




ARTICLE

A statistical population reconstruction model for wildlife populations: A case study with white-tailed deer and fisher

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Abstract

Harvested wildlife populations should ideally be monitored to inform harvest policies and decision-making to help achieve management objectives. When the age of harvested individuals can be obtained, these data (i.e., age-at-harvest data) can be used to estimate trends of abundances, demographic rates, and harvest probabilities by the statistical reconstruction of the living population. This approach was developed primarily within the frequentist framework and requires the inclusion of auxiliary data (e.g., radiotelemetry data). We developed a novel Bayesian hierarchical approach allowing the population reconstruction from the definition of the species' life cycle without auxiliary data. The hierarchical model assumes that individuals are harvested from an open population whose fluctuations result from demographic processes, and the definition of a superpopulation composed of pseudo-individuals from which the harvested population is drawn. We evaluated the ability of our model to estimate abundances, survival, recruitment, and harvest probabilities based on simulations guided by the demographic processes of a long-lived mammal population. We considered model performance across scenarios, including varying age and temporal structures, superpopulation size, and prior information. We showed how prior information selected based on life history characteristics affects the accuracy of estimated parameters. We found that the model estimates accurate demographic parameters and abundances when the age-at-harvest matrix comprises more than two age classes. Furthermore, an increase in demographic information (number of age groups and years) increased the precision of the estimated parameters. We apply our model to a population of harvested (2012–2021) white-tailed deer (*Odocoileus virginianus*) and a mammalian carnivore, the fisher (*Pekania pennanti*), from Rhode Island, USA. Our model estimated biologically realistic population size and demographic rates for both species. Our approach provides robustness to track the population abundance of harvested species through time and estimate fundamental demographic parameters. Such results can be used to monitor

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whether population objectives are being met and whether harvest policy changes are required. Furthermore, this information can be critical for evaluating the effect of harvest on population growth and projecting trajectories of age-structured populations under different harvest scenarios. Therefore, our framework can help to guide management decisions and species conservation.

KEYWORDS

age-at-harvest, Bayesian, demographic rates, fisher, harvest, life history, population size, superpopulation, white-tailed deer

INTRODUCTION

Robust inference to the population dynamics of harvested wildlife populations is needed to inform harvest management strategies (Nichols & Williams, 2006). Understanding the effects of harvest on the growth and viability of a population is essential to preserving a fluctuating population size that allows for sustainable harvest (Lande et al., 2003; May et al., 1978). Maintaining populations at a sustainable population size is necessary to enable their harvest and prevent overexploitation or the local extinction of the harvested species (Lande et al., 1995). Limiting the size of wildlife populations below their ecological carrying capacities can also be necessary for conserving ecosystems (Sinclair, 1997). Besides, environmental variations can influence a population's mortality and reproduction rates, leading to fluctuations in the population growth rate (May, 1973). Indeed, fluctuations in population size are driven by underlying interactions among factors, such as population density, weather, and the population structure (Lande et al., 2003). Also, these interactions can introduce heterogeneity in vital rates that can impact population dynamics (Coulson et al., 2001). Moreover, the associated effects of harvest and stochasticity in environmental conditions can also affect vital rates, which can reflect in the population structure and dynamics (Stenseth et al., 2022).

Wildlife management agencies manage the harvest of game species by making decisions to meet short- and long-term population objectives. It is critical to consider the species' ecology and have a thorough knowledge of its population dynamics when making decisions about the harvest of wild animal populations (Beddington & May, 1977; Bunnefeld & Keane, 2014; Lande et al., 1997). Ideally, a probabilistic monitoring strategy should relate population measurements to management objectives, and stakeholders' interest and engagement with the species should be clearly understood. Effective harvest management decisions require observational approaches that enable management processes to integrate an understanding of the population dynamics process and the effects of management actions over time (adaptive management)

(Gerber & Kendall, 2018; Williams, 2011). To this aim, managers must have affordable and logistically feasible monitoring options.

As part of population monitoring and management programs, age-at-harvest data of wild animal populations are often collected because it is commonly a priority of state management agencies and does not require intensive and extensive sampling (Skalski et al., 2005). Age-at-harvest data can be regarded as counts of the true age-structured population. These data can be summarized in an age-at-harvest matrix, where on the diagonals, one can find information about the cohort that has been harvested through the years (Appendix S1: Figure S1). These data can be viewed as finite realizations of stochastic demographic processes that contain information about the dynamics and size of the population. From age-at-harvest data, statistical reconstruction population models provide a way to estimate demographic parameters, such as survival and harvest probability, which are necessary to explain the variation in age-at-harvest data over time (Gove et al., 2002). Most applications of this approach use a frequentist likelihood function, which requires the integration of auxiliary data (e.g., radiotelemetry data, independent estimates of abundances and survival) to reconcile parameter redundancy and estimate unique demographic parameters (Clawson et al., 2017; Gove et al., 2002; Skalski et al., 2005). However, there may be situations where auxiliary data are lacking (Conn et al., 2008).

