

A flexible Bayesian approach for estimating survival probabilities from age-at-harvest data

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Abstract

1. Understanding survival probabilities is critical for the sustainable harvest of wildlife and fisheries populations. Age- and stage class-specific survival probabilities are needed to inform a suite of population models used to estimate abundance and track population trends. However, current techniques for estimating survival probabilities using age-at-harvest methods require restrictive assumptions or incorporate potentially unknown parameters within the model.
2. Using a Bayesian approach, we developed a flexible age-at-harvest model that incorporates either age- or stage-structured populations, while accounting for uncertainty in age structure, population growth rates and relative selectivity. Survival probabilities can vary by age or stage class, as well as by environmental covariates, and both population growth rates and selectivity for each age or stage class can be specified as fixed and known or these parameters can be specified as informative priors, allowing for the incorporation of expert opinion. We evaluated our model with simulations and empirical data from harvested bobcats *Lynx rufus* and American paddlefish *Polyodon spathula*.
3. Models fit to simulated age-at-harvest data yielded unbiased estimates of survival probability when population growth rates and selectivity were centered on the data-generating parameter. We obtained unbiased estimates of survival probability even with biased prior estimates of selectivity and random departures from the assumed stage distribution, although the latter increased uncertainty in those estimates. We found biased estimates of survival probability when the prior distribution for population growth rate was not centered on the data-generating value. When fit to empirical harvest data, our proposed age-at-harvest model produced estimates of survival probability congruent to those reported in the literature within similar geographic regions.

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4. We demonstrate the utility of a novel age-at-harvest model that estimates survival probability and realistically account for uncertainty in model parameters, transcending the restrictive assumptions and auxiliary data requirements of other methods. Furthermore, we advise collecting information about population trends and age structure alongside age-at-harvest data to help reduce bias. Although our model cannot replace more rigorous methods, we believe our model will be transformative for wildlife and fisheries practitioners who collect age-at-harvest data to estimate age- or stage-specific survival probabilities to help inform management decisions.

KEY WORDS

age-specific survival, age-at-harvest, age-structured populations, Bayesian analysis, fisheries populations, sampling scheme, survival, wildlife populations

1 | INTRODUCTION

Estimating species-specific survival is an important aspect of wildlife and fisheries management and conservation, with diverse applications (e.g. Buckland et al., 2004; Rota et al., 2014; Skalski et al., 1998). Estimates of survival probability can be used to better understand animal populations and to aid in harvest management and conservation planning. For example, estimating survival probabilities is a critical component of population modelling and is necessary to perform a population viability analysis, a tool frequently used to aid in conservation decision-making for wildlife populations (Beissinger & McCullough, 2002). By incorporating survival estimates into population models (e.g. Crouse et al., 1987; Lehman et al., 2018), we can identify the relative significance of different ages or stages on overall population dynamics, identify the greatest threats to an at-risk population, and prioritize science-based conservation actions. Estimates of survival probability are also instrumental in integrated population models, where numerous independent data sources are used to jointly estimate demographic parameters that could not be estimated from any single dataset (Schaub & Kéry, 2021).

Given the importance of survival probability in wildlife and fisheries sciences, there is plentiful literature describing statistical methods for estimating this demographic parameter. Perhaps, the simplest approaches are constructing life tables (Caughley, 1977; Roseberry & Woolf, 1991) and calculating return rates. More advanced mark-recapture methods are based on live encounters (e.g. Cormack-Jolly-Seber models), dead recoveries (e.g. band recovery models) or both (e.g. joint capture-recapture models; Barker, 1997; Williams et al., 2002). Known-fate models, wherein an individual is marked with a tracking device and regularly re-located to determine its status (i.e. alive or dead), permit estimates of survival probability with classical methods such as Kaplan–Meier, proportional hazard or parametric survival models (Efron, 1988).

Although mark-recapture and known-fate methods for estimating survival probability are well established, they usually require costly study design, in terms of funding, time and effort (e.g. the

expenses associated with capturing, marking, and monitoring individuals over long periods of time). An alternative approach to estimating survival probability is to collect age-at-harvest data (frequently called catch-at-age data in fisheries science). For example, many wildlife management agencies in the United States record the ages of harvested white-tailed deer *Odocoileus virginianus* at hunter check stations, while many fisheries managers collect large samples of fish, which they sort by age. Given the high cost of mark-recapture or known-fate survival studies, data from annual harvest efforts and routine sampling often represent a substantial proportion of data for a focal species. Furthermore, even for well-studied species, age-at-harvest data are usually collected much more routinely than formally designed survival studies and can be used to regularly update knowledge regarding current demographic trends. Thus, age-at-harvest data can potentially inform managers about species of interest by allowing them to obtain periodic and rapid estimates of survival and mortality rates in the absence of more expensive sources of data (e.g. mark-recapture studies).

As with mark-recapture and known-fate methods, there is a wide scope of literature describing methods for estimating survival probability from age-at-harvest data. Foundational approaches to estimating survival probability from age-at-harvest data were described by Chapman and Robson (1960). Additionally, regressing the log count in each age class against age is a frequently used method to estimate survival probability. These methods assume constant survival probability among ages, no trends in recruitment and equal detectability among ages (Smith et al., 2012). However, assuming equal detectability among ages often requires discarding data when age classes are under-represented (Allen & Hightower, 2010; Smith et al., 2012). Many advancements address these assumptions to various extents. For example, Thorson and Prager (2011) relax the assumption of constant mortality and detectability; Schnute and Haigh (2007) relax the assumptions of constant detectability and allow recruitment anomalies; and Udevitz and Ballachey (1998) and Udevitz and Gogan (2012) allow variation in survival probability among ages and population growth

rates among years. While these methods represent important advancements, they tend to relax only one or two assumptions at a time (e.g. Udevitz and Ballachey (1998) do not allow unequal selectivity among ages) and/or require additional parameters to be included as fixed and known (e.g. Thorson and Prager (2011) require assumptions of parameters of a Lorenzen mortality-at-age model). These methods may, therefore, still require restrictive assumptions and may not fully account for uncertainty in parameters that are assumed fixed and known. Alternatively, many approaches incorporate auxiliary data when estimating survival probability from age-at-harvest data (Broms et al., 2010; Conn et al., 2008; Gove et al., 2002). Such approaches no longer require many of the restrictive assumptions of basic age-at-harvest models, and uncertainty in auxiliary data can be appropriately propagated through the construction of joint likelihoods that simultaneously account for multiple demographic processes. However, appropriate data are likely to be available for only the most well-studied species, and integrated population models often require similar effort as mark-recapture or known-fate methods for estimating survival probability.

