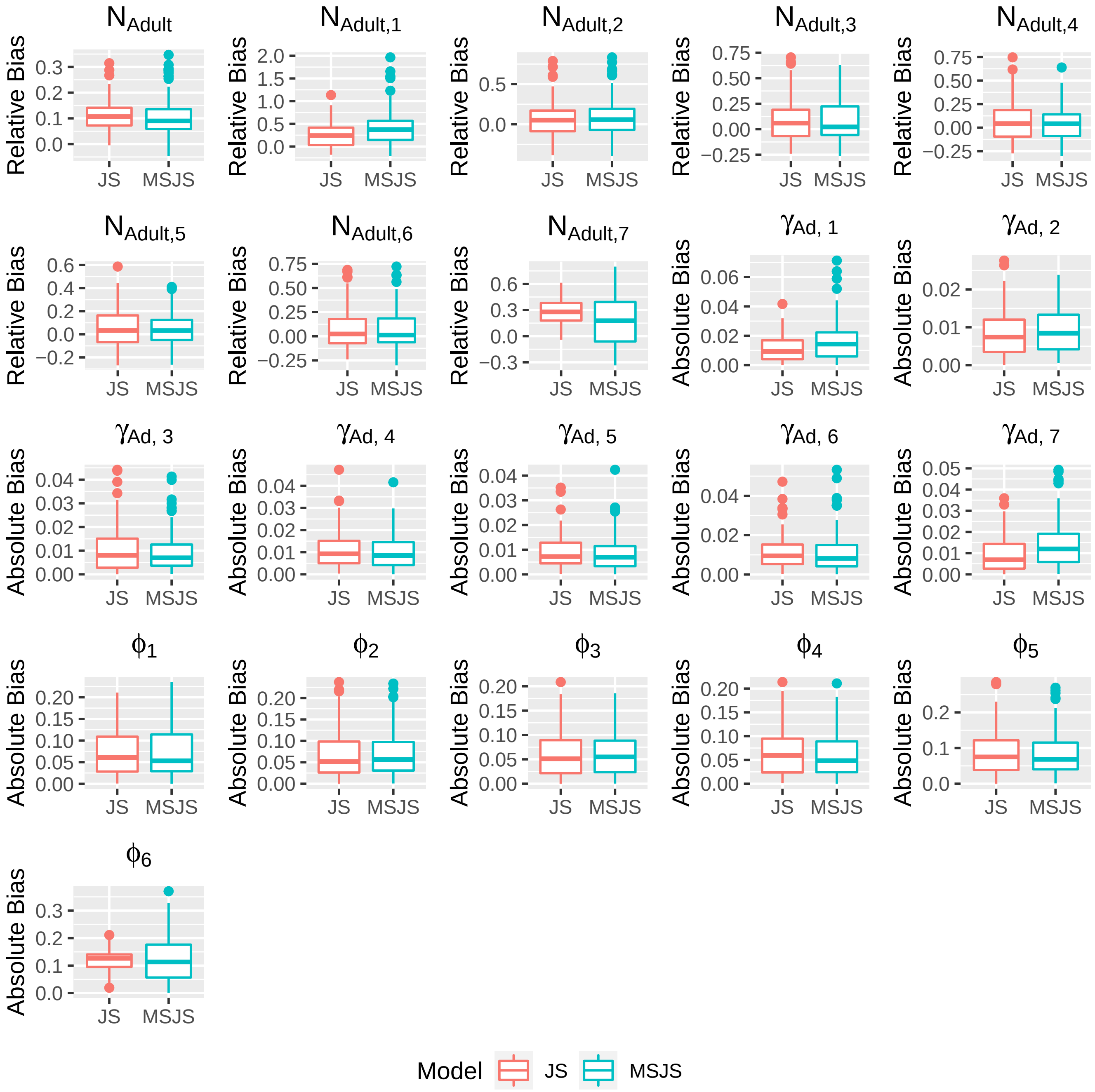

Figure A.9: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 11).

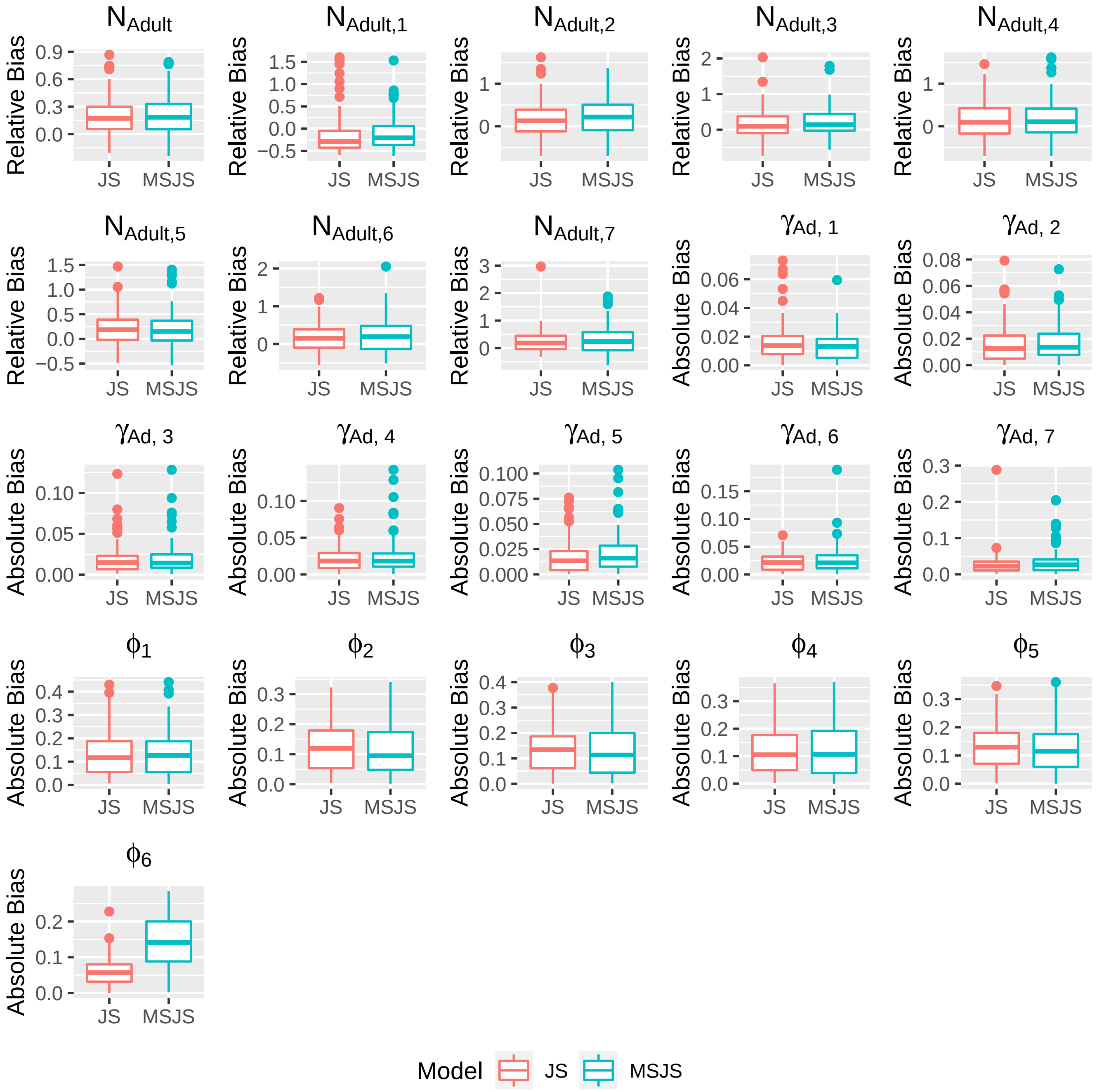

Figure A.10: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 12).

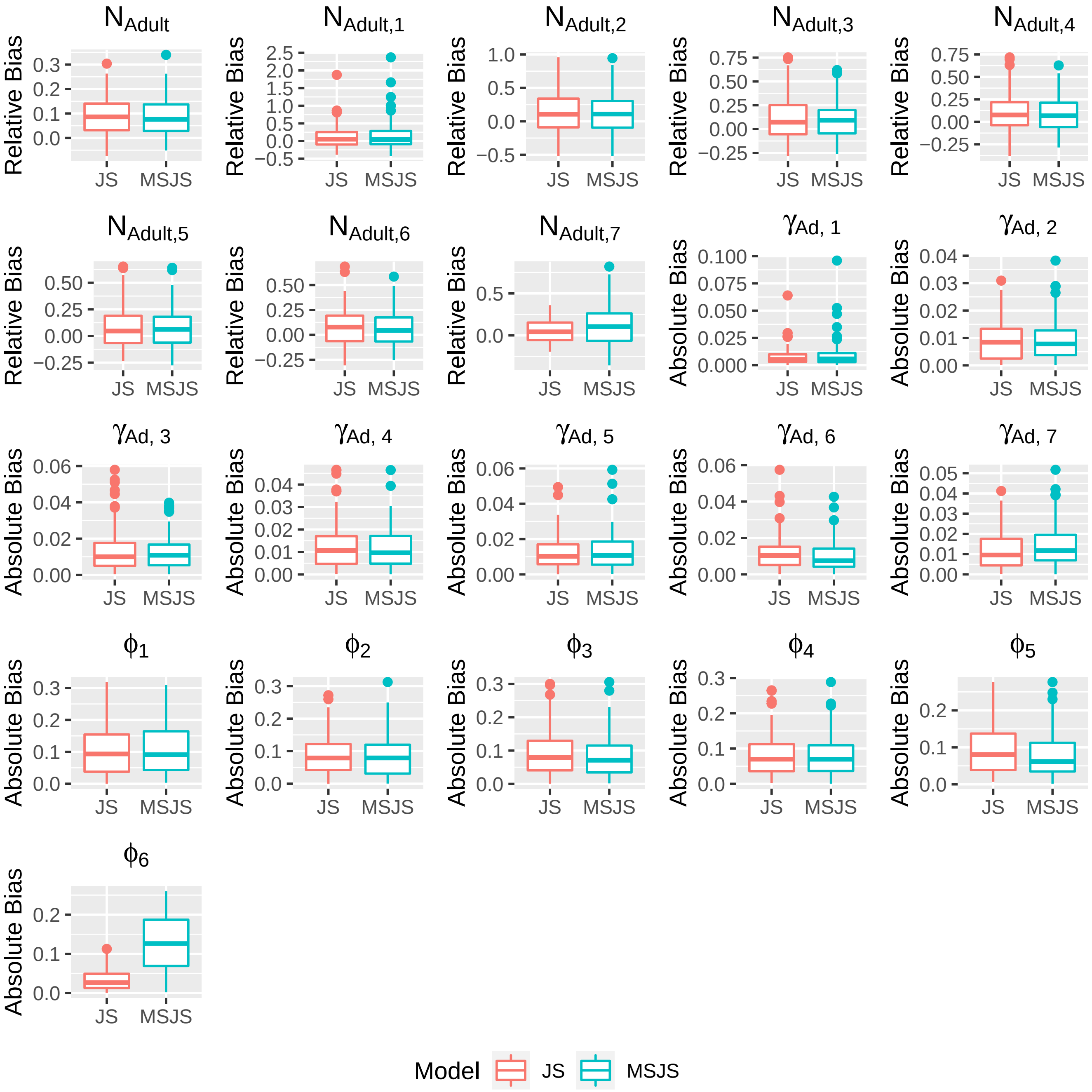

Figure A.11: Comparison of the distributions of relative bias for the population size parameters and of absolute bias for the capture, survival and entry parameters for the resulting 100 posterior medians when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\boldsymbol{\phi_{juv}} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 13).

