RESEARCH ARTICLE

Estimating reproductive and juvenile survival rates when offspring ages are uncertain: A novel multievent mark-resight model with beluga whale case study

Gina K. Himes Boor[1] | **Tamara L. McGuire**[2] | **Amanda J. Warlick**[3] |
Rebecca L. Taylor[4] | **Sarah J. Converse**[5] | **John R. McClung**[2] | **Amber D. Stephens**[2]

[1]Montana State University, Ecology Department, Bozeman, Montana, USA

[2]The Cook Inlet Beluga Whale Photo-ID Project, Anchorage, Alaska, USA

[3]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

[4]U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA

[5]U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Environmental and Forest Sciences & School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

Correspondence
Gina K. Himes Boor
Email: gkhimesboor@montana.edu

Handling Editor: Chris Sutherland

Abstract

1. Understanding the survival and reproductive rates of a population is critical to determining its long-term dynamics and viability. Mark-resight models are often used to estimate these demographic rates, but estimation of survival and reproductive rates is challenging, especially for wide-ranging, patchily distributed, or cryptic species. In particular, existing mark-resight models cannot accommodate data from populations in which offspring remain with parents for multiple years, are not always detected, and cannot be aged with certainty.

2. Here we describe a Bayesian multievent mark-resight modelling framework that uses all available adult and adult-offspring sightings (including sightings with older offspring of uncertain age) to estimate reproductive rates and survival rates of adults and juveniles. We extend existing multievent mark-resight models that typically only incorporate adult breeding state uncertainty by additionally accounting for age uncertainty in unmarked offspring and uncertainty in the duration of the mother-offspring association. We describe our model in general terms and with a simple illustrative example, then apply it in a more complex empirical setting using 13 years of photo-ID data from a critically endangered population of beluga whales *Delphinapterus leucas*. We evaluated model performance using simulated data under a range of sample sizes, and adult and offspring detection rates.

3. Applying our model to the beluga data yielded precise estimates for all demographic rates of interest (despite substantial uncertainty in calf ages), including nonbreeder survival and reproductive rates lower than in other beluga populations. Simulations suggested our model yields asymptotically unbiased parameter estimates with good precision and low bias even with moderate sample sizes and detection rates.

4. This work represents an important new development in multievent mark-resight modelling, allowing estimation of reproductive and juvenile survival rates for

populations with extended adult—offspring associations and uncertain offspring ages (e.g. some marine mammals, elephants, bears, great apes, bats and birds). Our model facilitated estimation of robust demographic rates for an endangered beluga population that were previously inestimable (e.g. nonbreeder and juvenile survival, reproductive rate) and that will yield new insights into this population's continued decline.

1 | INTRODUCTION

Understanding a population's survival and reproductive rates is critical to examining its long-term dynamics and viability, and foundational to effective management and conservation (Caswell, 2001; Morris & Doak, 2002). For wide-ranging, cryptic, or otherwise hard-to-study species, obtaining the mark-resight data typically used to estimate key demographic rates can be challenging, especially for reproduction (Etterson et al., 2011). For example, if young-of-the-year (YOY) are not always with their mother, or are hard to detect, definitively identifying which adults have reproduced may not be possible. Modelling techniques, such as multievent models, have been developed to deal with such state uncertainty (Gimenez et al., 2012; Kendall et al., 2003; Pradel, 2005), but if offspring remain with their mothers for multiple years and YOY cannot readily be distinguished from older offspring, existing modelling frameworks are inadequate for estimating reproductive rates or accurately estimating offspring survival.

In mark-resight studies designed to identify breeding state and estimate reproductive parameters, state uncertainty has traditionally been defined as arising when a breeding adult is seen without its offspring. Typically, observing a female with offspring is considered definitive evidence of her being in a breeding state (i.e. having given birth in the observation year), whereas a female seen without offspring may be in a nonbreeding state or may be a breeder whose offspring was not detected. Multievent models account for this uncertainty, but if a species exhibits extended maternal care, observing offspring with their mothers cannot be taken as definitive evidence of current breeding status unless offspring age is known. In such cases, observations of older or unknown-aged offspring can be excluded from the analysis (Kendall et al., 2004), but such an approach, at best, discards valuable information that could improve estimation, and, at worst, yields biased reproductive rate estimates if YOY are misidentified as older offspring or vice versa. Recently, researchers have begun incorporating sightings of older offspring into analyses to estimate offspring survival, but these methods assume that offspring age is determined with certainty (Arso Civil et al., 2019; Couet et al., 2019; Cubaynes et al., 2021; Lunn et al., 2016; Regehr et al., 2018; Verborgh et al., 2021). These methods also rely on either relatively high offspring detection rates or

high numbers of within-year surveys, and often assume a fixed (and known) mother-offspring association period. For many populations, however, offspring age cannot be determined with certainty, the mother-offspring association period is unknown and variable (sometimes extending beyond the birth of a sibling), and offspring may not be detected as YOY, only as older dependent young. Reproductive and juvenile survival rates cannot be estimated for such data with existing models.

To address these issues, we developed a new multievent mark-resight modelling framework that uses all available mother-offspring sighting data, including sightings of offspring of unknown age, to estimate reproductive rates and adult and juvenile survival rates. In standard multievent mark-resight studies designed to estimate reproductive rates, when a marked individual is observed, its apparent breeding status is recorded (i.e. presence of offspring); this observation 'event' is then used to infer the latent (unobserved) true state of the individual. Our model expands what is recorded during the observation event to include not only whether the marked individual was accompanied by offspring, but also the estimated age (or age category) of the offspring. This extension required us to account for uncertainty in both the latent breeding state and latent offspring age, given the observation event, and, in turn, required a host of modifications to the typical state-transition and observation matrices used in previously developed multievent models.

Below, we describe the basic structure of our model and use a simple example to illustrate its essential components. We demonstrate its usefulness for empirical data by applying it to photo-ID data from an endangered population of beluga whales, *Delphinapterus leucas*. Finally, we examine the precision and bias of our model with a simulation analysis under a range of detection probabilities and sample sizes using the matrices developed for our beluga application. We conclude by discussing the significance of our new modelling framework, its possible limitations, and how it can be applied to other data.

2 | MODEL STRUCTURE

Multievent models are a class of mark-resight models that account for the fact that the field observations of marked individuals (i.e. events)

may not fully reveal the true latent state of those individuals, such as their breeding status, disease state, or location (if unobserved). The multievent model likelihood function is comprised of three components: initial state vector, state process model, and observation (or event) process model (Gimenez et al., 2012; Pradel, 2005). The initial state vector defines the probabilities, upon first encounter, of an individual being in any one of the states defined in the model. On subsequent occasions, the individual can transition among states (or die) according to the state process model represented by a transition matrix with departure states in rows and arrival states in columns. The observation process model describes the possible observation events (columns) given the true state of marked individuals (rows). Data are in the form of sighting histories for marked individuals indicating the observation event (i.e. the observed status of the individual) on each sighting occasion.

As in other multievent models, our state process matrix describes the probability of a marked individual transitioning from one state at time t to another (or the same) state at $t+1$. For clarity, we construct the overall transition matrix by multiplying a series of four conditional transition matrices representing distinct portions of the state transition process, an approach described previously (e.g. Couet et al., 2019; Gimenez et al., 2012) but used infrequently. We refer to these as component matrices and they account for intermediate states that represent the transition between the states at time t and $t+1$. In order, the component matrices are (Step 1) adult survival, conditioned on state from the previous time-step; (Step 2) offspring survival, conditioned on adult survival; (Step 3) deterministic offspring aging conditioned on survival (i.e. offspring must age if they survive); and (Step 4) reproduction, conditioned on survival and offspring age.

Similar to the state process matrix, our observation process matrix results from the product of three conditional component matrices. In order, these are (Step 1) adult detection, conditioned on true state; (Step 2) offspring detection, conditioned on adult detection; and (Step 3) categorization of offspring age, conditioned on detection and offspring true age. This third step is a new addition in the multievent modelling canon.