In this paper, we aim to take a middle approach between age-at-harvest models with restrictive assumptions and costly integrated population models. We seek to develop a method for estimating survival probability from age-at-harvest data when auxiliary data are not available. However, we also aim to relax the restrictive assumptions required to do so and to simultaneously allow a full accounting of uncertainty in all model parameters. In our model, we account for the effects of both population growth rate and unequal selectivity among age or stage classes, while accommodating either age- or stage-structured populations. Specifically, by adopting a Bayesian approach, we allow flexible definitions of the likelihood and are able to account for uncertainty in age structure, population growth rate, and selectivity by assigning prior distributions to those parameters. We further allow survival probability to vary by age or stage class and as a function of environmental variables. Thus, this model allows for substantial flexibility, such that users can choose to adhere to standard assumptions by fixing those parameters in the model or choose to relax assumptions and assign prior distributions for parameters for which they have data. In this paper, we provide a general model overview, present the technical details of our statistical model, evaluate theoretical properties with a simulation study, and apply our proposed approach to two real-world case studies by estimating survival probabilities from bobcat *Lynx rufus* and American paddlefish *Polyodon spathula* harvest data.

2 | MATERIALS AND METHODS

2.1 | Model overview

The purpose of our proposed age-at-harvest model is to estimate age- or stage-specific survival probabilities of wildlife or fisheries populations using data from a subset of sampled animals. Specifically,

the model requires count data (i.e. number of individuals) organized by age or stage classes (i.e. groupings that consist of a range of ages that are assumed to have equivalent demographic rates). Our model can be applied to live animals if each sampled individual can accurately be assigned an age or stage class, but the majority of detailed age data typically comes from dead individuals that have been harvested, so henceforth, we concentrate on age-at-harvest data. We envision such data may arise from numerous sampling schemes that consist of wildlife species harvested by hunters and trappers or fish species harvested by anglers or sampled by fisheries managers. For example, biologists at hunter check stations for harvested deer may record the number of fawns (0.5 years old), yearlings (1.5 years old) and adults (2.5+ years old), yielding count data for three stage classes.

To use our model, the input age-at-harvest data should comprise counts of dead individuals segregated by age or stage class, which can be arranged in a simple table with columns indicating the age or stage classes and corresponding numbers of harvested individuals belonging to each age or stage class. If there is interest in allowing survival probability to vary as a function of covariates, the sampled individuals can also be grouped by sex, time period, geographical region or some other biologically relevant division. For example, biologists could segregate counts of harvested deer from hunter check stations by sex and county. In these cases, the data table would simply have additional columns indicating the category (e.g. 'Sex') and corresponding values within the category (e.g. 'Female' and 'Male').

Other inputs include population growth rate, relative selectivity, age or stage distribution, and age or stage class duration. A list and depiction of the model components, including inputs, parameters, and derived parameters, can be found in **Table 1** and **Figure 1**. For the purposes of our model, we define selectivity as the probability of individuals being harvested and included in the sample, assuming the statistical population from which we obtain the sample is all live individuals that are available in the biological population; thus, selectivity encompasses harvest effort, encounter or detection probability (for animals that are hunted), physical capture probability (for animals that are trapped or fished), sex or size harvest regulations, hunter/trapper/angler selection decisions and reporting probability. Relative selectivity for each age or stage class is then the probability of individuals in a particular age or stage class being harvested and included in the sample, relative to the probability of individuals in other age or stage classes being harvested and included in the sample. As real-world examples and consequences of harvest preferences, relative selectivity for fawns or yearlings would be lower than that of adult male deer because hunters will pass over a young deer with no or smaller antlers for an adult deer with larger antlers. Similarly, relative selectivity for juvenile brook trout *Salvelinus fontinalis* would be lower than that of older (and larger) adults because anglers would often rather release small fish to catch a bigger one later.

A strength of our proposed method is the diverse ways that population growth rates, selectivity and/or age structure can be

TABLE 1 List of key parameters of our proposed model to estimate survival probability from age-at-harvest data, including each parameter's corresponding state, technical definition, and potential data inputs.

Parameter	State	Definition	Inputs
Age-at-harvest data (y)	Fixed and known	Counts of harvested individuals segregated by age or stage class	Counts and ages of animals harvested by hunters/trappers/anglers
Population growth rate (λ)	Fixed and known, or assigned informative prior distributions	Rate of change in total population over a defined time period	Change in abundance or index data during a defined time period
Relative selectivity (α)	Fixed and known, or assigned informative prior distributions	Probability of individuals in a particular age or stage class being harvested and sampled, relative to individuals in other age or stage classes	Hunter effort, hunter/trapper/angler selection decisions, and reporting rates
Age/Stage distribution (C)	Fixed and known, assigned informative prior distributions or assumed stable age or stage distribution	Expected number of individuals in each age or stage class	Estimated probability an individual belongs to each age or stage class
Age/Stage class duration (d)	Fixed and known	Maximum duration for which an individual can remain in each age or stage class	Range of age or stage classes determined by biologists

incorporated into the model. Depending on the amount of information available, these parameters can be assumed fixed and known (e.g. if there are well-supported specific values from previous studies on the same focal population), allowed to vary within bounds assigned by the researcher (e.g. if there is an established range of values from previous studies of the same species) or assigned informative prior distributions (e.g. if there is a limited range of realistic values based on expert opinion or previous studies of similar species). Given no auxiliary information, one could make strong assumptions including constant population growth rate, equal selectivity among age or stage classes, and stable age distribution, although the value of output in such circumstances would depend on the validity of the assumptions.

In the end, wildlife and fisheries managers or biologists can use this age-at-harvest model to estimate survival probability overall (i.e. constant across all age or stage classes and groupings), by age or stage class or by combinations of age or stage and grouping (e.g. sex/time period/geographical region). Ultimately, results from our model are well suited to answering questions about spatiotemporal, abiotic/biotic and extrinsic/intrinsic factors influencing survival rates of wildlife and fisheries populations, as well as providing point estimates and credible intervals for survival probability that can be inputted into population models.

2.2 | Statistical model

The basic structure of our model is derived from Udevitz and Ballachey (1998), although we modify nearly every aspect of their model to relax assumptions and allow for greater generality. We assume the number of individuals within each age or stage class, denoted y_i , is a multinomial random variable:

$$y_i \sim \text{Multinomial}(\theta_i, H_i),$$

where H_i is the total number of individuals harvested within group i (which may represent sex, time period, geographical region, etc.) and θ_i is the probability a harvested individual within group i belongs to each age or stage class. We further model θ_i as a function of population growth rate, age- or stage-specific survival probabilities, selectivity, and age or stage distribution, which we describe in detail below.