A.2 Tables of MSE and 95% CI coverage for Common Parameters

Table A.1: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 1). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.17	0.15	0.98	1.00	0.01	0
N_2	0.00	0.00	0.97	0.97	0.02	0.02
N_3	0.00	0.00	0.95	0.95	0.02	0.02
N_4	0.00	0.00	0.97	0.96	0.02	0.02
N_5	0.00	0.00	0.94	0.95	0.02	0.02
N_6	0.00	0.00	0.95	0.95	0.02	0.02
N_7	0.00	0.00	1.00	1.00	0	0
N	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},1}$	0.17	0.15	0.98	1.00	0.01	0
$\gamma_{\text{Ad},2}$	0.15	0.13	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},4}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},5}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},6}$	0.00	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},7}$	0.00	0.00	1.00	1.00	0	0
ϕ_1	0.00	0.00	0.97	0.98	0.02	0.01
ϕ_2	0.00	0.00	0.95	0.94	0.02	0.02
ϕ_3	0.00	0.00	0.92	0.92	0.03	0.03
ϕ_4	0.00	0.00	0.95	0.94	0.02	0.02
ϕ_5	0.00	0.00	0.94	0.94	0.02	0.02
ϕ_6	0.00	0.00	1.00	1.00	0	0

Table A.2: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 3). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.12	0.13	1.00	1.00	0	0
N_2	0.07	0.08	0.98	0.97	0.01	0.02
N_3	0.02	0.03	0.95	0.96	0.02	0.02
N_4	0.01	0.02	0.94	0.95	0.02	0.02
N_5	0.01	0.02	0.95	0.97	0.02	0.02
N_6	0.01	0.02	0.99	0.94	0.01	0.02
N_7	0.03	0.14	0.96	0.92	0.02	0.03
N	0.01	0.00	0.94	0.97	0.02	0.02
$\gamma_{\text{Ad},1}$	0.12	0.13	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.20	0.34	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.20	0.18	0.97	0.97	0.02	0.02
$\gamma_{\text{Ad},4}$	0.18	0.15	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},5}$	0.19	0.19	0.98	0.98	0.01	0.01
$\gamma_{\text{Ad},6}$	0.15	0.16	0.98	0.98	0.01	0.01
$\gamma_{\text{Ad},7}$	0.19	0.21	0.95	0.96	0.02	0.02
ϕ_1	0.01	0.01	0.98	0.98	0.01	0.01
ϕ_2	0.01	0.00	0.99	1.00	0.01	0
ϕ_3	0.00	0.00	0.99	1.00	0.01	0
ϕ_4	0.00	0.00	1.00	1.00	0	0
ϕ_5	0.00	0.01	1.00	0.99	0	0.01
ϕ_6	0.02	0.12	0.99	1.00	0.01	0

Table A.3: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 4). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.15	0.16	0.99	1.00	0	0.01
N_2	0.00	0.00	0.90	0.90	0.03	0.03
N_3	0.00	0.00	0.96	0.95	0.02	0.02
N_4	0.00	0.00	0.96	0.95	0.02	0.02
N_5	0.00	0.00	0.98	0.98	0.01	0.01
N_6	0.00	0.00	0.97	0.96	0.02	0.02
N_7	0.00	0.00	1.00	1.00	0	0
N	0.00	0.00	0.98	0.99	0.01	0.01
$\gamma_{\text{Ad},1}$	0.16	0.16	0.99	1.00	0.01	0
$\gamma_{\text{Ad},2}$	0.14	0.13	0.98	1.00	0.01	0
$\gamma_{\text{Ad},3}$	0.03	0.00	0.79	1.00	0.04	0
$\gamma_{\text{Ad},4}$	0.02	0.00	0.83	1.00	0.04	0
$\gamma_{\text{Ad},5}$	0.01	0.00	0.96	1.00	0.02	0
$\gamma_{\text{Ad},6}$	0.01	0.00	0.94	1.00	0.02	0
$\gamma_{\text{Ad},7}$	0.01	0.00	1.00	1.00	0	0
ϕ_1	0.00	0.00	0.94	0.95	0.02	0.02
ϕ_2	0.00	0.00	0.96	0.95	0.02	0.02
ϕ_3	0.00	0.00	0.96	0.96	0.02	0.02
ϕ_4	0.00	0.00	0.97	0.96	0.02	0.02
ϕ_5	0.00	0.00	0.93	0.93	0.03	0.03
ϕ_6	0.00	0.00	1.00	1.00	0	0

Table A.4: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 5). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.03	0.02	1.00	1.00	0	0
N_2	0.02	0.02	0.94	0.94	0.02	0.02
N_3	0.00	0.00	0.97	0.98	0.02	0.01
N_4	0.00	0.00	0.94	0.96	0.02	0.02
N_5	0.00	0.00	0.95	0.99	0.02	0.01
N_6	0.00	0.00	0.97	0.94	0.02	0.02
N_7	0.02	0.04	0.98	1.00	0.01	0
N	0.00	0.00	0.97	1.00	0.02	0
$\gamma_{\text{Ad},1}$	0.03	0.02	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.03	0.03	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.08	0.04	0.94	0.98	0.02	0.01
$\gamma_{\text{Ad},4}$	0.07	0.04	0.92	0.98	0.02	0.01
$\gamma_{\text{Ad},5}$	0.06	0.04	0.96	0.99	0.02	0.01
$\gamma_{\text{Ad},6}$	0.05	0.04	0.95	0.95	0.02	0.02
$\gamma_{\text{Ad},7}$	0.03	0.06	0.99	0.96	0.01	0.02
ϕ_1	0.00	0.00	0.98	0.98	0.01	0.01
ϕ_2	0.00	0.00	0.96	0.96	0.02	0.02
ϕ_3	0.00	0.00	0.95	0.96	0.02	0.02
ϕ_4	0.00	0.00	0.96	0.96	0.02	0.02
ϕ_5	0.00	0.00	0.96	0.95	0.02	0.02
ϕ_6	0.02	0.04	0.98	1.00	0.01	0

Table A.5: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 6). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.11	0.13	1.00	1.00	0	0
N_2	0.05	0.06	0.98	0.98	0.01	0.01
N_3	0.03	0.03	0.96	0.98	0.02	0.01
N_4	0.01	0.02	0.95	0.97	0.02	0.02
N_5	0.01	0.01	0.99	0.99	0.01	0.01
N_6	0.01	0.01	0.95	0.94	0.02	0.02
N_7	0.05	0.15	0.92	0.85	0.03	0.04
N	0.00	0.00	0.96	0.99	0.02	0.01
$\gamma_{\text{Ad},1}$	0.11	0.13	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.14	0.18	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.33	0.18	0.95	0.97	0.02	0.02
$\gamma_{\text{Ad},4}$	0.23	0.17	0.96	0.98	0.02	0.01
$\gamma_{\text{Ad},5}$	0.32	0.19	0.95	0.97	0.02	0.02
$\gamma_{\text{Ad},6}$	0.18	0.15	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},7}$	0.18	0.24	0.98	0.91	0.01	0.03
ϕ_1	0.01	0.01	0.98	0.99	0.01	0.01
ϕ_2	0.01	0.01	0.98	0.99	0.01	0.01
ϕ_3	0.00	0.00	1.00	1.00	0	0
ϕ_4	0.00	0.00	0.99	0.99	0.01	0.01
ϕ_5	0.00	0.01	1.00	0.99	0	0.01
ϕ_6	0.04	0.12	1.00	1.00	0	0

Table A.6: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 8). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.21	0.17	1.00	1.00	0	0
N_2	0.05	0.05	0.97	0.97	0.02	0.02
N_3	0.03	0.04	0.94	0.96	0.02	0.02
N_4	0.03	0.04	0.90	0.92	0.03	0.03
N_5	0.03	0.03	0.94	0.97	0.02	0.02
N_6	0.03	0.03	0.95	0.94	0.02	0.02
N_7	0.13	0.11	0.96	1.00	0.02	0
N	0.02	0.02	0.81	0.94	0.04	0.02
$\gamma_{\text{Ad},1}$	0.21	0.18	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.06	0.06	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},3}$	0.08	0.08	0.94	0.94	0.02	0.02
$\gamma_{\text{Ad},4}$	0.08	0.09	0.94	0.92	0.02	0.03
$\gamma_{\text{Ad},5}$	0.07	0.08	0.95	0.96	0.02	0.02
$\gamma_{\text{Ad},6}$	0.06	0.07	0.98	0.98	0.01	0.01
$\gamma_{\text{Ad},7}$	0.16	0.13	0.95	1.00	0.02	0
ϕ_1	0.03	0.03	0.99	0.99	0.01	0.01
ϕ_2	0.02	0.02	0.98	0.95	0.01	0.02
ϕ_3	0.02	0.02	0.96	0.95	0.02	0.02
ϕ_4	0.02	0.02	0.94	0.93	0.02	0.03
ϕ_5	0.04	0.04	0.93	0.93	0.03	0.03
ϕ_6	0.10	0.06	0.99	1.00	0.01	0

Table A.7: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 9). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.11	0.13	1.00	0.99	0	0.01
N_2	0.19	0.17	0.99	1.00	0.01	0
N_3	0.20	0.18	0.95	1.00	0.02	0
N_4	0.19	0.20	0.95	0.94	0.02	0.02
N_5	0.19	0.21	0.95	0.97	0.02	0.02
N_6	0.24	0.33	0.94	0.99	0.02	0.01
N_7	0.30	0.45	0.98	1.00	0.01	0
N	0.09	0.11	0.84	0.88	0.04	0.03
$\gamma_{\text{Ad},1}$	0.11	0.13	1.00	0.99	0	0.01
$\gamma_{\text{Ad},2}$	0.30	0.25	1.00	1.00	0	0
$\gamma_{\text{Ad},3}$	0.58	0.33	0.95	1.00	0.02	0
$\gamma_{\text{Ad},4}$	0.38	0.37	0.99	0.98	0.01	0.01
$\gamma_{\text{Ad},5}$	0.44	0.32	0.98	0.99	0.01	0.01
$\gamma_{\text{Ad},6}$	0.52	0.54	0.98	1.00	0.01	0
$\gamma_{\text{Ad},7}$	0.64	1.19	0.99	1.00	0.01	0
ϕ_1	0.11	0.11	0.99	0.98	0.01	0.01
ϕ_2	0.09	0.09	0.99	0.99	0.01	0.01
ϕ_3	0.07	0.08	0.98	0.99	0.01	0.01
ϕ_4	0.08	0.09	0.97	0.94	0.02	0.02
ϕ_5	0.10	0.10	0.98	1.00	0.01	0
ϕ_6	0.10	0.02	1.00	1.00	0	0

Table A.8: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 10). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.09	0.11	0.99	0.98	0.01	0.01
N_2	0.00	0.00	0.95	0.94	0.02	0.02
N_3	0.00	0.00	0.97	0.97	0.02	0.02
N_4	0.00	0.00	0.99	0.97	0.01	0.02
N_5	0.00	0.00	0.95	0.95	0.02	0.02
N_6	0.00	0.00	0.98	1.00	0.01	0
N_7	0.14	0.21	0.92	1.00	0.03	0
N	0.01	0.01	0.54	0.45	0.05	0.05
$\gamma_{\text{Ad},1}$	0.09	0.11	1.00	0.98	0	0.01
$\gamma_{\text{Ad},2}$	0.03	0.03	0.99	1.00	0.01	0
$\gamma_{\text{Ad},3}$	0.01	0.00	1.00	1.00	0	0
$\gamma_{\text{Ad},4}$	0.00	0.00	0.99	1.00	0.01	0
$\gamma_{\text{Ad},5}$	0.00	0.00	0.99	1.00	0.01	0
$\gamma_{\text{Ad},6}$	0.00	0.00	0.99	1.00	0.01	0
$\gamma_{\text{Ad},7}$	0.09	0.22	0.99	1.00	0.01	0
ϕ_1	0.01	0.01	0.95	0.95	0.02	0.02
ϕ_2	0.01	0.01	0.93	0.93	0.03	0.03
ϕ_3	0.00	0.00	0.96	0.96	0.02	0.02
ϕ_4	0.01	0.01	0.94	0.94	0.02	0.02
ϕ_5	0.00	0.00	0.96	0.96	0.02	0.02
ϕ_6	0.14	0.20	0.88	0.91	0.03	0.03