In our model, states describe a combination of a marked individual's breeding status (e.g. nonbreeder or breeder) and the age(s) of any dependent offspring. The observation events describe detection of marked individuals as well as the estimated age of any accompanying offspring. Offspring age estimates are assigned using a set of age categories, some of which incorporate uncertainty (e.g. 0–1 year old [yo], 1 yo, ≤2 yo). The specific age categories used in the model can be defined to match the particular circumstances of any given study (i.e. the level of visual, or other, information available to determine offspring age), which will then guide parameterization of the offspring age-categorization matrix (see Section 3).

In addition to the standard assumptions of all multievent models, our model relies on two additional simplifying assumptions. We assume no false-positive offspring sightings (i.e. no marked adults without offspring are identified as having offspring), but offspring can be missed if present. Uncertainty in offspring ages is captured via the age categories used in the observation matrix and we assume no error in offspring age categorization (e.g. a 3 yo offspring will not be categorized as a ≤2 yo, but could be categorized as a ≤3 yo, or ≤4 yo). To meet this latter assumption, age-categories must be chosen to adequately represent the study-specific offspring-age-categorization uncertainty.

As in all multievent models, the precise form of our full state and observation matrices (and thus the conditional component matrices) will depend on the number of states and observation events used in a given study. Below, we illustrate the flexibility of our modelling framework using, first, a simple hypothetical example, followed by a more complex application with empirical data.

3 | SIMPLE EXAMPLE

In this example, we use five live states, eight observation events and 14 parameters with the following characteristics. Adult females are marked. During annual sighting occasions, offspring accompanying marked females are recorded, as are any age-distinguishing characteristics of the offspring (e.g. relative size, neonate features). Offspring must remain with their mother through their second year (i.e. as 1 yo) to survive, but sometimes remain longer (only rarely, however, remaining dependent as ≥3 yo). Females will not give birth if they have dependent young, but if offspring do not survive the transition from t to $t+1$, the adult can give birth in $t+1$.

In this example, the five true, live states include nonbreeder (NB), breeder with no offspring (B), breeder with a YOY (B_Y), breeder with a 1-year old (B_{c1}), and a breeder with a 2-year old or older offspring (B_{c2*}). The initial state vector gives the probabilities of being in each of these five live states upon initial capture/sighting: $\prod = [\pi_N \ \pi_B \ \pi_{By} \ \pi_{Bc1} \ \pi_{Bc2*}]$, where, $\pi_{Bc2*} = 1 - (\pi_N + \pi_B + \pi_{By} + \pi_{Bc1})$.

The state matrix includes six state parameters related to adult and juvenile survival and reproduction (Figure 1). Step 1: The adult survival component matrix allows marked individuals to survive (with probability φ_N for nonbreeders and φ_B for breeders) or die (i.e. with probability $1 - \varphi_N$ or $1 - \varphi_B$, respectively). In this step, they can only transition to the 'dead' state or stay in their same alive state. Step 2: The offspring survival matrix allows surviving marked individuals to transition to a state without offspring if the offspring dies, with probability $1 - S_Y$ for obligately dependent offspring (≤1 yo) or $1 - \varphi_J$ for older offspring (≥2 yo). S_Y represents true offspring survival probability, since we assume that offspring ≤1 yo cannot survive if separated from their mother. All other survival rates (denoted by φ) represent apparent survival, as true adult survival is confounded with permanent emigration, and true older offspring survival is confounded with gaining independence. Because the offspring survival matrix is conditioned on adult survival, we need to account post-hoc for offspring that die or become independent when their mothers die; thus, marginal offspring survival is calculated as $S\prime_Y = S_Y \times \varphi_B$ and $\varphi\prime_J = \varphi_J \times \varphi_B$. Step 3: The offspring-aging matrix advances surviving offspring from one age to the next, thus transitioning the marked individual to a state with an offspring that is 1 year older.
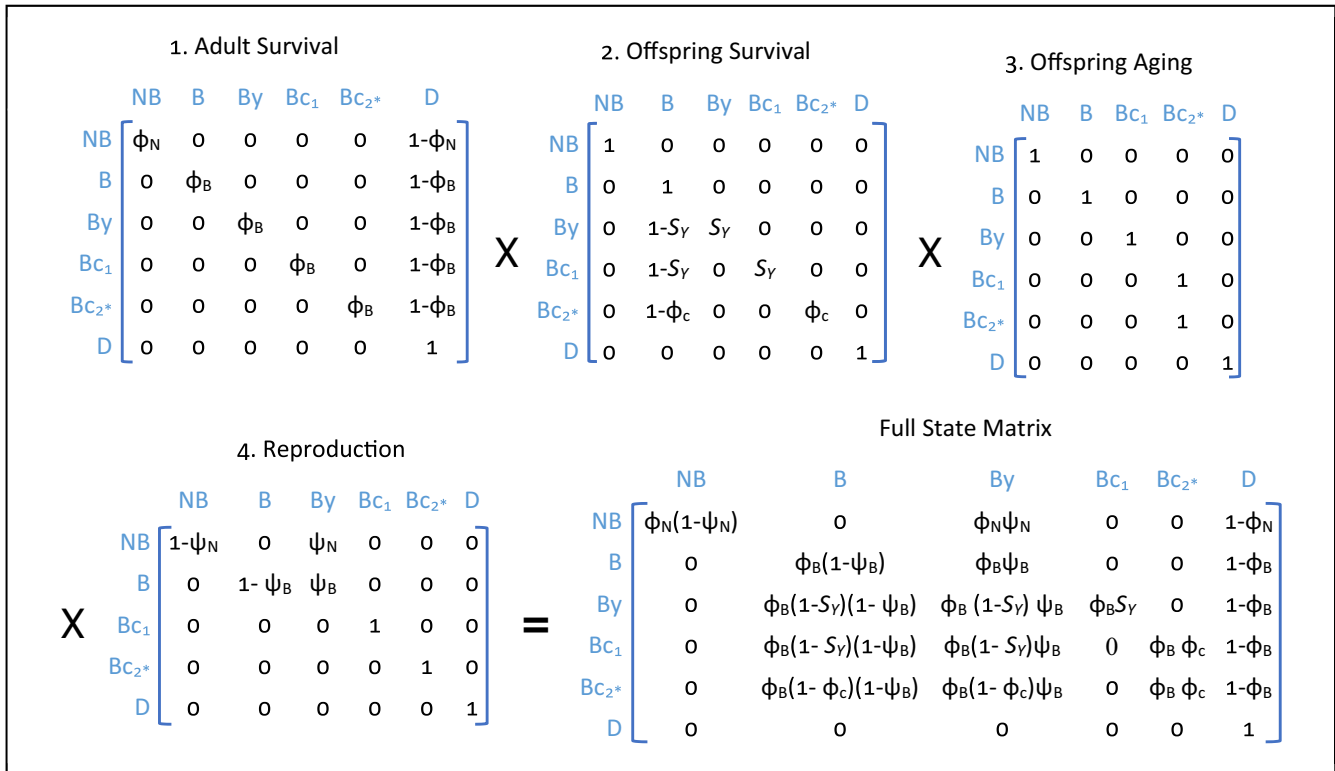
1. Adult Survival

$$\begin{array}{c c} & \begin{array}{cccccc} NB & B & By & Bc_1 & Bc_{2*} & D \end{array} \\ \begin{array}{c} NB \\ B \\ By \\ Bc_1 \\ Bc_{2*} \\ D \end{array} & \left[\begin{array}{cccccc} \phi_N & 0 & 0 & 0 & 0 & 1-\phi_N \\ 0 & \phi_B & 0 & 0 & 0 & 1-\phi_B \\ 0 & 0 & \phi_B & 0 & 0 & 1-\phi_B \\ 0 & 0 & 0 & \phi_B & 0 & 1-\phi_B \\ 0 & 0 & 0 & 0 & \phi_B & 1-\phi_B \\ 0 & 0 & 0 & 0 & 0 & 1 \end{array}\right] \end{array}$$