We can derive an expression for θ_i by considering the age or stage structure of a population and the relative selectivity of individuals within each age or stage class. Allow A_i to represent any age- or stage-structured (i.e. Leslie or Lefkovich) matrix projection model with S age or stage classes (Caswell, 2001) and allow $s \in 1, 2, \dots, S$ to index each discrete age or stage class. Within projection matrix A_i , parameters p_{is} describe the probability an individual within stage class s survives 1 time step and are the principle estimand of our model. Note that unlike Udevitz and Ballachey (1998), our formulation does not require all individuals in age or stage class S to die. The number of animals in any age or stage class $s > 1$ at time t , denoted n_{ist} , can be calculated as:

$$n_{ist} = N_{i,t-1} A_{i[s]} C_i,$$

where $N_{i,t-1}$ is the total abundance at time $t - 1$, $A_{i[s]}$ represents row s of projection matrix A_i , and C_i is a conformable vector describing the age or stage distribution of individuals within group i , such that $\sum C_i = 1$. We define the finite rate of increase as $\lambda_{it} = \frac{N_{it}}{N_{i,t-1}}$ (Caswell, 2001). Without information on age- or stage-specific reproductive rates, we can obtain the number of animals in age or stage class 1 at time t as:

$$\begin{aligned} n_{1it} &= N_{it} - \sum_{s=2}^S N_{i,t-1} A_{i[s]} C_i \\ &= N_{i,t-1} \left(\lambda_{it} - \sum_{s=2}^S A_{i[s]} C_i \right). \end{aligned}$$

Alternatively, if there is information on reproductive rates, we can obtain the number of animals in age or stage class 1 at time t as:

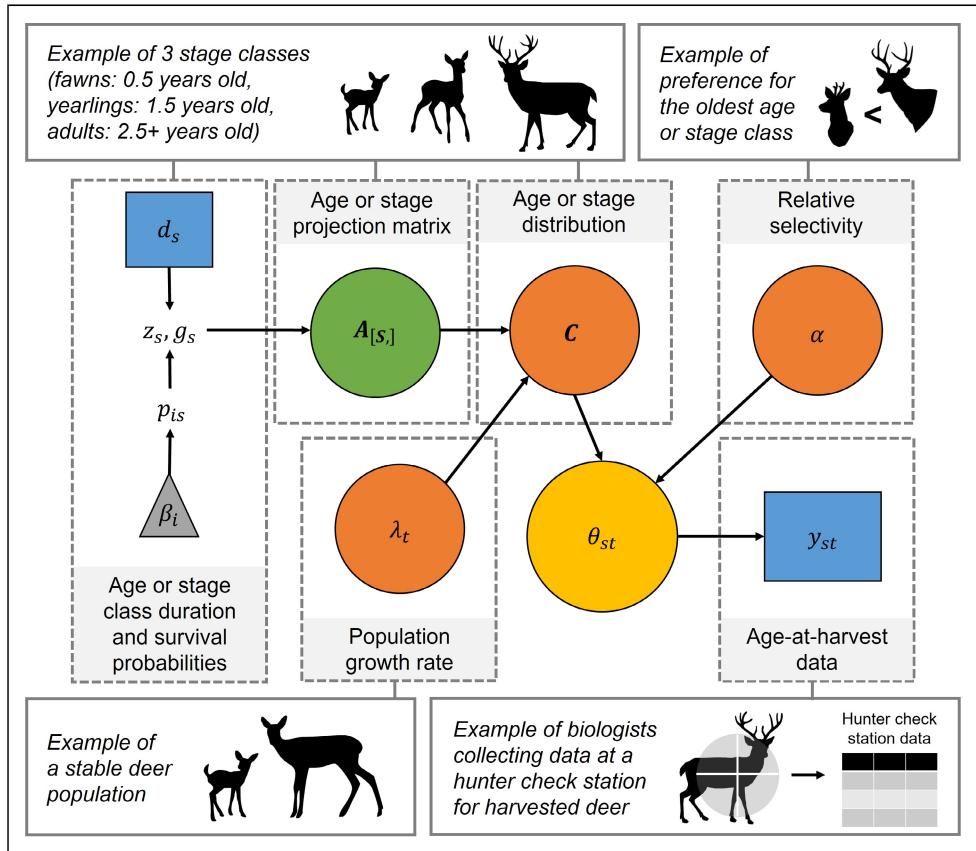


FIGURE 1 Conceptual diagram of the components of our proposed model to estimate survival probability from age-at-harvest data. The parameters of the model are colour-coded such that: blue boxes represent available data that has been collected or determined (d_s = fixed maximum duration for which an individual can remain in each age or stage class s ; y_{st} = the number of harvested individuals within each age or stage class s during time t); the grey triangle represents covariate data (β_i = predictor variable influencing age- or stage-specific survival probabilities); the green circle indicates a parameter derived from data (A_i = an age- or stage-structured matrix projection model with S age or stage classes); orange circles represent parameters that can be treated as either fixed and known from available data or estimated using a prior distribution (λ_t = population growth rate at time t ; C = the age or stage distribution; α = relative selectivity); and the yellow circle is a derived parameter and the process of interest (θ_{st} is the probability a harvested individual belongs to age or stage class s during time t). Boxes corresponding with certain parameters give corresponding real-world examples for white-tailed deer, a popular game species for which age-at-harvest data are often collected at hunter check stations.

$$n_{i1t} = N_{i,t-1} \mathbf{A}_{i[1]} \mathbf{C}_i,$$

where $\mathbf{A}_{i[1]}$ is calculated as a function of survival and reproduction, depending on whether \mathbf{A}_i is a pre- or post-birth pulse projection matrix (Mills, 2007).

Differential selectivity may cause the observed number of animals in each stage class to differ from age or stage distribution \mathbf{C}_i . Therefore, the expected number of animals observed in age or stage class s at time t is the product of age- or stage-specific selectivity α_{is} and age- or stage-specific abundance:

$$E(y_{ist}) = \alpha_{is} n_{ist},$$

and the probability a harvested individual belongs to age or stage class s at time t is

$$\theta_{ist} = \frac{E(y_{ist})}{\sum_{s=1}^S E(y_{ist})}. \quad (1)$$

Note that calculation of θ_{ist} does not depend on knowledge of $N_{i,t-1}$, since this term cancels from the numerator and denominator in Equation (1); α_{is} also cancels if it is assumed constant across age or stage classes. Additionally, when α_{is} varies among age or stage classes, only estimates of relative selectivity are necessary (i.e. we do not need to estimate absolute selectivity).