Table A.9: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 11). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.32	0.14	0.99	1.00	0.01	0
N_2	0.06	0.05	0.94	0.94	0.02	0.02
N_3	0.05	0.05	0.92	0.95	0.03	0.02
N_4	0.03	0.04	0.94	0.94	0.02	0.02
N_5	0.03	0.03	0.92	0.94	0.03	0.02
N_6	0.04	0.05	0.89	0.93	0.03	0.03
N_7	0.12	0.10	1.00	1.00	0	0
N	0.02	0.02	0.87	0.90	0.03	0.03
$\gamma_{\text{Ad},1}$	0.32	0.14	0.99	1.00	0.01	0
$\gamma_{\text{Ad},2}$	0.08	0.08	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},3}$	0.10	0.10	0.96	0.94	0.02	0.02
$\gamma_{\text{Ad},4}$	0.09	0.10	0.92	0.93	0.03	0.03
$\gamma_{\text{Ad},5}$	0.05	0.07	0.97	0.97	0.02	0.02
$\gamma_{\text{Ad},6}$	0.09	0.10	0.94	0.94	0.02	0.02
$\gamma_{\text{Ad},7}$	0.10	0.11	1.00	1.00	0	0
ϕ_1	0.03	0.03	0.96	0.97	0.02	0.02
ϕ_2	0.03	0.03	0.95	0.96	0.02	0.02
ϕ_3	0.02	0.02	0.96	0.97	0.02	0.02
ϕ_4	0.02	0.03	0.94	0.94	0.02	0.02
ϕ_5	0.04	0.04	0.91	0.93	0.03	0.03
ϕ_6	0.09	0.06	0.99	1.00	0.01	0

Table A.10: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\boldsymbol{\phi_{juv}} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 12). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.15	0.22	1.00	1.00	0	0
N_2	0.23	0.24	0.98	0.97	0.01	0.02
N_3	0.20	0.21	0.97	0.98	0.02	0.01
N_4	0.24	0.23	0.93	0.94	0.03	0.02
N_5	0.18	0.17	0.94	0.99	0.02	0.01
N_6	0.25	0.19	0.93	0.98	0.03	0.01
N_7	0.36	0.22	1.00	1.00	0	0
N	0.09	0.08	0.85	0.85	0.04	0.04
$\gamma_{\text{Ad},1}$	0.15	0.21	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.29	0.32	1.00	0.99	0	0.01
$\gamma_{\text{Ad},3}$	0.39	0.31	0.98	0.98	0.01	0.01
$\gamma_{\text{Ad},4}$	0.46	0.33	0.98	0.99	0.01	0.01
$\gamma_{\text{Ad},5}$	0.31	0.28	0.97	1.00	0.02	0
$\gamma_{\text{Ad},6}$	0.34	0.27	0.95	0.98	0.02	0.01
$\gamma_{\text{Ad},7}$	0.58	0.60	1.00	1.00	0	0
ϕ_1	0.11	0.11	0.97	0.96	0.02	0.02
ϕ_2	0.08	0.08	0.99	0.98	0.01	0.02
ϕ_3	0.11	0.11	0.94	0.97	0.02	0.02
ϕ_4	0.09	0.09	0.96	0.99	0.02	0.01
ϕ_5	0.10	0.10	0.97	0.99	0.02	0.01
ϕ_6	0.10	0.02	1.00	1.00	0	0

Table A.11: Comparison of relative mean squared error, MSE, in the 100 posterior medians for common model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\boldsymbol{\phi_{juv}} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 13). Coverage is the proportion of 95% CI containing the true value and MCE of Coverage gives the estimated Monte Carlo error of the coverage.

Parameter	Relative MSE		Coverage		MCE of Coverage	
	MSJS	JS	MSJS	JS	MSJS	JS
N_1	0.17	0.10	1.00	1.00	0	0
N_2	0.10	0.11	0.94	0.95	0.02	0.02
N_3	0.05	0.07	0.93	0.94	0.03	0.02
N_4	0.04	0.07	0.93	0.89	0.03	0.03
N_5	0.04	0.04	0.93	0.95	0.03	0.02
N_6	0.03	0.04	0.97	0.98	0.02	0.01
N_7	0.07	0.02	0.99	1.00	0.01	0
N	0.01	0.01	0.89	0.94	0.03	0.02
$\gamma_{\text{Ad},1}$	0.17	0.10	1.00	1.00	0	0
$\gamma_{\text{Ad},2}$	0.13	0.13	0.99	0.99	0.01	0.01
$\gamma_{\text{Ad},3}$	0.16	0.18	0.97	0.97	0.02	0.02
$\gamma_{\text{Ad},4}$	0.15	0.16	0.97	0.95	0.02	0.02
$\gamma_{\text{Ad},5}$	0.15	0.14	0.96	0.99	0.02	0.01
$\gamma_{\text{Ad},6}$	0.08	0.12	0.99	0.98	0.01	0.01
$\gamma_{\text{Ad},7}$	0.12	0.08	1.00	0.98	0	0.01
ϕ_1	0.05	0.05	0.95	0.96	0.02	0.02
ϕ_2	0.03	0.03	0.96	0.94	0.02	0.02
ϕ_3	0.03	0.04	0.94	0.93	0.02	0.03
ϕ_4	0.03	0.03	0.95	0.96	0.02	0.02
ϕ_5	0.03	0.03	0.94	0.96	0.02	0.02
ϕ_6	0.06	0.00	1.00	1.00	0	0

A.3 Distributions of Relative and Absolute Bias for Juvenile Parameters

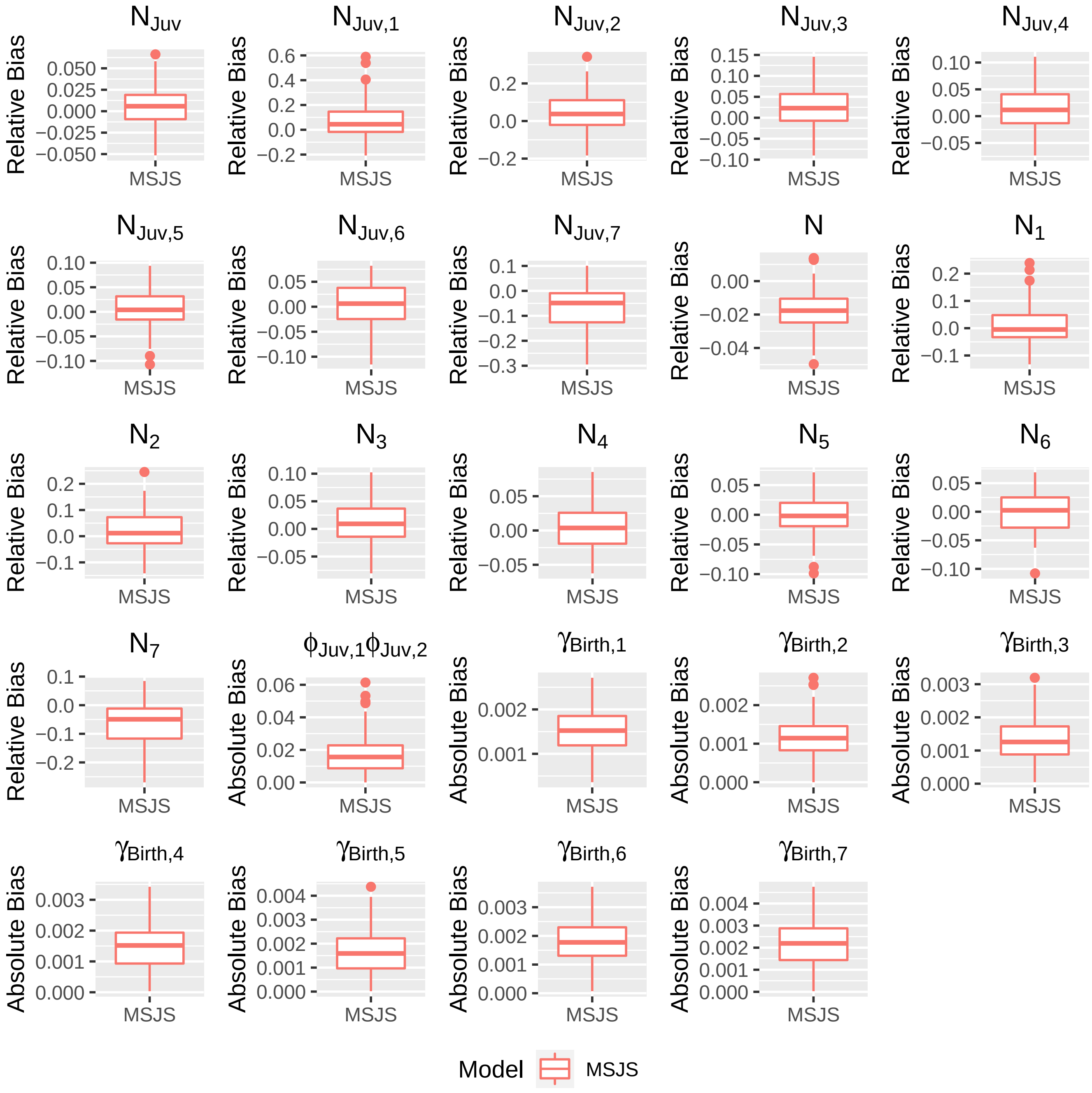

Figure A.12: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 2, MSJS model).