$\times$

2. Offspring Survival

$$\begin{array}{c c} & \begin{array}{cccccc} NB & B & By & Bc_1 & Bc_{2*} & D \end{array} \\ \begin{array}{c} NB \\ B \\ By \\ Bc_1 \\ Bc_{2*} \\ D \end{array} & \left[\begin{array}{cccccc} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 1-S_Y & S_Y & 0 & 0 & 0 \\ 0 & 1-S_Y & 0 & S_Y & 0 & 0 \\ 0 & 1-\phi_c & 0 & 0 & \phi_c & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{array}\right] \end{array}$$

$\times$

3. Offspring Aging

$$\begin{array}{c c} & \begin{array}{ccccc} NB & B & Bc_1 & Bc_{2*} & D \end{array} \\ \begin{array}{c} NB \\ B \\ By \\ Bc_1 \\ Bc_{2*} \\ D \end{array} & \left[\begin{array}{ccccc} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{array}\right] \end{array}$$

4. Reproduction

$\times$

$$\begin{array}{c c} & \begin{array}{cccccc} NB & B & By & Bc_1 & Bc_{2*} & D \end{array} \\ \begin{array}{c} NB \\ B \\ Bc_1 \\ Bc_{2*} \\ D \end{array} & \left[\begin{array}{cccccc} 1-\psi_N & 0 & \psi_N & 0 & 0 & 0 \\ 0 & 1-\psi_B & \psi_B & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{array}\right] \end{array}$$

$=$

Full State Matrix

$$\begin{array}{c c} & \begin{array}{cccccc} NB & B & By & Bc_1 & Bc_{2*} & D \end{array} \\ \begin{array}{c} NB \\ B \\ By \\ Bc_1 \\ Bc_{2*} \\ D \end{array} & \left[\begin{array}{cccccc} \phi_N(1-\psi_N) & 0 & \phi_N\psi_N & 0 & 0 & 1-\phi_N \\ 0 & \phi_B(1-\psi_B) & \phi_B\psi_B & 0 & 0 & 1-\phi_B \\ 0 & \phi_B(1-S_Y)(1-\psi_B) & \phi_B(1-S_Y)\psi_B & \phi_BS_Y & 0 & 1-\phi_B \\ 0 & \phi_B(1-S_Y)(1-\psi_B) & \phi_B(1-S_Y)\psi_B & 0 & \phi_B\phi_c & 1-\phi_B \\ 0 & \phi_B(1-\phi_c)(1-\psi_B) & \phi_B(1-\phi_c)\psi_B & 0 & \phi_B\phi_c & 1-\phi_B \\ 0 & 0 & 0 & 0 & 0 & 1 \end{array}\right] \end{array}$$

FIGURE 1 The four component conditional transition matrices and the full state matrix derived from the component matrices used in our simple example to illustrate our modelling approach. The full state matrix shows the probability of a marked individual transitioning from a state at time t (rows) to a state at time $t+1$ (columns). The following previously undefined abbreviations are used in the columns and row labels in the component matrices: By^D = breeder whose young-of-year offspring died, $Bc_1{}^D$ = breeder whose 1-year-old offspring died, $Bc_{2*}{}^D$ = breeder whose 2-year-old or older offspring died.

These transitions are deterministic, that is, entries in the matrix are all probabilities equal to zero or one. Step 4: The reproduction matrix allows marked individuals without offspring to transition to a state with a YOY and is based on two parameters: the probability of breeding for the first time (ψ_N), and the probability of a breeder giving birth again (ψ_B).

The observation model is defined by eight parameters and eight possible observation events: not seen, seen without offspring, and seen with offspring in one of six age categories (Figure 2). Step 1: The adult detection matrix is based on a single detection rate for all adults (p). Step 2: The offspring detection matrix is based on detection rates for young, obligately dependent offspring (i.e. ≤1 yo; δ_Y) and older offspring (i.e. ≥2 yo; δ_C), conditional on the mother being detected. Step 3: The offspring-age-categorization matrix includes six age categories: 'J0' for offspring that can be definitively identified as having been born in the observation year (i.e. YOY), 'J1−' for offspring determined to be a maximum of one year old but possibly younger, 'J1' for offspring that can be definitively identified as 1 year old, 'J1+' for offspring 1 year old or older, 'J2+' for offspring 2 years old or older, and 'Unk' for offspring whose age category could not be determined. We use five parameters to characterize the age-categorization process, where each parameter represents the probability of a binary age-categorization decision, conditional on any previous decision(s). Specifically, γ represents the probability

that the offspring can be assigned to an age category (vs. unknown). Parameters α and β apply to YOY and 1 yo, respectively, and, given they can be categorized, are the probabilities they can be assigned to a definitive age category (i.e. YOY assigned to 'J0', or 1 yo assigned to 'J1'). Parameter κ represents the probability that a 1 yo offspring, given it was not assigned to the definitive category 'J1', is assigned to the 'younger than or equal to' age category (e.g. 'J1−') versus the 'equal to or older than' category (e.g. 'J1+'). Parameter ω applies to offspring 2 years old or older and is the probability that the 2 yo will be placed in the 'J1+' category versus the 'J2+' category, given it could be categorized. The probability of a particular age assignment for any given true age will be equal to the product of all parameters along the binary decision path leading to that assignment. For example, a 1 yo will be assigned to the 'J1+' category with probability $\gamma(1-\beta)(1-\kappa)$ to account for the fact that it could be put into an age category, it could not be aged definitively, and it was not assigned to the 'younger than' category, but to the 1 yo 'or older' category (see matrix 3 in Figure 2).

This example illustrates a simple application of our model, but the basic framework is designed to be flexible enough to accommodate a wide range of study designs and data from any population with extended offspring care and uncertainty in offspring age determination. As described above, the key characteristics of our model are, (1) the construction of the state transition matrix using a series
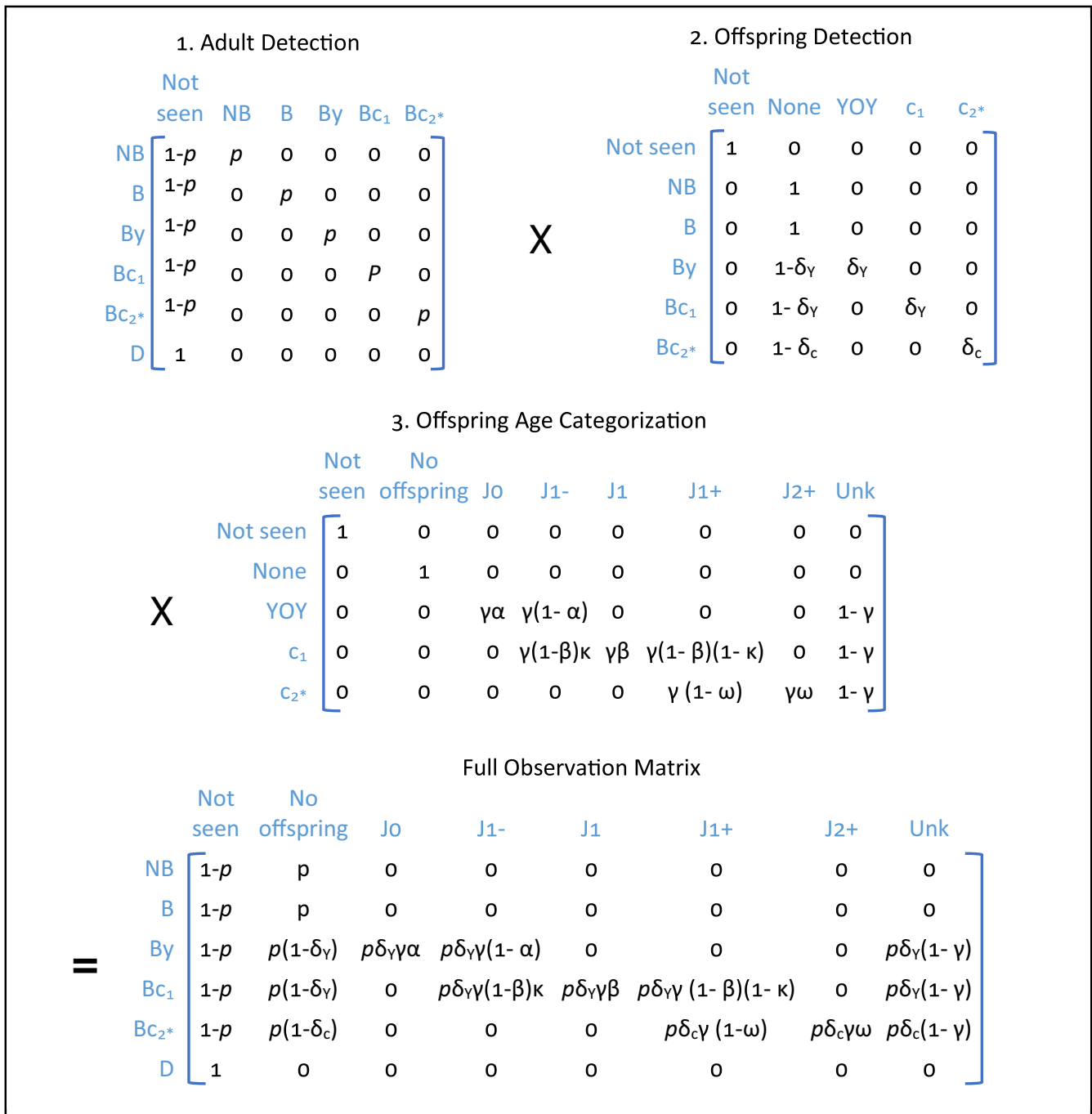
1. Adult Detection