From this expression for θ_{ist} , there is considerable flexibility in specifying model components. If there is sufficient information, \mathbf{C}_i , λ_{it} and α_{is} can all be specified as fixed and known. Alternatively, prior distributions can be induced on these variables, with uncertainty quantified via the variance of the prior distribution.

Additional flexibility arises when defining the age or stage distribution \mathbf{C}_i , which may be assumed to follow the stable age or stage distribution if there is no other information available. Caswell (2001) provides convenient expressions for calculating stable age distributions (Caswell, 2001, p. 87) and stable stage distributions (Caswell, 2001, p. 186) as a function of age- or stage-specific survival

probabilities and λ_t . These expressions assume an individual can remain in each age or stage class s for a fixed maximum duration d_s (i.e. dwell time). Assuming an animal remains in age or stage class s for up to d_s time steps, and assuming an individual survives an individual time step with probability p_{is} , the probability an individual survives and remains within stage class s is calculated as:

$$z_{is} = \frac{1 - p_{is}^{d_s-1}}{1 - p_{is}^{d_s}} p_{is},$$

The probability of an individual graduating to the next age or stage class is calculated as:

$$g_{is} = \frac{p_{is}^{d_s} (1 - p_{is})}{1 - p_{is}^{d_s}}.$$

Note that if $d_s = 1$, the probability that an individual remains in stage class s is 0 and the probability an individual graduates to the next age or stage class is p_{is} . Using these definitions for z_{is} and g_{is} , we can obtain the stable stage distribution. First, we calculate a vector \mathbf{w}_i that is proportional to the stable age or stage distribution. We fix the first element of \mathbf{w}_i at 1:

$$w_{i1} = 1.$$

Then, for all $s > 1$:

$$w_{is} = \frac{g_{i,s-1}}{\lambda_{it} - z_{is}} w_{i,s-1}.$$

Finally, the stable age or stage distribution is obtained by scaling \mathbf{w}_i :

$$\mathbf{C}_i = \frac{\mathbf{w}_i}{\sum_{s=1}^S w_{is}},$$

where S is the total number of age or stage classes. Note that the expression for calculating the stable age or stage distribution above assumes specific dwell times within age or stage classes. However, there is substantial flexibility in specifying age or stage class transition probabilities (i.e. the probability an individual graduates to the next age or stage class). For instance, dwell times in size-structured models could be a function of survival probabilities and growth rates, or dwell times could be assumed to follow a specific distribution.

There is also considerable flexibility in modelling age- and stage-specific survival probabilities. Survival probability can be assumed constant or to vary by age or stage class. Additionally, age- or stage-specific survival probabilities can be modelled as a linear function of covariates associated with group i (e.g. sex, time period, geographical region).

Finally, if overdispersion is present, age- or stage-specific selectivity can be modelled as a Dirichlet random variable:

$$\boldsymbol{\theta}_i \sim \text{Dirichlet}(\boldsymbol{\alpha}_i \times \mathbf{n}_{it}), \quad (2)$$

where $\boldsymbol{\alpha}_i \times \mathbf{n}_{it}$ represents element-wise multiplication of the vectors of age- or stage-specific selectivity and (relative) abundance. Note that

this multinomial-Dirichlet model is the multivariate equivalent of a beta-binomial model.

2.3 | Simulation study

We used a simulation study to evaluate the theoretical properties of our age-at-harvest model. We were interested in (1) evaluating bias and precision in estimates of survival probability over realistic sample sizes when prior knowledge of relative selectivity and population growth rates were unbiased and when the simulated stage distribution matched the stage distribution assumed by the model; (2) evaluating how estimates of survival probability varied when prior knowledge of selectivity and population growth rates were increasingly biased and (3) evaluating how estimates of survival probability varied when the simulated stage distribution departed from the stage distribution assumed by the model.

To do this, we simulated a realization of age-at-harvest data with five stage classes. We assumed the probability of surviving to the next time step was constant ($p = 0.8$) across all stages. At the end of each time step, individuals graduated to the next stage class, except for individuals in the oldest stage class, which could survive and remain within the oldest stage class. We assumed a constant population growth rate of $\lambda = 1.01$ and that relative selectivity of individuals in the youngest stage class was half that of individuals in older stage classes. We, therefore, fixed $\alpha_1 = 0.5$, and fixed $\alpha_s = 1$ for all remaining stage classes >1 . For objectives 1 and 2, we simulated data assuming stage classes were distributed according to the stable stage distribution. For objective 3, we simulated age-at-harvest data assuming both random and systematic departures from the stable stage distribution. For scenarios assuming random departures from the stable stage distribution, we simulated a realized stage distribution \mathbf{C}_r as a Dirichlet random variable:

$$\mathbf{C}_r \sim \text{Dirichlet}(\mathbf{C} \times 100).$$

For scenarios assuming systematic departures from the stable stage distribution, we initialized a population with a uniform stage distribution and allowed that population to grow until it arrived at the stable stage distribution. A population with the vital rates described above ($p = 0.8$ and $\lambda = 1.01$, which implies constant per-capita fecundity of 0.21) will take approximately four time steps to transition from a uniform stage distribution to the stable stage distribution (Figure 2). We, therefore, simulated age-at-harvest data from populations with age distributions reflecting the four time steps required to transition from a uniform stage distribution to a stable stage distribution.