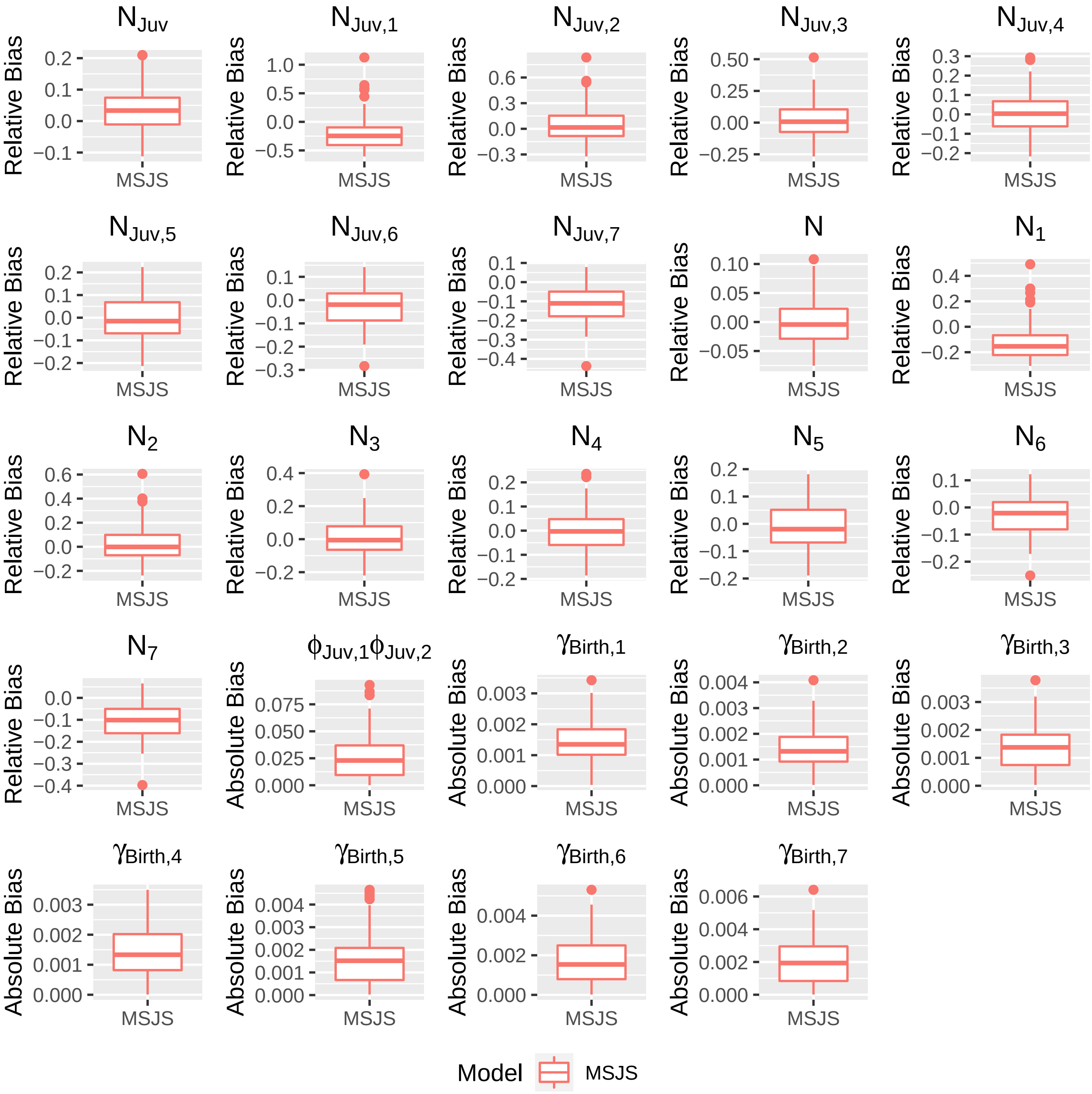

Figure A.13: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 3, MSJS model).

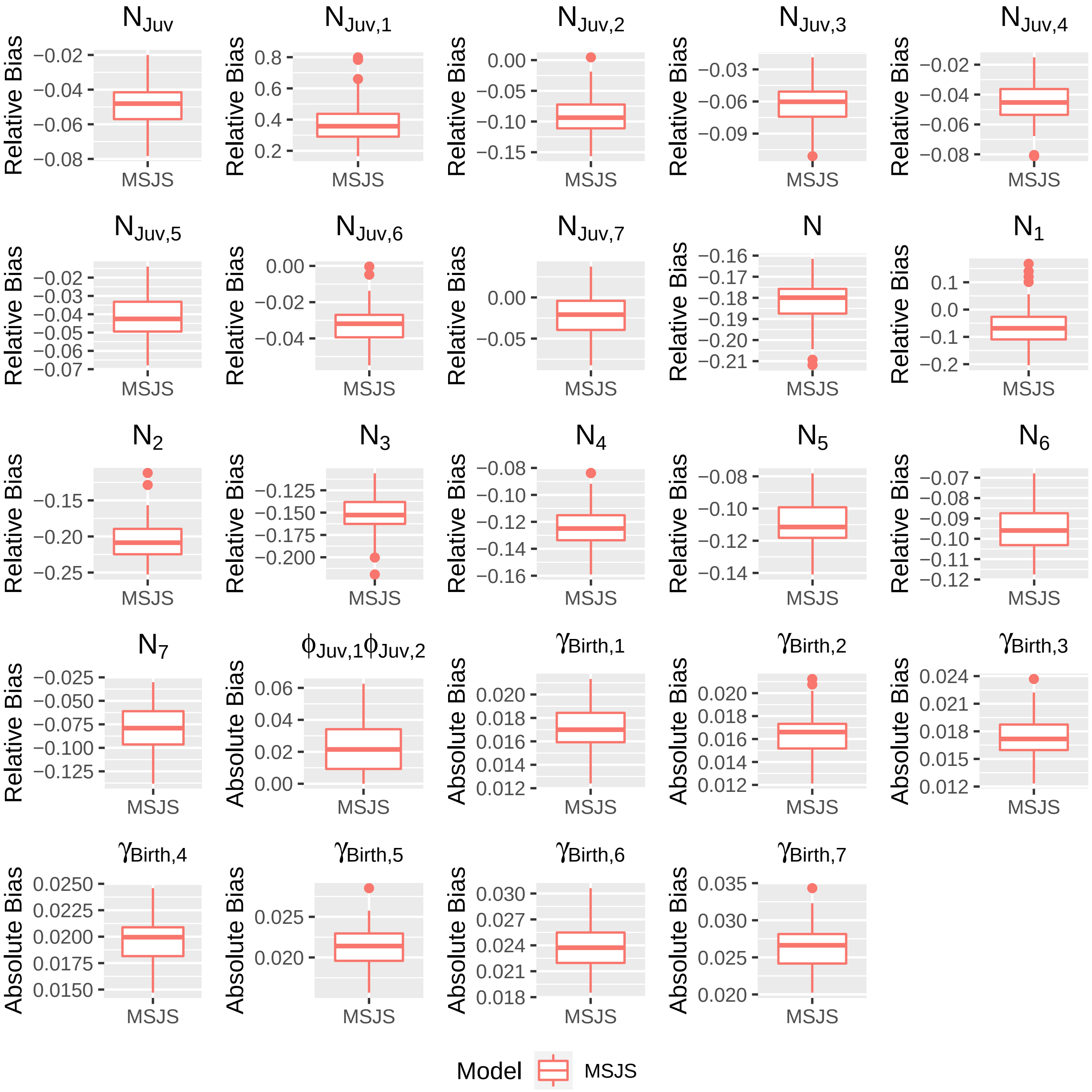

Figure A.14: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.9$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 4, MSJS model).

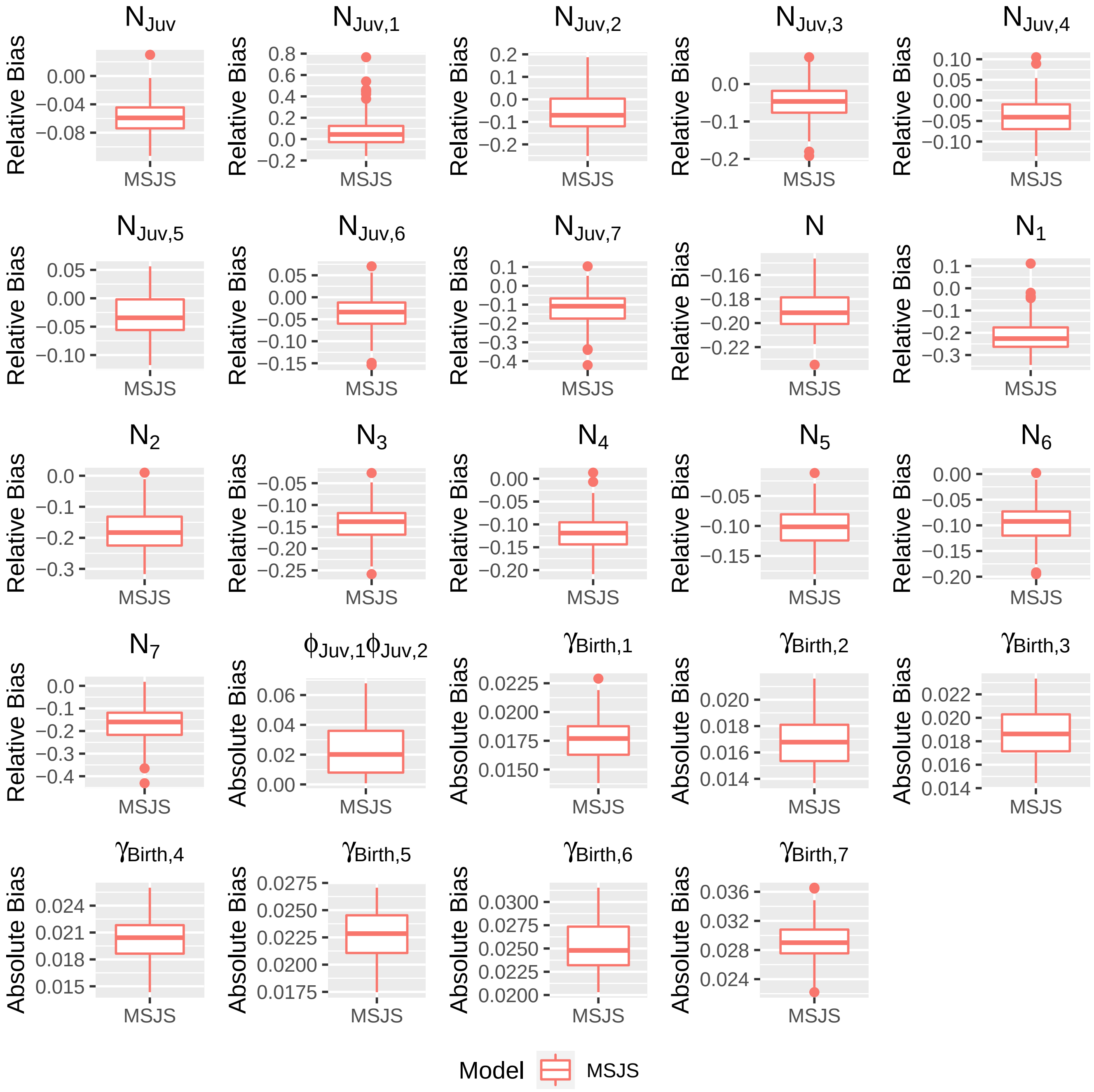

Figure A.15: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.5$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 5, MSJS model).