	Not seen	NB	B	By	Bc_1	Bc_{2*}
NB	$1-p$	p	0	0	0	0
B	$1-p$	0	p	0	0	0
By	$1-p$	0	0	p	0	0
Bc_1	$1-p$	0	0	0	P	0
Bc_{2*}	$1-p$	0	0	0	0	p
D	1	0	0	0	0	0

X

2. Offspring Detection

	Not seen	None	YOY	c_1	c_{2*}
Not seen	1	0	0	0	0
NB	0	1	0	0	0
B	0	1	0	0	0
By	0	$1-\delta_Y$	δ_Y	0	0
Bc_1	0	$1-\delta_Y$	0	δ_Y	0
Bc_{2*}	0	$1-\delta_c$	0	0	δ_c

3. Offspring Age Categorization

X

	Not seen	No offspring	J0	J1-	J1	J1+	J2+	Unk
Not seen	1	0	0	0	0	0	0	0
None	0	1	0	0	0	0	0	0
YOY	0	0	$\gamma\alpha$	$\gamma(1-\alpha)$	0	0	0	$1-\gamma$
c_1	0	0	0	$\gamma(1-\beta)\kappa$	$\gamma\beta$	$\gamma(1-\beta)(1-\kappa)$	0	$1-\gamma$
c_{2*}	0	0	0	0	0	$\gamma(1-\omega)$	$\gamma\omega$	$1-\gamma$

Full Observation Matrix

=

	Not seen	No offspring	J0	J1-	J1	J1+	J2+	Unk
NB	$1-p$	p	0	0	0	0	0	0
B	$1-p$	p	0	0	0	0	0	0
By	$1-p$	$p(1-\delta_Y)$	$p\delta_Y\gamma\alpha$	$p\delta_Y\gamma(1-\alpha)$	0	0	0	$p\delta_Y(1-\gamma)$
Bc_1	$1-p$	$p(1-\delta_Y)$	0	$p\delta_Y\gamma(1-\beta)\kappa$	$p\delta_Y\gamma\beta$	$p\delta_Y\gamma(1-\beta)(1-\kappa)$	0	$p\delta_Y(1-\gamma)$
Bc_{2*}	$1-p$	$p(1-\delta_c)$	0	0	0	$p\delta_c\gamma(1-\omega)$	$p\delta_c\gamma\omega$	$p\delta_c(1-\gamma)$
D	1	0	0	0	0	0	0	0

FIGURE 2 The three component conditional transition matrices and the full observation matrix (derived from multiplying the component matrices) used in our simple example to illustrate our modelling approach. The full observation matrix shows the probability of an observation event (columns) occurring given a marked individual's true state (rows) in time t. The following previously undefined abbreviations are used in the columns and row labels in the component matrices: YOY = young-of-year offspring observed with marked adult, c_1 = 1-year-old offspring observed with marked adult, c_{2*} = 2-year-old or older offspring observed with marked adult.

of conditional transition matrices that account for adult and juvenile survival, juvenile aging, and adult reproduction, and (2) construction of the observation matrix using a series of matrices that account for adult and juvenile detection and juvenile age categorization. Using this basic framework, we are able to build a substantially more complex example to accommodate the ecology and observation of the Cook Inlet beluga whale.

4 | CASE STUDY: COOK INLET BELUGA

In this section, we apply our model to empirical data from the endangered Cook Inlet beluga whale population, for which managers currently lack robust estimates of reproductive and juvenile survival rates. This beluga case study demonstrates how the structure of our model matrices can be adapted to account for different kinds of data,

life histories and model assumptions by modifying the states, events, matrices and parameters while using the same basic model structure. We also use this empirical example to describe the Bayesian model fitting procedure.

4.1 | Data collection and processing

We applied our model to photo-ID data collected from the endangered beluga whale population that resides in Cook Inlet, Alaska, USA (Laidre et al., 2000; O'Corry-Crowe et al., 1997; Wade et al., 2019). Detailed data collection protocols can be found in McGuire et al. (2020), but we briefly describe them here. Photo-ID surveys were conducted under General Authorization, Letter of Confirmation No. 481-1759, and National Marine Fisheries Service Scientific Research Permits #14210 and #18016. The Cook Inlet Beluga Whale Photo-ID Project (CIBW-PIP; https://www.cookinletbelugas.com/) photographs Cook Inlet beluga whales (CIBWs) on surveys conducted multiple times annually, April–October, and identifies individual whales from distinct permanent marks on their dorsal and lateral surfaces. We applied our model to data from the catalogue of left-side photographs taken between 2005 and 2017 ($n = 471$ individuals; $n = 13$ sightings occasions), where our sighting records consist of the aggregate sightings of an individual made during each field season ($n = 1931$ aggregate sighting records). Based on previous studies and field observations (Bors et al., 2021; McGuire et al., 2020, 2021; Shelden et al., 2020), we assumed that catalogued individuals are a combination of male and female (which are indistinguishable in the field) adults and subadults. We define subadults as independent whales (i.e. no longer with mother) ≥5 yo but not yet of reproductive age (<13–14 yo).

Calves in close association with adults were also photographed ($n = 367$ adult-calf sightings), but generally could not be individually identified. Calves are thought to remain with their mothers between 2 and 5 years, and can remain closely associated beyond the birth of a sibling (McGuire et al., 2020). In the extremely turbid waters of Cook Inlet, darker-coloured calves are frequently undetected, and for those that are detected, their age is difficult to determine.

During post-survey photo-processing, calves photographed in close association with an adult (their presumed mother) were assigned to an age category based on size relative to adult, colour, and neonate and YOY features (i.e. fetal folds, 'peanut-shaped' head, and presence of an eye ring; McGuire et al., 2020). We assumed presence of neonate or YOY features was definitive evidence the calf was a YOY. Most calves, however, were assigned to a calf-age category that included uncertainty. At least two photo-analysts independently assigned an age category to each calf sighting, with discrepancies resolved by using the most-inclusive category or by a third analyst. In general, age categories were assigned independently across years (i.e. without consideration of previous offspring age categorizations) to avoid age categorization bias and propagation of errors. However, because a few YOY were individually identifiable from distinct

permanent markings, following the initial age-categorization process, photo-analysts checked for distinct marks that linked to a YOY sighting in previous years, which enabled assignment of a definitive age category (e.g. 'J2'; 2.7% of calf sightings). When marked adults were observed in close association with two calves of different sizes on a single sighting occasion or on different occasions within the same year, the adult was associated with both calves, and ages were assigned to both (3.8% of calf sightings).