For each scenario described above, we evaluated five different sample size scenarios of $n = 50$, $n = 100$, $n = 250$, $n = 500$, and $n = 1000$. The smaller sample sizes may reflect species with lower harvest rates (e.g. bobcat harvest records), while the larger sample size scenarios may reflect abundant, well-sampled species (e.g. white-tailed deer reported to hunter check stations). We simulated

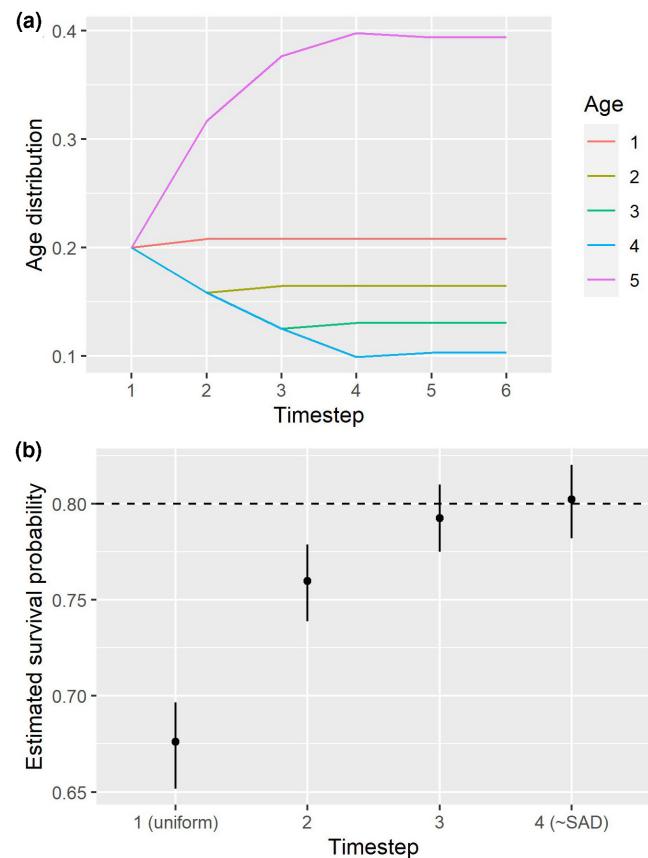


FIGURE 2 (a) Transient dynamics expressed as changes in age distribution as a population moves from a uniform stage distribution at time step 1 to (approximately) the stable stage distribution at time step 4. This panel assumes a five-stage population, where individuals spend 1 time step in stage classes 1–4, and remain in the final stage class until death. We assume a constant survival probability of 0.8 across all stage classes and a population growth rate of 1.01 (which implies a constant per capita fecundity of 0.21). (b) Estimated survival probability when simulated age-at-harvest data are drawn from a population with the stage distribution corresponding to the matching time step in panel (a). Estimates are derived from an age-at-harvest model with a sample size of 1000 aged individuals, assuming unbiased normal prior distributions for population growth and relative selectivity and assuming a stable stage distribution.

age-at-harvest data by assuming counts of individuals by stage class were a multinomial random variable:

$$\gamma_{\text{sim}} \sim \text{Multinomial}(\theta_{\text{sim}}, n),$$

where θ_{sim} is calculated as described above using the population structure and parameter values described in this section. We assume a stable stage distribution for all models fit to simulated data.

For all simulated scenarios, we quantified uncertainty in population growth rates and relative selectivity by inducing both a uniform and a normal prior distribution for λ and α_1 . To evaluate the influence of biased prior estimates of relative selectivity and population growth rates on estimates of survival probability, we varied the bounds of the prior distribution around λ and α_1 . We evaluated three different levels of prior bias for each parameter: (1) prior distributions centered on the truth (i.e. unbiased prior information); (2) prior distributions not centered on the truth but within bounds of the uniform prior distribution or within 95% of the probability density of the normal prior distribution and (3) outside the bounds of the uniform prior distribution or outside 95% of the probability density of the normal prior distribution. This led us to assume the prior distributions listed in Table 2. Note that the standard deviation of the normal prior distributions listed in Table 2 is such that 95% of the probability density falls within the limits of the lower and upper bounds of the uniform distribution for each particular scenario. Note also that values of $\alpha > 1$ correspond to greater selectivity of stage class 1 relative to other stage classes.

We assumed a uniform (0,1) prior distribution for survival probability over all 6 age distributions \times 5 sample sizes \times 2 prior distributions \times 3 levels of selectivity bias \times 3 levels of population growth bias = 540 different simulation scenarios. We simulated 1000 datasets for each scenario, recording the posterior mean survival probability from each scenario. We fit models in JAGS (Plummer, 2003) using the *jagsUI* package (Kellner, 2019) in program R (R Core Team, 2020). We used the *autojags* function within *jagsUI* to ensure all models achieved convergence (assuming convergence is achieved when $\hat{R} < 1.1$).

TABLE 2 Prior distributions for relative selectivity of stage class 1 (α_1) and population growth rate (λ) used in simulation scenarios. Centered, Uncentered, and Outside refer to the simulation scenario corresponding to prior distributions being centered on the data-generating value of the parameter; prior distributions not centered on data-generating values of the parameter, but the data-generating value falls within 95% of prior probability density; and the data-generating value of the parameter falling outside of 95% of prior probability density.

Simulation scenario			
Parameter	Centered	Uncentered	Outside
α_1	Uniform (0.25, 0.75) Normal ($\mu = 0.50$, $\sigma = 0.13$)	Uniform (0.45, 0.95) Normal ($\mu = 0.70$, $\sigma = 0.13$)	Uniform (0.65, 1.15) Normal ($\mu = 0.90$, $\sigma = 0.13$)
λ	Uniform (0.960, 1.060) Normal ($\mu = 1.010$, $\sigma = 0.026$)	Uniform (0.985, 1.085) Normal ($\mu = 1.036$, $\sigma = 0.026$)	Uniform (1.020, 1.120) Normal ($\mu = 1.070$, $\sigma = 0.026$)

2.4 | Bobcat survival study

To demonstrate the utility of our method, we used our age-at-harvest model to estimate bobcat survival probability in West Virginia, USA. To obtain updated estimates of bobcat vital rates, the West Virginia Division of Natural Resources collected carcasses of legally harvested bobcats during the 2014/2015 and 2015/2016 trapping years (Landry, 2017). Bobcats were sexed, and teeth were pulled from carcasses and aged by counting rings of cementum annuli (Crowe, 1972). Our data, therefore, consisted of counts of bobcat individuals by age, sex, and year collected (Table S1). No permits were needed to conduct this work.

We assumed a six stage-class model (Table S1). We assumed individuals remain within the first five stage classes for 1 year ($d_1, d_2, \dots, d_5 = 1$), while individuals in the oldest stage class (aged 5+) can survive and remain within that stage class. We assumed survival probability varied by stage class, but fixed survival probability in stage class 5 (age 4–5) equal to stage class 6 to ensure survival probability was identifiable (Conn et al., 2008). We additionally allowed survival probability to vary among sex and year. When survival probability varied by year, we also allowed λ to vary by year. To find a parsimonious model of bobcat survival probability, we evaluated eight models with various combinations of sex, year, and stage-specific survival probability (Table S2). We assumed logistic(0, 1) prior distributions for all survival regression coefficients.