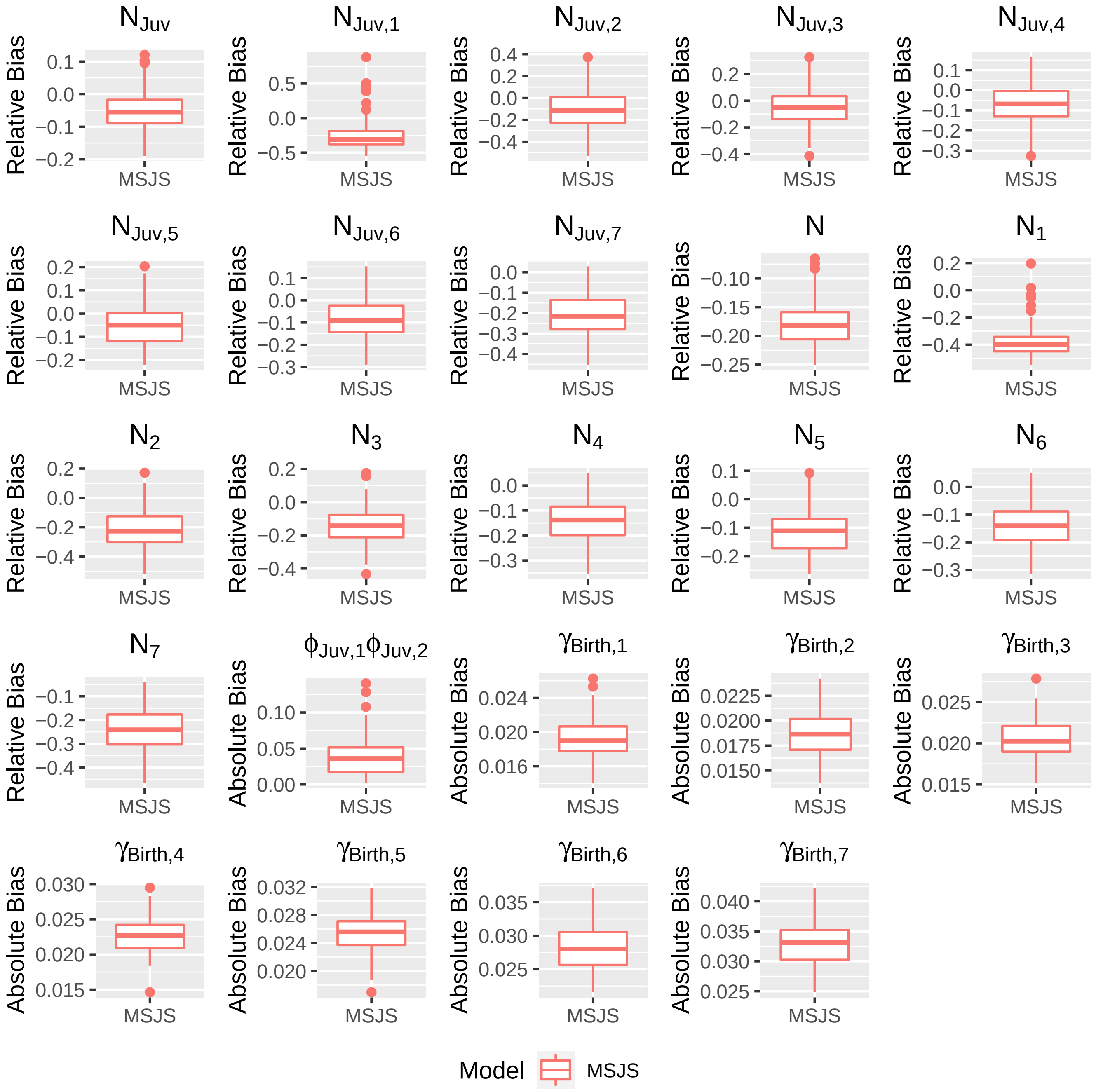

Figure A.16: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.9$, $p_{ad} = 0.2$, $\phi_{juv} = (0.5, 0.7)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 6, MSJS model).

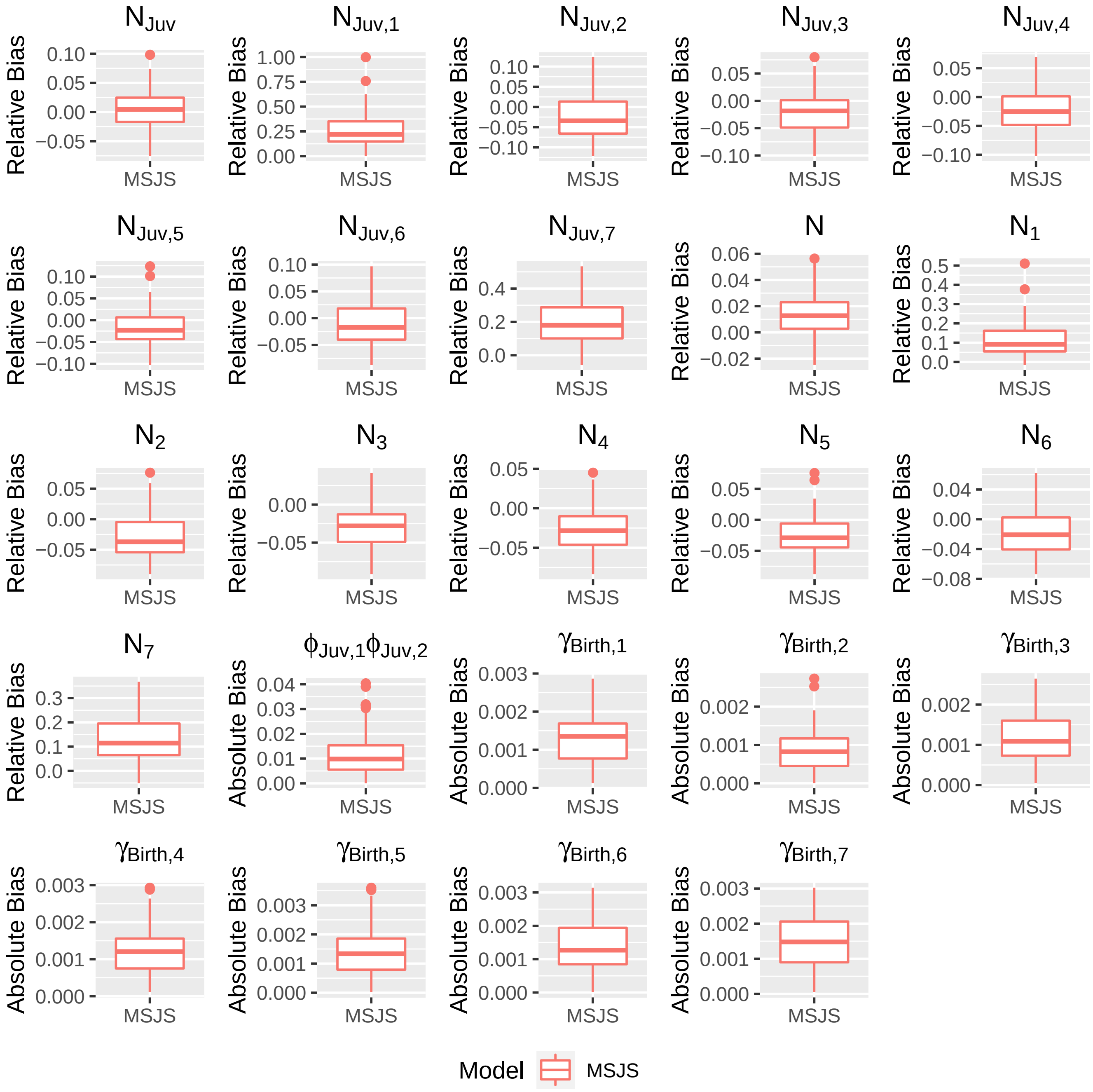

Figure A.17: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 7, MSJS model).

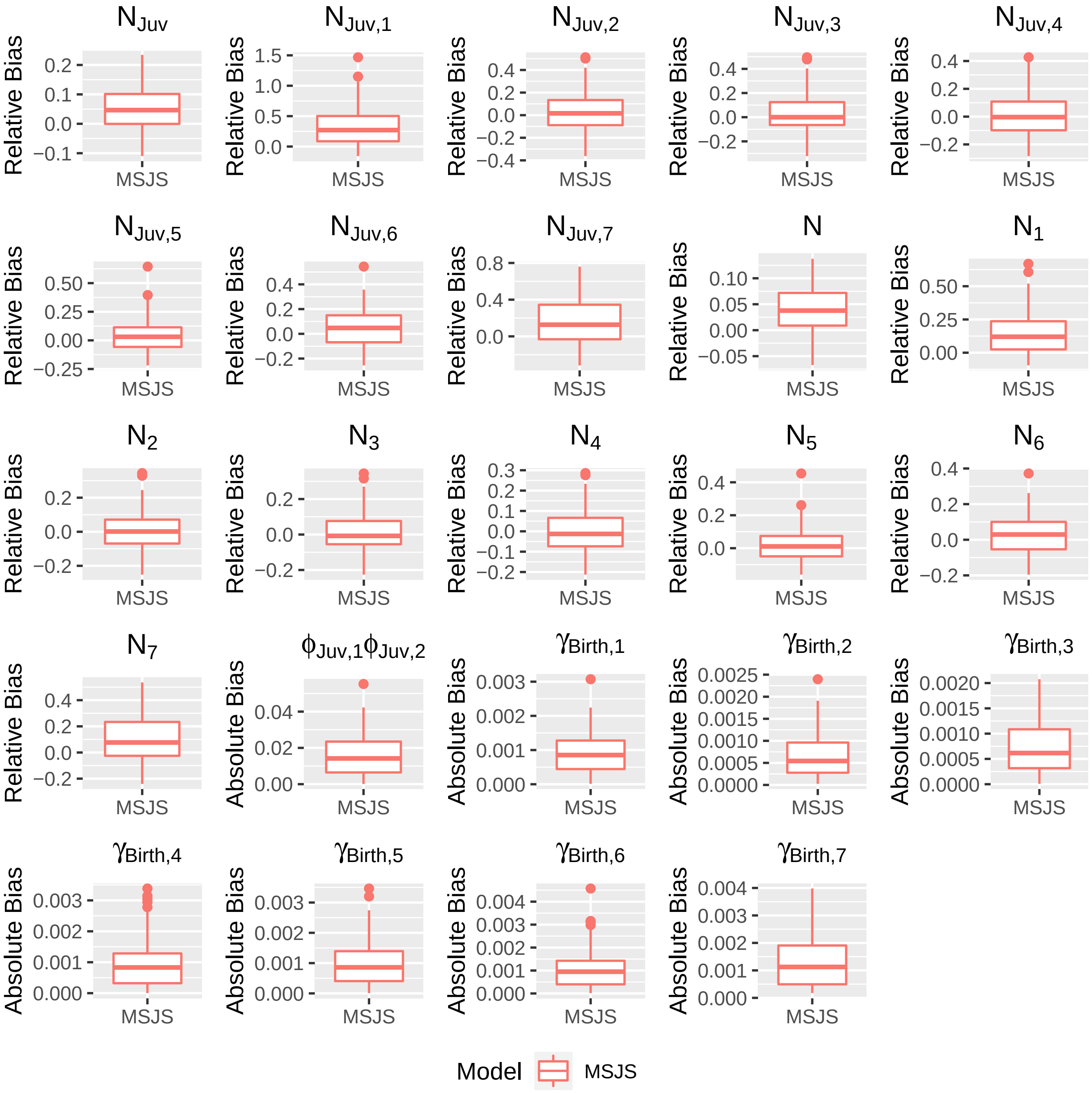

Figure A.18: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 8, MSJS model).