4.2 | Model and parameters

Our beluga application included more states and observation events than the simple example described above. The initial state vector included 13 parameters (π_i), one for each possible live state (Table 1). We used a total of 72 observation events, with 70 of those corresponding to observation of a marked adult with one or two calves in any combination of 12 calf-age observation categories (Table 1). Below, we describe the parameters of biological interest, but we list all parameters and present all matrices in Appendix S1.

The state process model included six parameters that differed only slightly from the analogous parameters in the simple example (Figure 3; Appendix S1). We separated adult survival into breeder and nonbreeder survival (S_B and S_N, respectively), where breeders are defined as females that have given birth at least once and nonbreeders include subadults, males, and nonbreeding females. These adult survival rates represent true survival because CIBWs are geographically isolated in Cook Inlet and their summer range is currently limited to the portion of the Inlet where CIBW-PIP surveys are conducted. Thus, we assumed no immigration from or emigration to locations outside the study area. As in the simple example, we estimated two age-specific calf survival rates (S_Y for ≤1 yo, and φ_C for ≥2 yo). We assumed, based on the literature and our own records (McGuire et al., 2020), that beluga calves do not wean before their second ice-free season and therefore must remain with their mother for at least that long in order to survive. Thus, our young calf survival parameter (S_Y) represents true survival probability, and the older calf survival parameter (φ_C) represents apparent survival (the probability that the calf both survives and remains with its mother until the next ice-free season). Given that older calves that survive must become independent at some point, this will by necessity be a negatively biased estimate of true older calf survival. Marginal calf survival was calculated as in the simple example: $S\prime_Y = S_Y \times S_B$ and $\varphi\prime_C = \varphi_C \times S_B$. We did not assume an upper age for calf dependence on its mother, but we did assume a mother would care for no more than two calves concurrently. Our reproductive parameters included a nonbreeder transition parameter (i.e. the probability a nonbreeder gives birth for the first time; ψ_N) and an established breeder reproductive rate parameter (ψ_B). Based on the biology of CIBWs, we assume that births cannot occur in consecutive years, thus our reproductive rate is defined as the probability that an established breeder without a YOY in the previous year gives birth. Relatedly, we assume that a breeder whose YOY dies cannot give birth the next year.

TABLE 1 The states and events used in the Cook Inlet beluga photo-ID case study. (a) The 13 possible true states in which marked individuals can first be detected, plus the 'dead' state used in the state transition matrix. (b) The first 14 sighting history event codes and their definitions. The events that include calf ages represent observations of a marked adult with a single calf that was assigned to the specified age category. Appendix S1 lists the 58 remaining events used in the model that represent sightings of a marked adult with two associated calves of all possible combinations of age-categorizations

Code	Definition
(a) True state codes and definitions	
NB	Nonbreeder
B	Breeder with no calf
Byoy	Breeder with YOY calf
Bc1	Breeder with 1 yo calf
Bc2	Breeder with 2 yo calf
Bc2yoy	Breeder with YOY & 2 yo calves
Bc3	Breeder with 3 yo calf
Bc3yoy	Breeder with YOY & 3 yo calves
Bc3c1	Breeder with 1 yo & 3 yo calves
Bc4*	Breeder with 4 yo or older calf
Bc4*yoy	Breeder with YOY & 4 yo or older calves
Bc4*c1	Breeder with 1 yo & 4 yo or older calves
Bc4*c2	Breeder with 2 yo & 4 yo or older calves
D	Dead
(b) First 14 observation event codes and definitions	
0	Marked individual not seen
1	Marked individual seen alone
J0	Observed with calf assigned to YOY age category
J1−	Observed with calf assigned to 1 yo or younger age
J1	Observed with calf assigned to 1 yo age category
J1+	Observed with calf assigned to 1 yo or older age
J2−	Observed with calf assigned to 2 yo or younger age
J2	Observed with calf assigned to 2 yo age category
J2+	Observed with calf assigned to 2 yo or older age
J3	Observed with calf assigned to 3 yo age category
J3+	Observed with calf assigned to 3 yo or older age
J4	Observed with calf assigned to 4 yo age category
J4+	Observed with calf assigned to 4 yo or older age
Unk	Observed with calf whose age category could not be determined (was unknown)

The observation model included 13 parameters—five to account for detection and eight to account for the calf-age-categorization processes. Adult detection was defined as the probability that an identified individual was detected on at least one of the surveys conducted each year. To account for any potential differences in sociability, habitat use, or photographer bias toward whales with calves, we estimated three separate adult detection probabilities, one for nonbreeders (p_N), one for breeders with one

or more calves of any age (p_{Bc}), and one for established breeders with no calf in a given year (p_{Bn}). We estimated two calf-detection probabilities corresponding to young calves (δ_{Yc}) and older calves (δ_C). Our calf-age-categorization matrix used eight parameters to account for calf-age-categorization uncertainty that together describe the probability a photo-analyst assigned an observed calf to 1 of 12 calf-age categories conditional on its true age and detection (Appendix S1). We accomplished this using the type of binary decision-path approach described in our simple example (and illustrated in detail in Appendix S2), which allowed us to describe 72 observations events using eight parameters.

4.3 | Model fitting

We fit the beluga model using a Bayesian statistical framework with vague prior distributions for all parameters, including a Dirichlet [1…1] prior for the initial state parameters (π_i), and Uniform [0, 1] priors for all others. Models were fit by running four chains of 55,000 Markov chain Monte Carlo (MCMC) iterations with a burn-in of 10,000 iterations and a thin rate of 10; thus, we retained 18,000 samples from each posterior distribution. Below we report the posterior median and 95% credible intervals (CrIs) for all demographic and detection parameters (see Appendix S1 for the complete set of parameter estimates). We performed statistical analyses in R version 3.6.1 (R Core Team, 2017), using a Gibbs sampler algorithm implemented in JAGS version 4.3 (Plummer, 2022), and used the R packages RJAGS (Plummer, 2019) and JAGSUI (Kellner, 2019) to interface with JAGS. We assessed MCMC chain convergence using visual examination of trace plots as well as Gelman-Rubin diagnostics ($\hat{R} \leq 1.1$) (Brooks & Roberts, 1998; Gelman & Rubin, 1992).

4.4 | Results

Our model produced precise estimates of all demographic rates. Breeding females had an estimated survival rate of 0.962 (95% CrI: 0.945–0.975), and nonbreeders of 0.931 (0.917–0.944; Table 2). We estimated a breeding probability for established breeders without a YOY in the previous year of 0.279 (0.226–0.34), which translates to an inter-birth interval of 4.6 years (3.9–5.4; calculated as, $\frac{1}{\Psi_B} + 1$). Nonbreeders entered the breeding population at a rate of 0.072 (0.059–0.085) per year. Young calves (≤1 yo) had an estimated survival rate of 0.926 (0.85–0.964), and older calves (≥2 yo) had an estimated apparent survival rate (i.e. probability of surviving and remaining with the mother) of 0.492 (0.398–0.595).