It is common for trappers to release bobcat kittens, and surveys indicate that ~63% of kittens that are trapped are released alive (Landry, 2017). We, therefore, assume a normal($\mu = 0.37, \sigma = 0.026$) prior distribution for relative selectivity of kittens aged 0–1 year, which puts 95% of the prior probability density for relative selectivity between 0.32 and 0.42.

The population growth rates of bobcats within West Virginia are unknown. Based on trends in reported harvests between 2005 and 2016 (Landry, 2017), we assumed a normal($\mu = 1.01, \sigma = 0.026$) prior distribution on λ , which assumes a slightly growing population on average but puts 95% of prior density between 0.96 (a declining population) and 1.06 (an increasing population).

Finally, we assumed a stable stage distribution. Because kittens are likely to be released alive, empirical stage structure data are likely to be biased. Given the lack of other information regarding the bobcat stage structure, a stable stage distribution is the best available approximation. The adequacy of this assumption would likely be apparent following model checking.

We evaluated model fit using posterior predictive checks (Kéry, 2010). We calculated the G-statistic (defined as $G = 2 \sum_i O_i \log(O_i/E_i)$, with O_i representing observed counts and E_i representing expected counts; Udevitz & Ballachey, 1998) from observed counts (G_{obs}) and from simulated counts (G_{sim}), and calculated a Bayesian p -value as $\Pr(G_{\text{sim}} \geq G_{\text{obs}})$. We assume adequate fit if $(0.05 < p < 0.95)$ (Gelman et al., 2014).

We fit models in JAGS (Plummer, 2003) using the JAGSUI interface (Kellner, 2019) to program R (R Core Team, 2020). We ran models for 11,000 iterations, discarding the first 1000 iterations as burn-in and

keeping every iteration thereafter. This was enough to achieve adequate convergence ($\hat{R} < 1.1$ for all parameters; Gelman et al., 2014).

2.5 | Paddlefish survival study

We also used our age-at-harvest model to estimate American paddlefish survival probability in the Mississippi (rkm 587–322, rkm 313–0, rkm 1535–1353), Ohio (rkm 1160–1579), and Missouri (rkm 233–0) rivers, USA. Paddlefish were collected from these rivers using hobbled (6.1 m height, 60.1 m length, 127 mm bar mesh) floating monofilament gill nets (Scholten & Bettoli, 2007). No permits were needed to conduct this work.

The left dentary of each paddlefish was removed, cleaned and air-dried. Dentaries were sectioned (~0.635 mm thick) using a low-speed water saw. Multiple thin sections were obtained from each dentary to ensure reliable age estimates (Scarneccia et al., 1997). Dentary sections were aged under a dissecting scope (10–40 \times) using transmitted light. All sections were independently aged by two observers. If observers disagreed on age, the structure was viewed in concert to resolve discrepancies. In cases where a consensus could not be achieved, the sample was removed from the analysis. In total, <3% of all sampled paddlefish were discarded due to a lack of agreement on age. Our data, therefore, consisted of counts of paddlefish individuals by age and river reach (Table S3).

We assumed a five stage-class model (Table S3). We assumed survival probability varied by stage class, but fixed survival probability in stage class 5 (age 18+) equal to stage class 4 (age 17) to ensure survival probability was identifiable (Conn et al., 2008). We additionally allowed survival probability and λ to vary by river reach. To find a parsimonious model of paddlefish survival probability, we evaluated four models with various combinations of river reach and stage-specific survival probability (Table S4). We assumed logistic(0, 1) prior distributions for all survival regression coefficients.

Sampling paddlefish across all life stages (i.e. stage classes) is imperative for unbiased demographic representation (Ricker, 1975; Scholten & Bettoli, 2007). However, capturing young paddlefish has proven difficult since the onset of paddlefish population evaluations (Allen, 1911; Phelps et al., 2009; Purkett, 1961; Stockard, 1907) because the gear used to sample paddlefish has a low probability of capturing individuals in the youngest stage class. We, therefore, assume a logistic selectivity curve to allow relative selectivity to vary by age:

$$\alpha_a = \frac{1}{1 + \exp(-\beta(a - \gamma))},$$

where a is the age of the fish, β governs how selectivity varies with age, and γ is the age at which selectivity = 0.50. Note that we assumed the median age of each age category when fitting the logistic selectivity curve. We assumed the following prior distributions for logistic selectivity curve parameters: $\beta \sim \text{gamma}(1, 1)$; $\gamma \sim \text{uniform}(0, 18)$.

Population growth rates of paddlefish within the Mississippi River are unknown. Given the lack of information on population growth rates, we assume a normal ($\mu = 1.0$, $\sigma = 0.026$) prior distribution on λ , which assumes a stable population on average but puts 95% of prior density between 0.95 (a declining population) and 1.05 (an increasing population).

Finally, we assumed a stable stage distribution. Because paddlefish within the youngest stage class are poorly sampled, empirical stage structure data are likely to be biased. Given the lack of other information regarding paddlefish stage structure, a stable stage distribution is the best available approximation.

We evaluated model fit with posterior predictive checks (Kéry, 2010) using identical techniques as described in the bobcat survival analysis. Preliminary analyses indicated poor fit when assuming counts by stage class were a multinomial random variable. We, therefore, assumed the multinomial-Dirichlet model from Equation (2).

We fit models in JAGS (Plummer, 2003) using the JAGSUI interface (Kellner, 2019) to program R (R Core Team, 2020). We ran models for 11,000 iterations, discarding the first 1000 iterations as burn-in and keeping every iteration thereafter. This was enough to achieve adequate convergence ($\hat{R} < 1.1$ for all parameters; Gelman et al., 2014).

3 | RESULTS

3.1 | Simulation study

We found that estimates of survival probability were unbiased when stage classes were distributed according to the stable stage distribution and when prior distributions for λ and α_1 were centered on their data-generating value (Figure 3, Table S5). There appeared to be no advantage to assuming either a normal or uniform prior distribution for these parameters. In addition, there was a substantial gain in precision when moving from 50 to 1000 samples (Figure 4). The model appeared to be more sensitive to errors in estimates of population growth rate compared to relative selectivity. When the prior distribution for λ was centered on its data-generating parameter, the model could produce unbiased estimates of survival probability even with biased prior distributions for α_1 . Provided that 95% of the prior density for α_1 contained its data-generating value (i.e. the 'uncentered' scenario), estimates of survival probability were largely unbiased. When 95% of the prior density for α_1 did not contain its data-generating value (i.e. the 'outside' scenario), unbiased estimates of survival probability only occurred at the larger sample sizes and when assuming a normal prior distribution for both α_1 and λ . In contrast, estimates of survival probability were always biased if prior distributions of λ were not centered on its data-generating value.