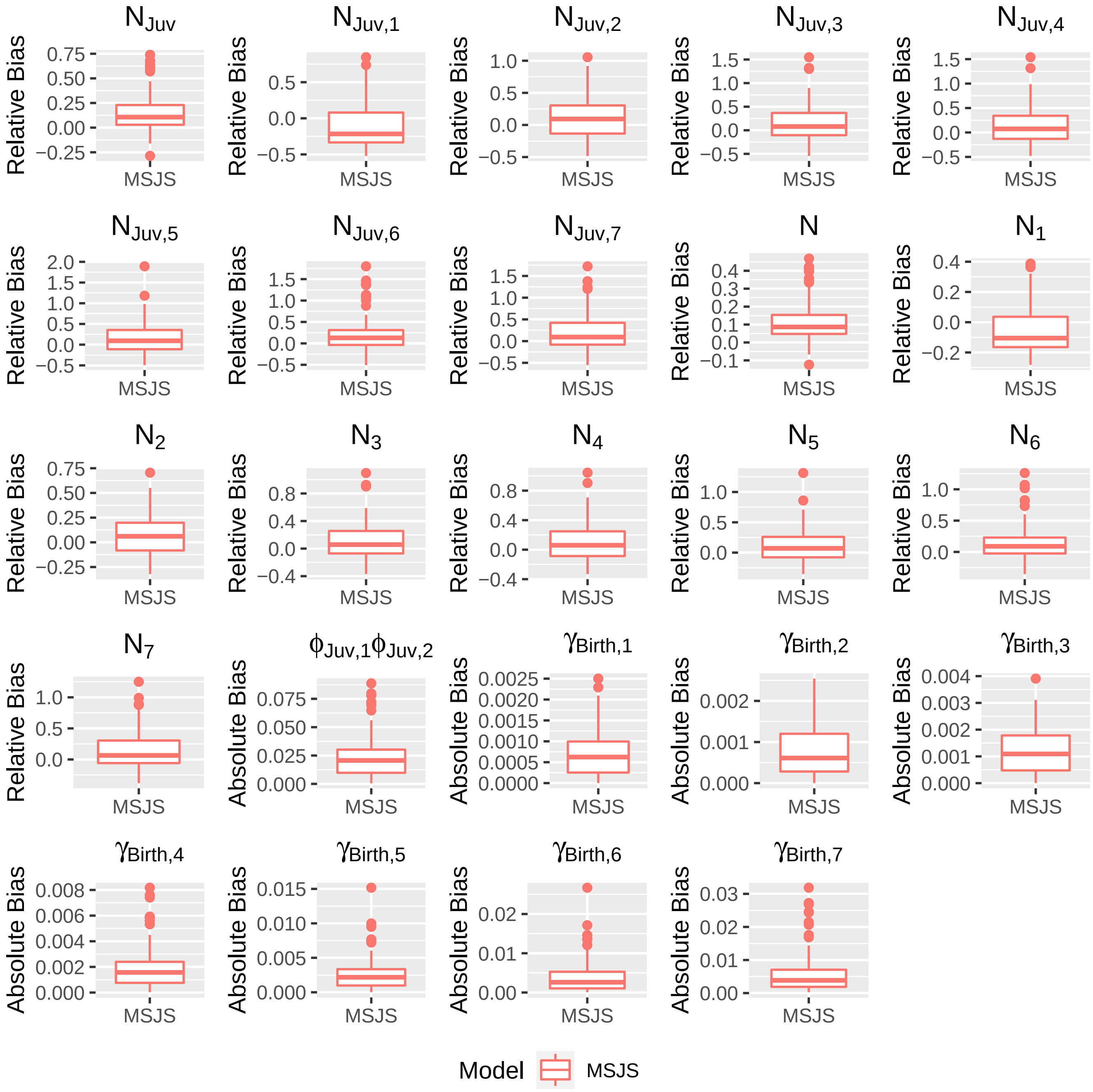

Figure A.19: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 9, MSJS model).

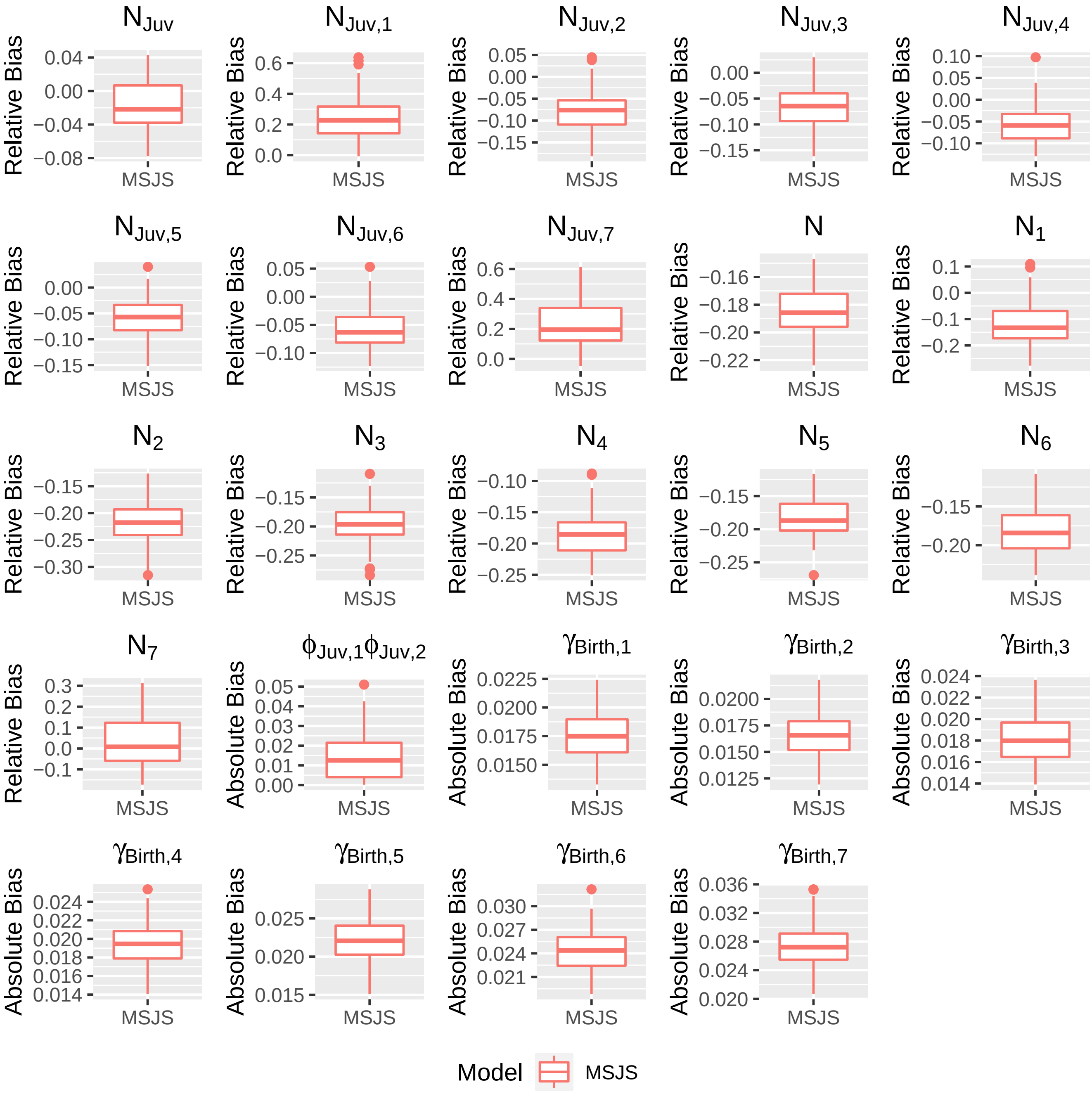

Figure A.20: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.9$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 10, MSJS model).

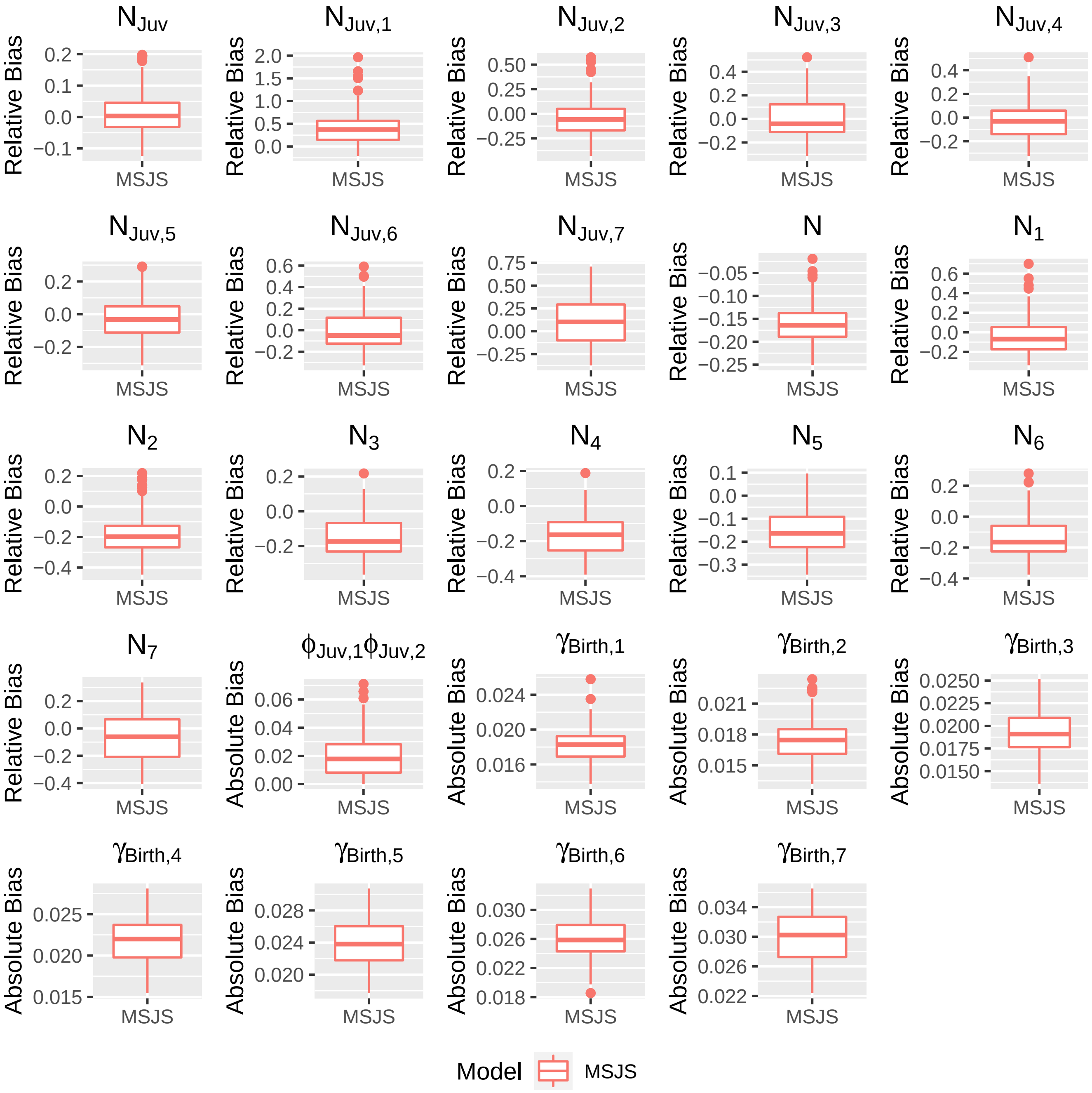

Figure A.21: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.5$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 11, MSJS model).