Detection rates for all classes of whales were moderate to high (Table 2). For adults and subadults, detection rates varied among breeding classes, ranging from 0.456 (0.43–0.484) for nonbreeders to 0.715 (0.606–0.83) for established breeders with no calf. Calves were detected about half the time they were present with their detected mothers.
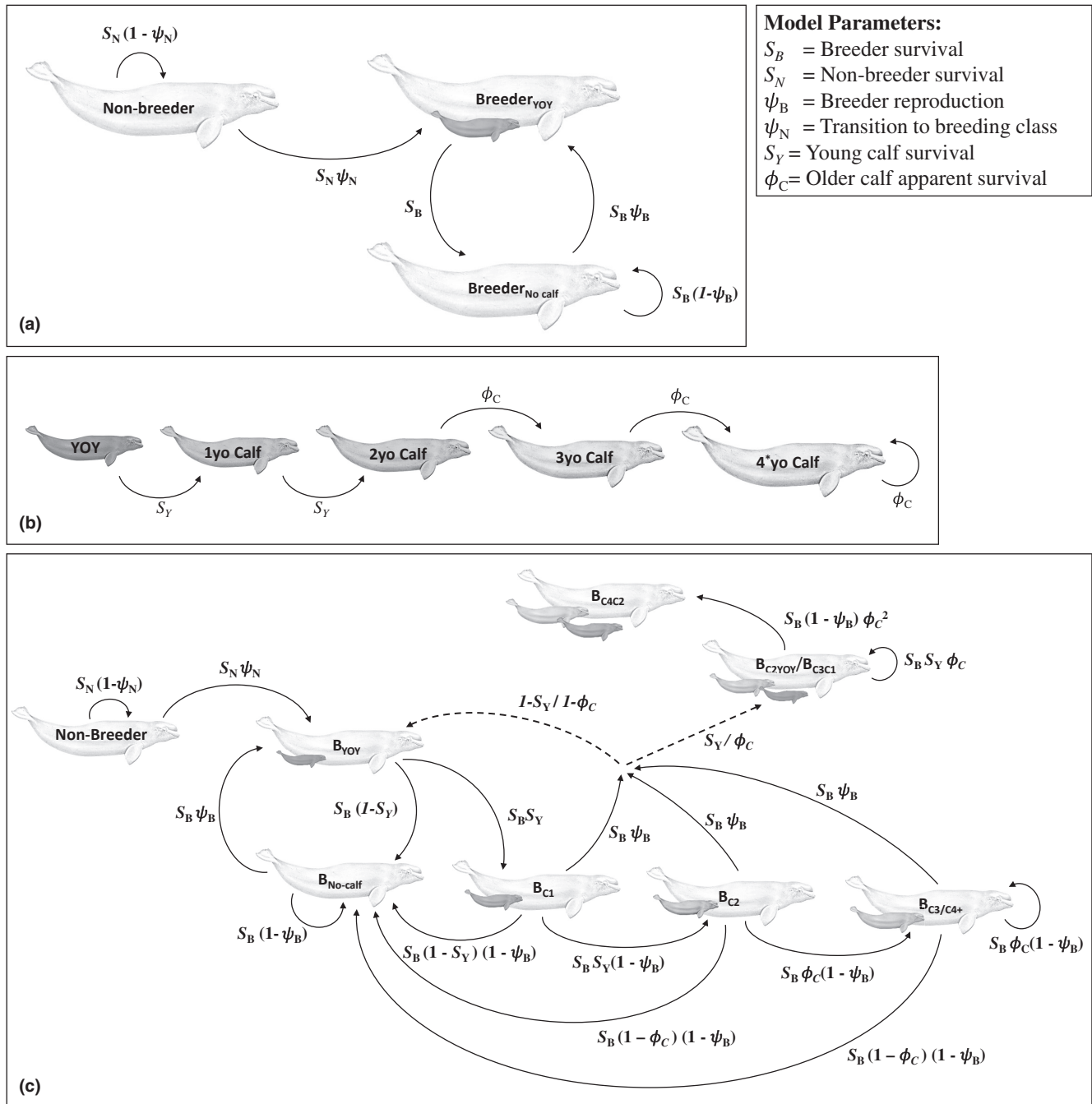
FIGURE 3 Illustration of our beluga case study state model parameters and their relationship to one another for (a) adult and subadult survival and reproductive rates only, (b) calf survival rates only, and (c) the full model. For simplicity, the full model illustration does not depict the possible transitions from a breeder with two calves (upper right portion of illustration) to a breeder with one or no calves (i.e. one or both calves die or gain independence), but those transitions are part of the model. Beluga drawing by Dawn Witherington.

5 | SIMULATION ANALYSIS

5.1 | Methods

To assess bias and precision in our model, we applied it to simulated mark-resight data. The simulated data resembled the empirical beluga data, with 72 possible observation events and

13 possible live states, and we used the same parameters and model structure used in the beluga case study. We simulated three levels of sample sizes (250, 475, 1000) corresponding to the total number of marked individuals, three levels of adult and calf detection (0.25, 0.5, 0.75), and fixed demographic rate values similar to our empirically based beluga estimates. We generated $n = 50$ datasets for each fully crossed combination

TABLE 2 Parameter estimates from our Bayesian state-space multievent mark-resight model applied to Cook Inlet beluga whale photo-ID data from the left-side catalogue

Parameter description	Parameter	Median	Standard deviation	2.5%	97.5%
Nonbreeder survival	S_N	0.931	0.007	0.917	0.944
Adult female breeder survival	S_B	0.962	0.008	0.945	0.975
YOY-1 yo calf survival	S'_Y	0.926	0.030	0.850	0.964
≥2 yo calf apparent survival	Φ'_C	0.492	0.050	0.398	0.595
Transition from nonbreeder to breeder	Ψ_N	0.072	0.007	0.059	0.085
Birth rate for established breeders	Ψ_B	0.279	0.029	0.226	0.340
Nonbreeder detection	p_N	0.456	0.014	0.430	0.484
Breeder-with-no-calf detection	p_{Bn}	0.715	0.057	0.606	0.830
Breeder-with-calf detection	p_{Bc}	0.672	0.021	0.631	0.712
YOY-1 yo calf detection	δ_{Yc}	0.546	0.029	0.489	0.602
≥2 yo calf detection	δ_C	0.473	0.050	0.383	0.580
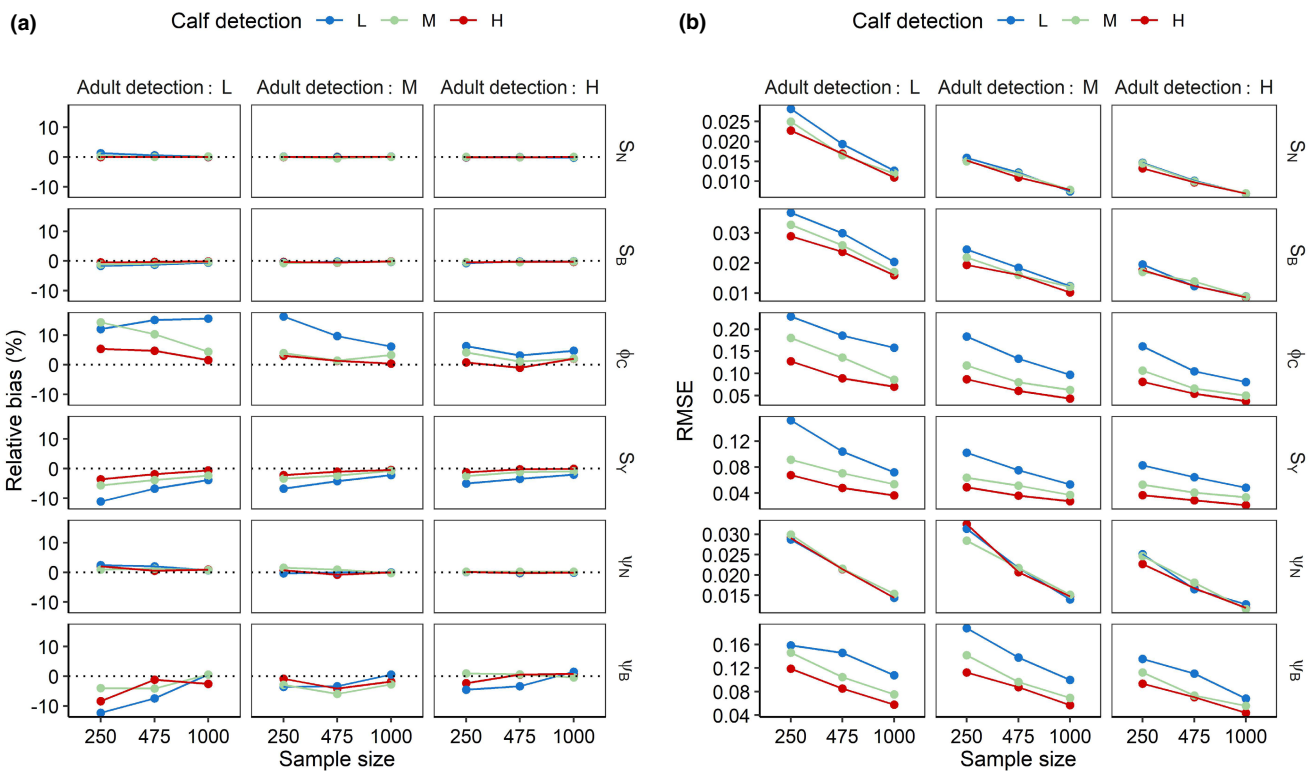
FIGURE 4 Results from simulations to examine model bias and precision. Relative bias (a) and root median square error (RMSE; b) mean values for each batch of 50 simulations conducted under three sample sizes (250, 475, 1000) and three adult and calf detection rates (L = 0.25, M = 0.5, H = 0.75).

of sample size and detection probability. For each parameter and scenario, we calculated relative bias as $RB = \left| \frac{(\sum_{i=1}^{n} f_{0.5,i}) - t}{t} \right| \times 100$, and root median square error as $RMSE = \sqrt{\frac{\sum_{i=1}^{n}(f_{0.5,i} - t)^2}{n}}$, where $f_{0.5,i}$ is the estimated posterior median for the ith simulation and true value, t. To determine CrI coverage, we calculated the mean proportion of simulations in which the 95% CrIs included t, that is, $f_{0.025} \leq t \leq f_{0.975}$.