We found that random departures from the stable stage distribution introduced additional uncertainty into estimates of survival probability but did not add additional bias (Table S6). In contrast,

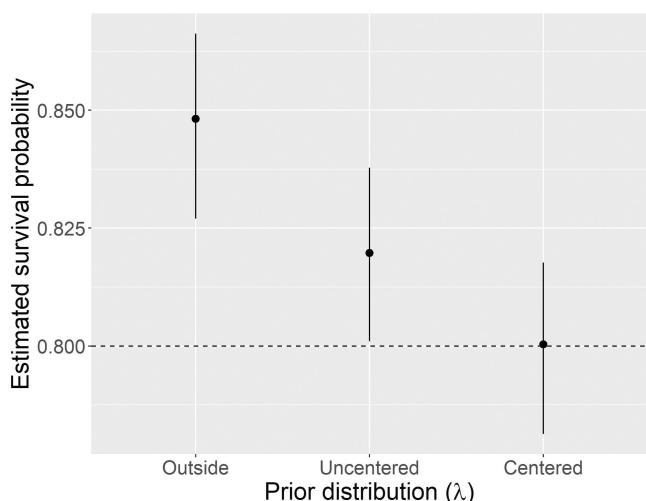


FIGURE 3 Mean estimates of survival probability (with 95% CI) obtained from simulated age-at-harvest data. Each scenario had 1000 replicates from which the mean estimates and 95% CI were determined from the posterior means. Centered, Uncentered, and Outside refer to whether the prior distribution for population growth rate (λ) was centered on its data-generating value (1.01), within 95% of prior density or outside 95% of prior density, respectively. Relative selectivity (α_1) was centered on its data-generating value (0.5) for each scenario. The horizontal dashed line is the data-generating value for survival probability. Prior distributions for each scenario are listed in Table 2.

systematic departures from the stable stage distribution led to biased estimates of survival probability, but this bias diminished as the population approached the stable stage distribution (Figure 2, Tables S7–S10).

3.2 | Bobcat survival

We fit our age-at-harvest model with data obtained from 524 harvested bobcats (Table S1). The top model demonstrated a strong effect of year on bobcat survival probability (Table S2). Although the 2nd ranked model included an effect of sex and year, 95% credible intervals of the slope coefficient for sex overlapped 0. Since only the top models exhibited reasonable fit, and the effect of sex was not strongly different from 0, we draw inference exclusively from the top model, which included an effect of year only. The mean survival probability over all years was 0.62 (95% CI = 0.58–0.65). Survival probability was greater (mean regression coefficient = 0.46, 95% CI = 0.16–0.77) in the 2014 / 2015 harvest season (0.67; 95% CI = 0.62–0.72) relative to the 2015 / 2016 harvest season (0.56; 95% CI = 0.51–0.62).

3.3 | Paddlefish survival

We fit our age-at-harvest model with data obtained from 424 American paddlefish (Table S3). All models exhibited reasonable fit,

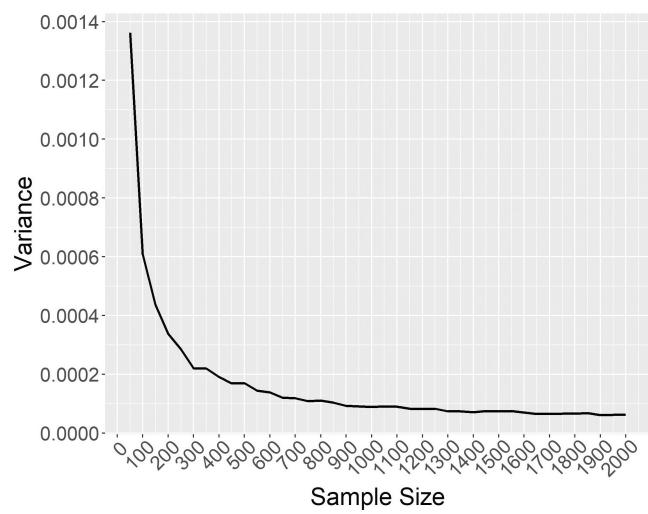


FIGURE 4 Estimates of variance for survival probability obtained from simulated age-at-harvest data as a function of sample size. Each sample size variance estimate was calculated using 1000 replicates assuming a normal distribution with relative selectivity (α_1) and population growth rate (λ) centered on their respective data-generating values, 0.5 and 1.01.

and all models were within 1 ΔDIC unit of each other (Table S4). The top model included an effect of both age and river reach, and 95% credible intervals for the age 17+ slope coefficient in this model did not overlap 0. While the direction and magnitude of estimated slope coefficients were consistent across the remaining models, all 95% credible intervals of slope coefficients in the remaining models overlapped 0. Therefore, while acknowledging substantial model selection uncertainty, we report results only from the top model and pertaining to age.

We found 0.95 (95% CI = 0.85–1) annual survival probability of 0 to 8-year-old fish; 0.97 (95% CI = 0.88–1) annual survival probability of 9- to 12-year-old fish; and 0.97 (95% CI = 0.83–1) annual survival probability of 13- to 16-year-old fish. Slope coefficients for the 9–12 and 13- to 16-year stage classes included credible intervals that overlapped 0, suggesting no strong difference in survival probability among the younger stage classes. However, we found 0.65 (95% CI = 0.23–0.92) annual survival probability of 17+-year-old fish, and 95% credible intervals of the slope coefficient did not overlap 0, suggesting lower survival probability among the oldest stage classes of fish. We found relative selectivity was lowest for the youngest age class but quickly approached 1 for older individuals (Figure 5).