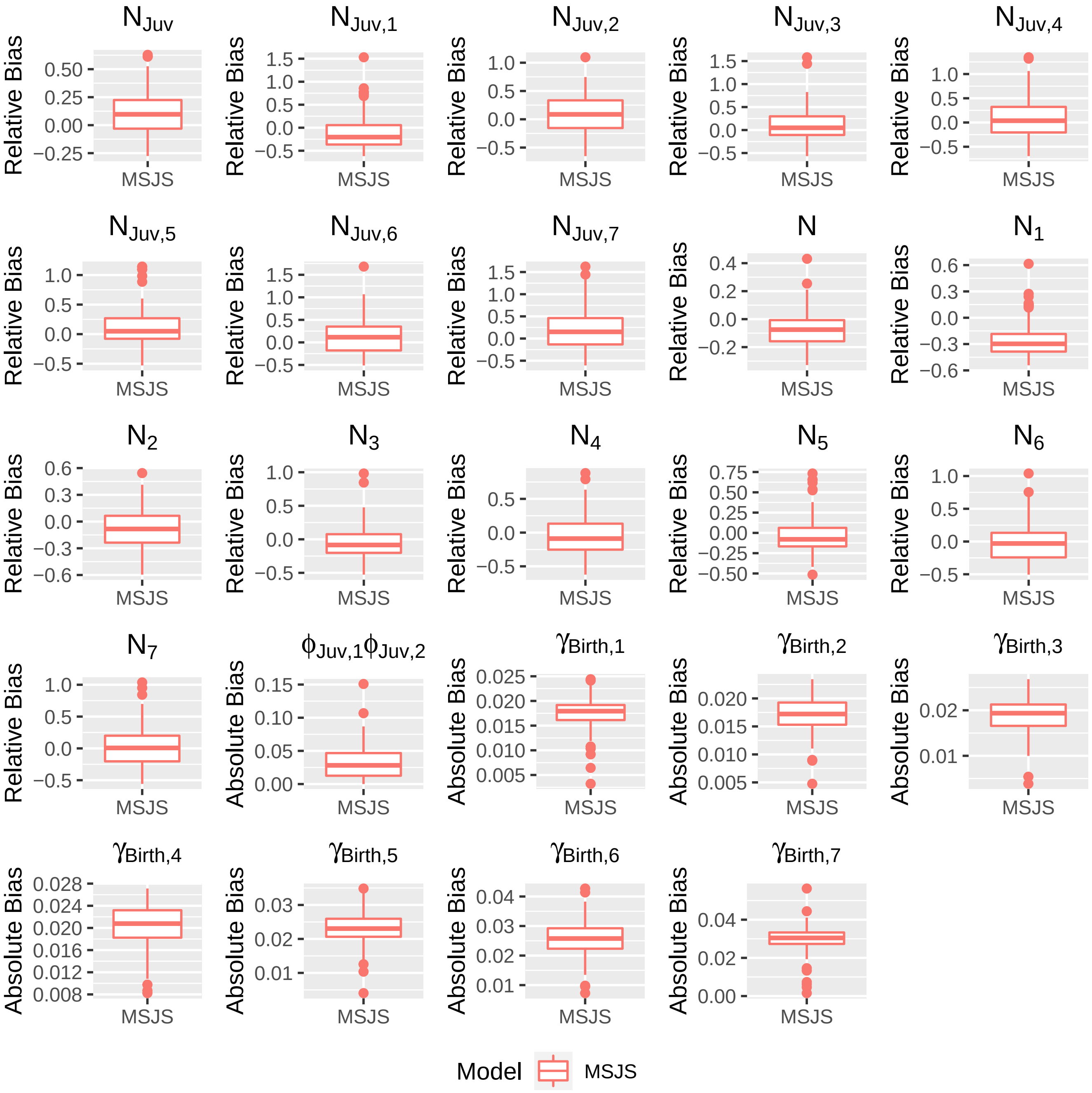

Figure A.22: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.5$, $p_{ad} = 0.2$, $\phi_{juv} = (0.3, 0.4)$, and $\mathbf{p}_{juv} = (0.5, 0)$ (Scenario 12, MSJS model).

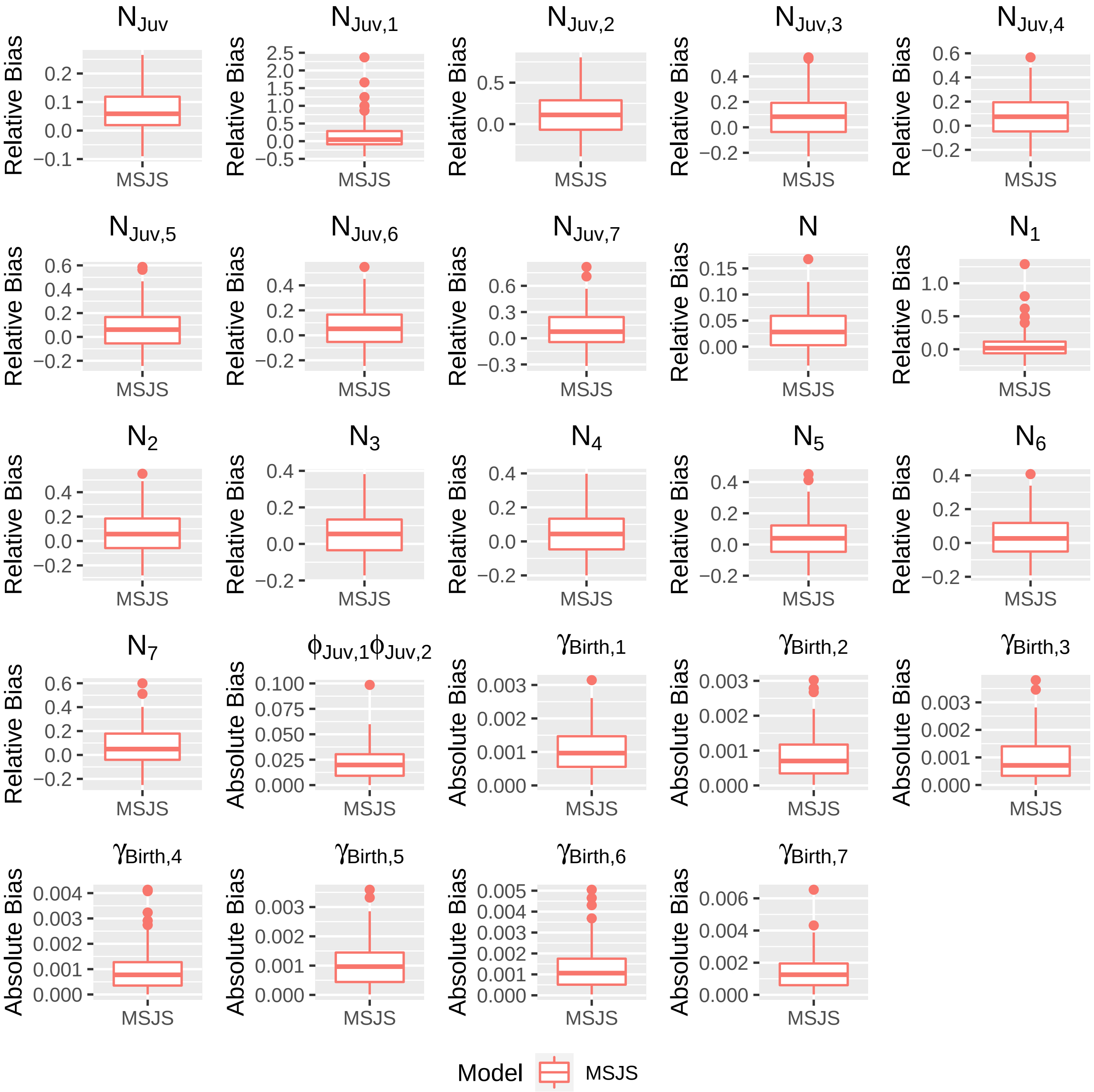

Figure A.23: Distributions of relative bias for juvenile model parameters when the data is simulated for 1000 adults and 1000 births and with parameters $\phi_{ad} = 0.6$, $p_{ad} = 0.35$, $\phi_{juv} = (0.3, 0.5)$, and $\mathbf{p}_{juv} = (0.95, 0)$ (Scenario 13, MSJS model).