5.2 | Results

The simulation analysis indicated that our model is asymptotically unbiased and performed well under a broad range of detection rates and sample population sizes. Both RB and RMSE decreased at higher sample sizes and higher levels of adult and calf detection rates (Figure 4; Appendix S3). At the highest sample size and

detection rates, all survival and reproductive parameters had RMSE <0.03 and RB <1%. Some offspring-age-categorization parameters suffered from high bias at low adult and offspring detection, but the bias did not appear to negatively impact parameters of biological interest (Appendix S3). Credible intervals across all model parameters included the data-generating value in an average of 95% of the simulations.

6 | DISCUSSION

We developed a novel multievent mark-resight model that addresses many of the challenges associated with estimating reproductive and survival rates in long-lived species with complex social structures. This model is the first to produce reproductive rate and juvenile survival estimates in a scenario with classic reproductive state uncertainty coupled with an extended, variable parental care period and uncertain offspring ages. Simulations indicated the model is asymptotically unbiased and performs well under a broad range of detection rates and samples sizes. Our model is applicable to any population for which mark-resight-type data are collected on adults along with information on presence and relative size or age of accompanying offspring.

In our case study, we were able to estimate reproductive and survival rates for the Cook Inlet beluga population that were previously inestimable from mark-resight data due to a combination of reproductive state uncertainty, offspring age uncertainty, and an unknown and variable offspring-dependency period that can result in overlapping sibling dependency. The vital rate estimates enabled by our new model yield important new information suggesting that nonbreeder survival and reproductive rate may be low and contributing to the population's decline. This knowledge may further the effort to elucidate the exogenous stressors affecting this population.

6.1 | Model assumption violations

In our model, as in all mark-recapture models, capture heterogeneity can negatively bias survival rates (Abadi et al., 2013; Williams et al., 2002, p. 434). The beluga application of our model accounted for potential differences in detection between breeders with calves, breeders without calves, and nonbreeders, but not for the subgroups within the nonbreeder class (subadults, males, nonbreeding females) because those groups were not distinguishable in our data. This has the potential to misrepresent survival of these subgroups. In applying the model to other systems, separate detection parameters should be used for any classes of individuals with potentially different detection patterns to avoid biased survival estimates.

Our model results rely on the assumption that we have no false-positive adult-offspring sightings. In the beluga case study, we excluded ambiguous mother-calf associations from the data, but assumed an adult whale photographed in unambiguous association with a calf was the mother of that calf. If calves commonly associate closely with individuals that are not their mother (i.e. allocare; Aubin et al., 2021), our reproductive rates could be biased. To assess how erroneous adult-offspring associations might impact demographic rate estimates, we applied our model to a modified beluga dataset in which we excluded the 60 adult-calf sightings that occurred on only a single survey for any given adult, under the unrealistic, but instructive, assumption that these observations were all erroneous associations. These 60 sightings represented 16% of all adult-calf sightings and 3% of all sightings. The results from this exploration indicated that violations of the no-false-positive assumption in the beluga case study would result in an overestimate of the transition rate from nonbreeder to breeder and an underestimate of established breeder reproductive rates. Quantitatively, a 16% false positive rate in adult-offspring associations could result in an 80% overestimate of nonbreeder transition and an 18% underestimate of the reproductive rate. In addition, survival rates in the different breeding classes could change because the pool of individuals in the breeder and nonbreeder classes would be different. With respect to the beluga data, we know that ~1/3 of the excluded single adult-calf sightings came from whales that were seen with calves in years after the end of the present study (T.M., unpublished data) suggesting that the previous single adult-calf sightings for those individuals were correct. Notably, however, this assessment yields important information about the potential direction and magnitude of bias if allocare or similar misspecification of adult-offspring association is common within a dataset.

6.2 | Modifying the model for other applications

The structure of the state and observation matrices used in our model are driven by the two related, but distinct, adaptations of the multievent modelling framework that we leveraged: (1) defining adult reproductive status in terms of offspring age, and (2) extending state uncertainty to include offspring-age-categorization uncertainty. To estimate reproductive rate, offspring ages must be tracked through time to link observations of older offspring (i.e. >YOY) to their birth year, and thus to a reproductive event for the adult. As a result, the 'reproductive state' of an adult must include offspring age, and each offspring age must be explicitly accounted for as a separate adult reproductive state in both the state and observation matrices. Thus, for the full state matrix to account for each offspring age plus a breeder-with-no-offspring state and a dead state, its minimum dimensions must equal the number of potential offspring age classes plus two. In addition, the state matrix must account for offspring survival and their transition to the next age-category. As illustrated in the beluga application, the transition between offspring ages will be deterministic, conditional on offspring (apparent) survival.

In both the simple example and the beluga case study, we defined the oldest adult-offspring state to be the specified offspring age 'or older'. This approach was a practical decision to minimize the size of the state matrix while allowing for occasional sightings of older offspring and for uncertainty in how old the oldest offspring

is. We found that rare instance of offspring older than the nominal state will not bias model results. However, the model matrices can be constructed to include all possible ages of offspring if that information is available. We also note that use of an 'or older' state will bias model results if sightings of the 'older' offspring are frequent.

The observation matrix must account for both offspring detection (conditional on adult detection) and offspring age-categorization. By defining reproductive state in terms of offspring age, we can incorporate this uncertainty in the same way that reproductive state uncertainty has been incorporated in previous work with conditional transition matrices (e.g. Gimenez et al., 2012), albeit with somewhat more complexity. The number of, and relationship between, the offspring-age-classification parameters will depend on the number of reproductive states and the complexity and overlap among the age-categorization categories. Our simple example demonstrated a parameter reduction method based on binary categorization decisions, and we extended that for our extremely complex beluga data with 72 observation events (Appendix S2). Careful a priori decisions about what offspring-age-categorization categories will be allowed during the age-categorization process could help minimize the complexity of the age-categorization matrix.

7 | CONCLUSIONS

The novel multievent model structure we developed is an important step forward in using mark-resight models to estimate reproductive rates and juvenile survival for species with extended parental care and uncertain offspring ages. Many cetaceans (i.e. whales and dolphins) exhibit social dynamics amenable to our model, as do bears, elephants, and some great apes, bats, and birds (Stearns, 1976; Uomini et al., 2020; van Noordwijk & van Schaik, 2005). In addition to expanding the number of populations for which reproductive rates may be estimable, our model could yield important ecological insights and improved parameter estimates through application to datasets previously analysed under restrictive assumptions (e.g. fixed parental-offspring association periods, offspring age certainty) or datasets in which observations of older or unknown-aged offspring were previously discarded. Our model can be adapted to include time-varying survival and reproductive parameters as well as covariates that can account for variability in demographic and detection rates (A.W., unpublished data).

With respect to the Cook Inlet beluga population, our model provides critical new demographic rate estimates for this endangered and declining population that suggest nonbreeder survival and established breeder reproductive rates are low relative to other beluga populations and likely contributing to negative growth. We suggest our model may yield similarly elucidating information for other hard-to-study species with extended parental care.