4 | DISCUSSION

We demonstrate the utility of a novel age-at-harvest model that can estimate survival probability without many of the restrictive assumptions of established approaches. To our knowledge, this is the first such model that can simultaneously account for variation in relative selectivity, population growth or reproductive rates, age or stage structure, and survival probability among age/stage groups or

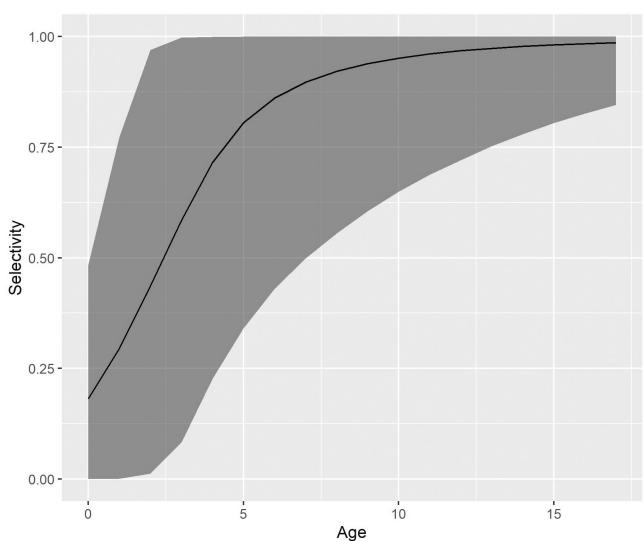


FIGURE 5 Relative selectivity of American paddlefish *Polyodon spathula* by age in the Mississippi, Ohio, and Missouri Rivers, USA.

as a function of covariates, all while fully accounting for uncertainty in each of these processes. Our simulations demonstrate that estimates of survival probability are unbiased when model assumptions are met, but are biased if poor estimates of population growth are supplied or if the stage distribution assumed by the model deviates strongly from the actual stage distribution. Therefore, while our proposed model may not require ancillary data, we caution that poor estimates of population growth rates or stage structure may yield inaccurate estimates of survival probability.

We expect that this model will be most useful when estimating survival probabilities for species that are primarily monitored through harvest records or for which counts of dead individuals by age can be obtained. Given the bias that is likely to occur if estimates of population growth rates or reproduction are poor, we do not advocate this model as a replacement for more rigorous mark-recapture or known-fate survival studies. Instead, we advocate the use of this model as a method for deriving estimates of survival probability when estimates from other rigorously designed studies are not available. In such circumstances, we envision that many of the required prior distributions can be provided as expert opinions. The Bayesian paradigm then allows for a full accounting of uncertainty when estimating survival probability from such prior information. While this may lead to imprecise estimates of survival probability, such an approach is probably a more accurate reflection of uncertainty relative to established age-at-harvest models.

Alternatively, our age-at-harvest likelihood could be substituted into integrated population models (Schaub & Kéry, 2021) for species with auxiliary data. For example, Gove et al. (2002) describe an integrated population model that uses an age-at-harvest likelihood in addition to likelihoods derived for auxiliary data. In such situations, estimates of population growth rates, reproduction, relative selectivity, etc. could be supplied as auxiliary data, potentially improving the accuracy and precision of survival probability and other model parameters.

Our simulations indicate that accurate estimates of population growth rates are critical for unbiased estimates of survival probability from age-at-harvest data. We note that if good estimates of population growth rates are unavailable, estimates of reproductive rates could instead be substituted into our model. We expect accurate estimates of survival probability will still depend on accurate estimates of reproduction, but such estimates may be more widely available than population growth rates for some species. For example, estimates of reproductive rates could be derived from the primary literature and used to construct prior distributions for this parameter.

Importantly, our estimates of bobcat survival probability are congruent with other estimates reported in the literature. For example, a recent known-fate analysis of bobcats within West Virginia suggested annual survival probabilities of approximately 0.74 between 2018 and 2020 (Edwards et al., 2021). Other regional studies suggest annual survival probabilities between 0.61 and 0.84 in West Virginia (Fox, 1980) and Massachusetts (Fuller et al., 1995), respectively. This suggests that despite uncertain prior knowledge on population growth rates, relative selectivity of juvenile bobcats, and assumption of stable stage distributions, our model appears to produce realistic and reasonable estimates of bobcat survival probability.

Our estimate of American paddlefish annual survival probability was also similar to other published accounts. For example, Glassic et al. (2020) report annual survival probability of 0.92 and 0.82 for females and males, respectively, in the Missouri River. Similarly, Boone and Timmons (1995) and Donabauer et al. (2009) both report annual survival probability of 0.91 in the absence of commercial or recreational harvest. We note that output from our American paddlefish model may not be much different than what could be obtained using established methods. However, it relaxes assumptions of established methods, incorporates uncertainty into model components that allow greater complexity, allows inference on other factors that may have influenced survival probability (even if we found no difference in survival probability along different stretches of the Mississippi River), and probably represents a more honest accounting of uncertainty relative to established methods.

Ultimately, we present a Bayesian model that advances our ability to estimate survival probability from age-at-harvest data. We demonstrated that it can produce reasonable estimates of survival probability, while relaxing many of the assumptions of more established techniques. Our approach is highly flexible, both in terms of model components (e.g. specification of age or stage structure, reproduction or population growth) and likelihood structure (e.g. straightforward implementation of multinomial-Dirichlet model for overdispersed data). We expect our proposed model will be useful to a wide array of practitioners seeking to understand demographic parameters of wildlife and fisheries populations from age-at-harvest data.

AUTHOR CONTRIBUTIONS

Christopher T. Rota conceived the ideas and developed the methodology; Stephanie Landry, Rich Rogers, Quinton Phelps, and James T. Anderson contributed data; Brett P. Skelly, Hannah L. Clipp, and

Christopher T. Rota performed simulations and statistical analysis; Brett P. Skelly, Hannah L. Clipp, and Christopher T. Rota wrote and revised the manuscript. All authors contributed to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14077>.

DATA AVAILABILITY STATEMENT

All data and R code used in simulations and the two real-world examples are available from the Zenodo data repository at <https://doi.org/10.5281/zenodo.7447900> (Skelly, 2022).

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SUPPORTING INFORMATION

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

Table S1: Counts by age, sex, and year of bobcat (*Lynx rufus*) carcasses obtained by trappers during 2014–2016 in West Virginia, USA.

Table S2: Model selection and Bayesian *p*-values for bobcat (*Lynx rufus*) survival models for West Virginia, USA, 2014–2016.

Table S3: Counts by age and river reach of American paddlefish (*Polyodon spathula*) obtained within the Mississippi River, USA.

Table S4: Model selection and Bayesian *p*-values for American paddlefish (*Polyodon spathula*) survival models for the Mississippi River, USA.

Table S5: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models when the data-generating population is at the stable stage distribution.

Table S6: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models when the data-generating age distribution is a Dirichlet random variable with expectation equal to the stable stage distribution.

Table S7: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models when the data-generating age distribution is uniform across all stage classes.

Table S8: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models during the second time step of transient dynamics.

Table S9: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models during the third time step of transient dynamics.

Table S10: Mean point estimate (standard deviation) of survival probability estimated from Bayesian age-at-harvest models during the fourth time step of transient dynamics, when the age distribution is approximately equal to the stable stage distribution.

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