Appendix B

MSJS and JS Model Code

B.1 MSJS model code

```
library(coda)
library(R2jags)
library(rjags)

# cat("
#  model{

    #### Priors and Constraints ####

      # Dirichlet Prior for entry removal probabilities
      # for removal entry probabilities
#      for(j in 1:(n.occasions-1)){
#        for(i in 1:3){
#          temp[j,i] ~ dgamma(1,1)
#          gamma_Matrix[j,i] <- temp[j,i]/sum(temp[j,1:3])
#        }
#      }

      # Prior for time-dependent adult survival
#      for(j in 1:(n.occasions-1)){
#        phi[j] ~ dunif(0,1)
#      }
      # Prior for constant juvenile survival
#      for(i in 1:2){
#        phi_juv[i] ~ dunif(0,1)
#      }
      # Prior for time-dependent adult capture
```

```
#      for(j in 1:n.occasions){
#        p[j] ~ dunif(0,1)
#      }
      # Prior for constant juvenile capture
#      for(i in 1:2){
#        p_juv[i] ~ dunif(0,1)
#      }

    #### Define State-transitions and Observation matrices ####
#    for(i in 1:M){

      # Define probabilities of S(j+1) given S(j)

      # Dimension 1: state of departure
      # Dimension 2: state of arrival
      # Dimension 3: individual
      # Dimension 4: time

#      for(j in 1:(n.occasions-1)){
#        pstate[1,1,i,j] <- gamma_Matrix[j,1]
#        pstate[1,2,i,j] <- gamma_Matrix[j,2]
#        pstate[1,3,i,j] <- 0
#        pstate[1,4,i,j] <- gamma_Matrix[j,3]
#        pstate[1,5,i,j] <- 0
#
#        pstate[2,1,i,j] <- 0
#        pstate[2,2,i,j] <- 0
#        pstate[2,3,i,j] <- phi_juv[1]
#        pstate[2,4,i,j] <- 0
#        pstate[2,5,i,j] <- (1-phi_juv[1])


#        pstate[3,1,i,j] <- 0
#        pstate[3,2,i,j] <- 0
#        pstate[3,3,i,j] <- 0
#        pstate[3,4,i,j] <- phi_juv[2]
#        pstate[3,5,i,j] <- (1 - phi_juv[2])

#        pstate[4,1,i,j] <- 0
#        pstate[4,2,i,j] <- 0
#        pstate[4,3,i,j] <- 0
#        pstate[4,4,i,j] <- phi[j]
```

```
#        pstate[4,5,i,j] <- (1-phi[j])

#        pstate[5,1,i,j] <- 0
#        pstate[5,2,i,j] <- 0
#        pstate[5,3,i,j] <- 0
#        pstate[5,4,i,j] <- 0
#        pstate[5,5,i,j] <- 1

#      }

      # Define probabilities of ind. i being observed at time j given S(j)

#      for(j in 1:n.occasions){
#        pobs[1,i,j] <- 0
#        pobs[2,i,j] <- p_juv[1]
#        pobs[3,i,j] <- p_juv[2]
#        pobs[4,i,j] <- p[j]
#        pobs[5,i,j] <- 0
#      }
#    }

    #### Likelihood ####

#    for(i in 1:M){

      # Dummy occasion 1 where everyone is in state 1 (not yet in population)
#      state[i,1] <- 1

#      for(j in 2:n.occasions){

        # state of individual i at time j given previous state
#        state[i,j] ~ dcat(pstate[state[i,j-1],,i,j-1])

        # observation of individual i at time j given current state
#        X[i,j] ~ dbern(pobs[state[i,j],i,j])
#      }
#    }

    #### Derived Parameters ####

#    for(i in 1:M){
#      for(j in 2:n.occasions){
```

```
#       whenAlive_ever[i,j-1] <- equals(state[i,j],2) + equals(state[i,j],3) +
#                             equals(state[i,j],4)
#        whenAlive_adult[i,j-1] <-  equals(state[i,j],4)
#        whenAlive_juv[i,j-1] <- equals(state[i,j],3) + equals(state[i,j],4)
#      }
#      alive_ever[i] <- sum(whenAlive_ever[i,])
#      alive_adult[i] <- sum(whenAlive_adult[i,])
#      alive_juv[i] <- sum(whenAlive_juv[i,])
#    }

#    for(j in 1:(n.occasions-1)){
#      N_ever[j] <- sum(whenAlive_ever[,j])
#      N_adult[j] <- sum(whenAlive_adult[,j])
#      N_juv[j] <- sum(whenAlive_juv[,j])
#    }

#    for(i in 1:M){
#      z_ever[i] <- 1-equals(alive_ever[i],0)
#      z_adult[i] <- 1-equals(alive_adult[i],0)
#      z_juv[i] <- 1-equals(alive_juv[i],0)
#    }
#    N_super_ever <- sum(z_ever)
#    N_super_adult <- sum(z_adult)
#    N_super_juv <- sum(z_juv)
#  }

#    ",file="MultiStateJSWithJAGS.txt")

#### Determine Known States ####

# For Juveniles, they are first observed in State 2 (right after birth)
# If they are observed on the subsequent occasion, then they are in state 3
# if they are observed 2 or more occasions after birth they are in state 4

known.states.juv <- function(juv.ch){
  state <- matrix(NA,nrow=nrow(juv.ch),ncol=ncol(juv.ch))
  for(i in 1:nrow(juv.ch)){
    if(sum(juv.ch[i,])==0){
      next               # if never observed, skip to next individual
    }
    else{
      fst <- min(which(juv.ch[i,]==1))
```

```
      lst <- max(which(juv.ch[i,]==1))
      # don't know their state after last observation
      state[i,lst:(ncol(juv.ch))] <- NA
      # in State 1 before first observation (we redefine fst as state 2 next)
      state[i,1:fst] <- 1
      # in State 2 on first observation
      state[i,fst] <- 2
      # cover states between first and last observation
      if((lst - fst) >= 2){
        state[i,fst+1] <- 3
        state[i,(fst+2):lst] <- 4
      }
      if((lst-fst) == 1){
        state[i,fst+1] <- 3
      }
      else{
        next
      }
    }
  }
  return(state)
}


# For adult CH, we assume they are adults when they are first observed
# thus between the first and last observation, the state is 4, before that
# the state is unknown so NA
known.states.adult <- function(ad.ch){
  state <- matrix(NA,nrow=nrow(ad.ch),ncol=ncol(ad.ch))
  for(i in 1:nrow(ad.ch)){
    if(sum(ad.ch[i,])==0){
      next   # if never observed, skip to next individual
    }
    else{
      fst <- min(which(ad.ch[i,]==1))
      lst <- max(which(ad.ch[i,]==1))
      state[i,fst:lst] <- 4
    }
  }
  return(state)
}
```

```
# Add dummy occasion to Ad_CH
AD_CH.du <- as.matrix(cbind(rep(0,nrow(Ad_CH)),Ad_CH))
ad_state <- known.states.adult(AD_CH.du)

# Add dummy occasion to Juv_CH
JV_CH.du <- as.matrix(cbind(rep(0,nrow(Juv_CH)),Juv_CH))
juv_state <- known.states.juv(JV_CH.du)


# Combine the known state matrices together
known_states_du <- rbind(ad_state,juv_state)


# Combine the observations together with the dummy first occasion
# where no one is yet observed.

Xobs.du <- rbind(AD_CH.du,JV_CH.du)


#### Initial States for the latent values of the state matrix
# Put NA wherever the state is known and 1's before the known
# states.

initial.states <- function(ch,n.ad) {
  init_st <- matrix(NA,nrow=nrow(ch),ncol=ncol(ch))
  for(i in 1:n.ad){
    if(sum(ch[i,])==0){
      init_st[i,] <- rep(1,ncol(ch))
    }
    else{
      fst <- min(which(ch[i,]==1))
      lst <- max(which(ch[i,]==1))
      init_st[i,1:fst] <- 1
      init_st[i,fst] <- NA
      init_st[i,lst:ncol(ch)] <- 5
      init_st[i,lst] <- NA

    }
  }
  for(i in (n.ad+1):nrow(ch)){
    if(sum(ch[i,])==0){
      init_st[i,] <- rep(1,ncol(ch))
```

```
    }
    else{
      fst <- min(which(ch[i,]==1))
      lst <- max(which(ch[i,]==1))
      init_st[i,1:fst] <- NA
      init_st[i,lst:ncol(ch)] <- 5
      init_st[i,lst] <- NA
    }

  }
  return(init_st)
}

init_state_du <- initial.states(Xobs.du,nrow(AD_CH.du))

# Augment the data
n.aug <- 3000
M <- n.aug + nrow(Ad_CH) + nrow(Juv_CH)
X_aug <- rbind(Xobs.du, matrix(0,ncol=ncol(Xobs.du),nrow=n.aug))


# Augment Initial state matrix and known state matrix
known_states_aug <- rbind(known_states_du,
                          matrix(NA,nrow=n.aug,
                                 ncol=ncol(known_states_du)))
init_states_aug <- rbind(init_state_du,
                         matrix(1,nrow=n.aug,
                                ncol=ncol(init_state_du)))

# set the first column of init_states_aug and known_states_aug = NA
init_states_aug[,1] <- NA
known_states_aug[,1] <- NA


# Bundle Data
MSJS_data <- list(X = X_aug, M=nrow(X_aug),n.occasions = ncol(X_aug),
                  state = known_states_aug)

n.occasions <- ncol(X_aug)

#### INITIAL VALUES
```

```
# Bundle Initial Values

MSJS_inits <- function(){
  list(phi=runif(n.occasions-1,0,1),phi_juv = runif(2,0,1),
       p = runif(n.occasions,0,1),p_juv=runif(2,0,1),
       state = init_states_aug)
}


# Parameters to be monitored
MSJS_params <- c("phi","phi_juv","p","p_juv","N_ever","N_adult","N_juv",
                 "N_super_ever","N_super_adult","N_super_juv","gamma_Matrix")

# MCMC settings
ni <- 20000
nt <- 1
nb <- 5000
nc <- 3

# Run JAGS model
MSJS_jags.fit <- jags(model.file="MultiStateJSWithJAGS.txt",data = MSJS_data,
                      inits = MSJS_inits, parameters.to.save = MSJS_params,
                      n.iter = ni,n.chains = nc,n.burnin = nb,n.thin = nt)
```

B.2 JS model Code

```
library(coda)
library(R2jags)
library(rjags)

# cat("
#    model{

    #### Priors and Constraints ####

      # Prior for Time-dependent removal-entry
#      for(j in 1:(n.occasions-1)){
#        gamma[j] ~ dunif(0,1)
#      }
```

```
      # Prior for Time-dependent adult survival
#      for(j in 1:(n.occasions-1)){
#        phi[j] ~ dunif(0,1)
#      }

      # Prior for Time-dependent adult capture
#      for(j in 1:n.occasions){
#        p[j] ~ dunif(0,1)
#      }

    #### Define State-transitions and Observation matrices ####
#    for(i in 1:M){

      # Define probabilities of S(j+1) given S(j)

      # Dimension 1: state of departure
      # Dimension 2: state of arrival
      # Dimension 3: individual
      # Dimension 4: time

#      for(j in 1:(n.occasions-1)){
#        pstate[1,1,i,j] <- 1-gamma[j]
#        pstate[1,2,i,j] <- gamma[j]
#        pstate[1,3,i,j] <- 0


#        pstate[2,1,i,j] <- 0
#        pstate[2,2,i,j] <- phi[j]
#        pstate[2,3,i,j] <- (1-phi[j])


#        pstate[3,1,i,j] <- 0
#        pstate[3,2,i,j] <- 0
#        pstate[3,3,i,j] <- 1

#      }

      # Define probabilities of ind. i being observed at time j given S(j)

#      for(j in 1:n.occasions){
#        pobs[1,i,j] <- 0
#        pobs[2,i,j] <- p[j]
```

```
#        pobs[3,i,j] <- 0
#      }
#    }


    #### Likelihood ####

#    for(i in 1:M){

      # Dummy occasion 1 where everyone is in state 1 (not yet in population)
#      state[i,1] <- 1

#      for(j in 2:n.occasions){
        # state of individual i at time j given previous state
#        state[i,j] ~ dcat(pstate[state[i,j-1],,i,j-1])

        # observation of individual i at time j given current state
#        X[i,j] ~ dbern(pobs[state[i,j],i,j])
#      }
#    }

    #### Derived Parameters ####

#    for(i in 1:M){
#      for(j in 2:n.occasions){
#        whenAlive[i,j-1] <- equals(state[i,j],2)
#      }
#      alive[i] <- sum(whenAlive[i,])
#    }

#    for(j in 1:(n.occasions-1)){
#      N[j] <- sum(whenAlive[,j])  # Population size at each occasion
#    }

#    for(i in 1:M){
#      z[i] <- 1-equals(alive[i],0)    # if ind. i was never alive, z[i]=0
#    }
#    N_super <- sum(z)
#  }

#    ",file="JSWithJAGS.txt")
```

```
#### Determine Known States ####
# For adult CH, we assume they are adults when they are first observed
# thus between the first and last observation, the state is 5, before that
# the state is unknown so NA
known.states.js <- function(ch){
  state <- matrix(NA,nrow=nrow(ch),ncol=ncol(ch))
  for(i in 1:nrow(ch)){
    if(sum(ch[i,])==0){
      next                # if never observed, skip to next individual
    }
    else{
      fst <- min(which(ch[i,]==1))
      lst <- max(which(ch[i,]==1))
      state[i,fst:lst] <- 2
    }
  }
  return(state)
}

# Add dummy occasion to Ad_CH
Xobs.du.js <- as.matrix(cbind(rep(0,nrow(CH.js)),CH.js))
known_state.js <- known.states.js(Xobs.du.js)




#### Initial States for the latent values of the state matrix
# Put NA wherever the state is known and 1's before the known
# states. After the known states, put 3's

initial.states.js <- function(ch) {
  init_st <- matrix(NA,nrow=nrow(ch),ncol=ncol(ch))
  for(i in 1:nrow(ch)){
    if(sum(ch[i,])==0){
      init_st[i,] <- rep(1,ncol(ch))
    }
    else{
      fst <- min(which(ch[i,]==1))
      lst <- max(which(ch[i,]==1))
      init_st[i,1:fst] <- 1
      init_st[i,fst] <- NA
```

```
      init_st[i,lst:ncol(ch)] <- 3
      init_st[i,lst] <- NA

    }
  }
  return(init_st)
}

init_state.js <- initial.states.js(Xobs.du.js)

# Augment the data
n.aug.js <- 3000
X_aug.js <- rbind(Xobs.du.js, matrix(0,
                                     ncol=ncol(Xobs.du.js),nrow=n.aug.js))


# Augment Initial state matrix and known state matrix
known_states_aug.js <- rbind(known_state.js,
                             matrix(NA,nrow=n.aug.js,
                                    ncol=ncol(known_state.js)))
init_states_aug.js <- rbind(init_state.js,
                            matrix(1,nrow=n.aug.js,
                                   ncol=ncol(init_state.js)))

# set the first column of init_states_aug and known_states_aug = NA
init_states_aug.js[,1] <- NA
known_states_aug.js[,1] <- NA

# Bundle Data
JS_data <- list(X = X_aug.js, M=nrow(X_aug.js),n.occasions = ncol(X_aug.js),
                state = known_states_aug.js)

n.occasions.js <- ncol(X_aug.js)

#### INITIAL VALUES

# Bundle Initial Values

JS_inits <- function(){
  list(phi=runif(n.occasions.js-1,0,1), p = runif(n.occasions.js,0,1),
       state = init_states_aug.js)
}
```

```
# Parameters to be monitored
JS_params <- c("phi","p","N","N_super","gamma")

# MCMC settings
ni.js <- 20000
nt.js <- 1
nb.js <- 5000
nc.js <- 3

# Run JAGS model
JS_jags.fit <- jags(model.file="JSWithJAGS.txt",data = JS_data,
                    inits = JS_inits, parameters.to.save = JS_params,
                    n.iter = ni.js,n.chains = nc.js,
                    n.burnin = nb.js,n.thin = nt.js)
```

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