AUTHOR CONTRIBUTIONS

Tamara McGuire and Gina Himes Boor conceived of the project; Tamara McGuire developed the field methodologies and obtained the field funding and research permits; Tamara McGuire, Amber Stephens and John McClung collected and processed the photo-ID data; Gina Himes Boor designed the modelling methodology, analysed the data and obtained the analytical funding; Amanda Warlick developed and performed all model validation simulations; Rebecca Taylor provided statistical consulting and error-checking of the model structure; Sarah Converse provided feedback on model structure and validation. Gina Himes Boor led the writing of the manuscript, but all authors contributed critically to multiple drafts of the manuscript and gave final approval for publication.

CONFLICT OF INTEREST

None of the authors have any conflicts of interest related to this research.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/2041-210X.14032.

DATA AVAILABILITY STATEMENT

Model and simulation code and the beluga data are available via GitHub: https://github.com/gkhimesboor/HimesBoor_etal_2022_MEE, and Zenodo https://doi.org/10.5281/zenodo.7293607 (Himes Boor et al., 2022).

ORCID

Gina K. Himes Boor https://orcid.org/0000-0003-3924-5198
Tamara L. McGuire https://orcid.org/0000-0003-4536-007X
Amanda J. Warlick https://orcid.org/0000-0003-0926-1672
Rebecca L. Taylor https://orcid.org/0000-0001-8459-7614
Sarah J. Converse https://orcid.org/0000-0002-3719-5441

REFERENCES

Abadi, F., Botha, A., & Altwegg, R. (2013). Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: Does it matter? *PLoS ONE*, *8*, e62636.

Arso Civil, M., Cheney, B., Quick, N. J., Islas-Villanueva, V., Graves, J. A., Janik, V. M., Thompson, P. M., & Hammond, P. S. (2019). Variations in age- and sex-specific survival rates help explain population trend in a discrete marine mammal population. *Ecology and Evolution*, 9, 533–544.

Aubin, J. A., Michaud, R., & Vander Wal, E. (2021). Prospective evolutionary drivers of allocare in wild belugas. *Behaviour*, 158, 727–756.

Bors, E. K., Baker, C. S., Wade, P. R., O'Neill, K. B., Shelden, K. E. W., Thompson, M. J., Fei, Z., Jarman, S., & Horvath, S. (2021). An epigenetic clock to estimate the age of living beluga whales. *Evolutionary Applications*, 14, 1263–1273.

Brooks, S. P., & Roberts, G. O. (1998). Convergence assessment techniques for Markov chain Monte Carlo. *Statistics and Computing*, 8, 319–335.

Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation* (2nd ed.). Sinauer Associates.

Couet, P., Gally, F., Canonne, C., & Besnard, A. (2019). Joint estimation of survival and breeding probability in female dolphins and calves with uncertainty in state assignment. *Ecology and Evolution*, 9, 13043–13055.

Cubaynes, S., Aars, J., Yoccoz, N. G., Pradel, R., Wiig, Ø., Ims, R. A., & Gimenez, O. (2021). Modeling the demography of species providing extended parental care: A capture–recapture multievent model with a case study on polar bears (*Ursus maritimus*). *Ecology and Evolution*, 11, 3380–3392.

Etterson, M. A., Ellis-Felege, S. N., Evers, D., Gauthier, G., Grzybowski, J. A., Mattsson, B. J., Nagy, L. R., Olsen, B. J., Pease, C. M., van der Burg, M. P., & Potvien, A. (2011). Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments. *Ecological Modelling*, 222, 2178–2190.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.

Gimenez, O., Lebreton, J.-D., Gaillard, J.-M., Choquet, R., & Pradel, R. (2012). Estimating demographic parameters using hidden process dynamic models. *Theoretical Population Biology*, 82, 307–316.

Himes Boor, G. K., McGuire, T. L., Warlick, A. J., Taylor, R. L., Converse, S. J., McClung, J. R., & Stephens, A. D. (2022). gkhimesboor/HimesBoor_etal_2022_MEE: Unknown-Aged-Offspring Multievent Mark-Resight Model Code and Data (v1.0). *Zenodo*, https://doi.org/10.5281/zenodo.7293607

Kellner, K. (2019) *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.5.1. https://CRAN.R-project.org/package=jagsUI

Kendall, W. L., Hines, J. E., & Nichols, J. D. (2003). Adjusting multistate capture-recapture models for misclassification bias: Manatee breeding proportions. *Ecology*, 84, 1058–1066.

Kendall, W. L., Langtimm, C. A., Beck, C. A., & Runge, M. C. (2004). Capture-recapture analysis for estimating manatee reproductive rates. *Marine Mammal Science*, 20, 424–437.

Laidre, K. L., Shelden, K. E., Rugh, D. J., & Mahoney, B. A. (2000). Beluga, *Delphinapterus leucas*, distribution and survey effort in the Gulf of Alaska. *Marine Fisheries Review*, 62, 27–36.

Lunn, N. J., Servanty, S., Regehr, E. V., Converse, S. J., Richardson, E., & Stirling, I. (2016). Demography of an apex predator at the edge of its range: Impacts of changing sea ice on polar bears in Hudson Bay. *Ecological Applications*, 26, 1302–1320.

McGuire, T. L., Stephens, A. D., McClung, J. R., Garner, C., Burek-Huntington, K. A., Goertz, C. E. C., Shelden, K. E. W., O'Corry-Crowe, G., Himes Boor, G. K., & Wright, B. (2021). Anthropogenic scarring in long-term photo-identification records of Cook Inlet beluga whales, *Delphinapterus leucas*. *Marine Fisheries Review*, 82, 20–40.

McGuire, T. L., Stephens, A. D., McClung, J. R., Garner, C. D., Shelden, K. E. W., Himes Boor, G. K., & Wright, B. (2020). Reproductive natural history of endangered Cook Inlet beluga whales: Insights from a long-term photo-identification study. *Polar Biology*, 43, 1851–1871.

Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer Associates.

O'Corry-Crowe, G. M., Suydam, R. S., Rosenberg, A., Frost, K. J., & Dizon, A. E. (1997). Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology*, 6, 955–970.

Plummer, M. (2019) *Rjags: Bayesian graphical models using MCMC*. R package version 4-10. https://CRAN.R-project.org/package=rjags

Plummer, M. (2022). *JAGS version 4.3.1*. https://mcmc-jags.sourceforge.io/

Pradel, R. (2005). Multievent: An extension of multistate capture-recapture models to uncertain states. *Biometrics*, 61, 442–447.

R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Regehr, E. V., Hostetter, N. J., Wilson, R. R., Rode, K. D., Martin, M. S., & Converse, S. J. (2018). Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. *Scientific Reports*, 8, 16780.

Shelden, K. E. W., Burns, J. J., McGuire, T. L., Burek-Huntington, K. A., Vos, D. J., Goertz, C. E. C., O'Corry-Crowe, G., & Mahoney, B. A. (2020). Reproductive status of female beluga whales from the endangered Cook Inlet population. *Marine Mammal Science*, 36, 690–699.

Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology*, 51, 3–47.

Uomini, N., Fairlie, J., Gray, R. D., & Griesser, M. (2020). Extended parenting and the evolution of cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 375, 20190495.

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, 127, 79–94.

Verborgh, P., Gauffier, P., Esteban, R., & de Stephanis, R. (2021). Demographic parameters of a free-ranging deep-diving cetacean, the long-finned pilot whale. *Marine Mammal Science*, 37, 463–481.

Wade, P. R., Boyd, C., Shelden, K. E. W., & Sims, C. L. (2019). Group size estimates and revised abundance estimates and trend for the Cook Inlet beluga population. In K. E. W. Shelden & P. R. Wade (Eds.), *Aerial surveys, distribution, abundance, and trend of belugas (Delphinapterus leucas) in Cook Inlet, Alaska, June 2018. AFSC processed report 2019-09* (p. 93). Alaska Fisheries Science Center, NOAA, National Fisheries Marine Service.

Williams, B., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations*. Academic Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.