To overcome this issue, we develop a novel Bayesian model that provides flexibility in integrating information to resolve the identifiability of model parameters. The applicability of Bayesian methods in problems of natural resources management and conservation has been recognized previously (Ellison, 2004; Wade, 2000). We integrate species life history information by defining informative priors on demographic parameters to eliminate the need for auxiliary data (Lemoine et al., 2016). In addition, it is preferable to adapt previous data from previous research and literature rather than to borrow specific data from another population than the one that is

being studied (McCarthy & Master, 2005). Even informative priors can still be diffuse but are biologically realistic, which provides little information but as the benefit of reconciling redundant parameters that are otherwise not separately estimated (Catchpole & Morgan, 1997). Adding logical biological realm should be a model goal and not thought of as bad. Several ecological studies have shown that prior knowledge can increase estimator precision without compromising accuracy (Morris et al., 2015). Non-informative priors can promote poor statistical practices and leave the full potential of the Bayesian analysis framework, which is to explicitly incorporate prior research and expertise into new science, unrealized in ecological applications (Banner et al., 2020; Hobbs & Hooten, 2015; Rodhouse et al., 2019). Choosing default priors (i.e., uninformative priors) for ecological models can result in inefficient conservation and management decisions for species of interest or concern (Banner et al., 2020; Dorazio & Johnson, 2003). Therefore, in this study, we propose that uncertainty about vital rates can be taken into account by defining informative priors based on the life history of the studied species and reconciling redundant parameters that are otherwise not separately estimable without additional data that may not be available for the population being studied. To evaluate the performance of our novel model, we perform an extensive simulation study composed of different scenarios that vary in terms of superpopulation size, the amount of demographic information, and prior information.

From our model, we reconstruct the population of harvested white-tailed deer (*Odocoileus virginianus*) and fisher (*Pekania pennanti*) in Rhode Island, USA. The white-tailed deer is one of the most harvested big game species in the United States, leading to important financial resources for managing game and other nongame species (Lueck, 2000). The fisher have experienced significant range contraction since the late 1800s. Protective measures, translocation efforts, and reforestation of agricultural land have enabled the fisher to recolonize their range in eastern North America (LaPoint et al., 2015). Increasing deer populations can have environmental implications through the degradation of the vegetation and the damage of habitats of other species (Hanberry, 2021) as well as public general consequences such as road collisions (Farrell & Tappe, 2007) and transmission of diseases such as Lyme diseases to humans (Levi et al., 2012). Differently, fisher populations can decrease quickly if their habitat is degraded (Powell, 1993), which can disrupt the functioning of their ecosystem as mesopredators are essential drivers of ecosystem function (Roemer et al., 2009). Also, variations in life history traits are much larger across species than among individuals and can be represented by the slow-fast continuum of life

history strategies (Pianka, 1970; Stearns, 1992). Ungulates are “slow” mammals having few offspring and higher survival rates, while mesocarnivores are relatively “fast” mammals with short lifespans (Heppell et al., 2000). Therefore, we predict that the white-tailed deer’s juvenile and adult survival will be higher than those of the fisher. Both species are harvested and should be monitored to ensure that the population size remains stable and can continue to be harvested. The objectives of this study are (1) to develop a model and reconstruct a population without auxiliary information but instead by incorporating biologically reasonable information to reconcile parameters; (2) evaluate the model by different scenarios to understand its performance regarding accuracy and precision; and (3) apply the model to monitor the trends and demographic parameters of the deer and fisher.

MATERIALS AND METHODS

Definition of the statistical population reconstruction model

We define our model by considering an observed harvested animal as a captured individual from an open population (Seber, 1982). We link the demographic process to the annual abundance (N_t) in year t through survival and recruitment probabilities that change the state of N (Figure 1). As the size of the living population is unknown, we introduce a superpopulation of $M \gg N$ individuals where M is fixed a priori for all the years of the study period (Royle & Dorazio, 2008, 2012; Schwarz & Arnason, 1996). We added $M - n$ zero histories to the data set comprising n observed individuals (Royle & Dorazio, 2012). This is referred to as data augmentation and is widely applied in fitting hierarchical models (Royle & Dorazio, 2012). See Appendix S1 for a schematic description of the data augmentation procedure for age-at-harvest data. We assume that the population is harvested T years yielding n unique harvested individuals. We proceed to data augmentation from a cohort (see Appendix S1: Figures S1–S3). A cohort is represented by $y_{i,t,a} = y_{i,1,1}, \dots, y_{M,T,A}$ where $y_{i,t,a} = 1$ if individual i is harvested during harvesting year t and 0 otherwise. We decompose the life cycle of the population, where $z_s(i, t, a)$ is the latent individual i at year t in summer before winter survival and $z_h(i, t, a)$ represents the latent individual i at year t after winter survival. For $t = 0$ and age = a , we define z_s as an individual having the probability of being recruited before the summer from the superpopulation M with a recruitment rate γ at year t such that

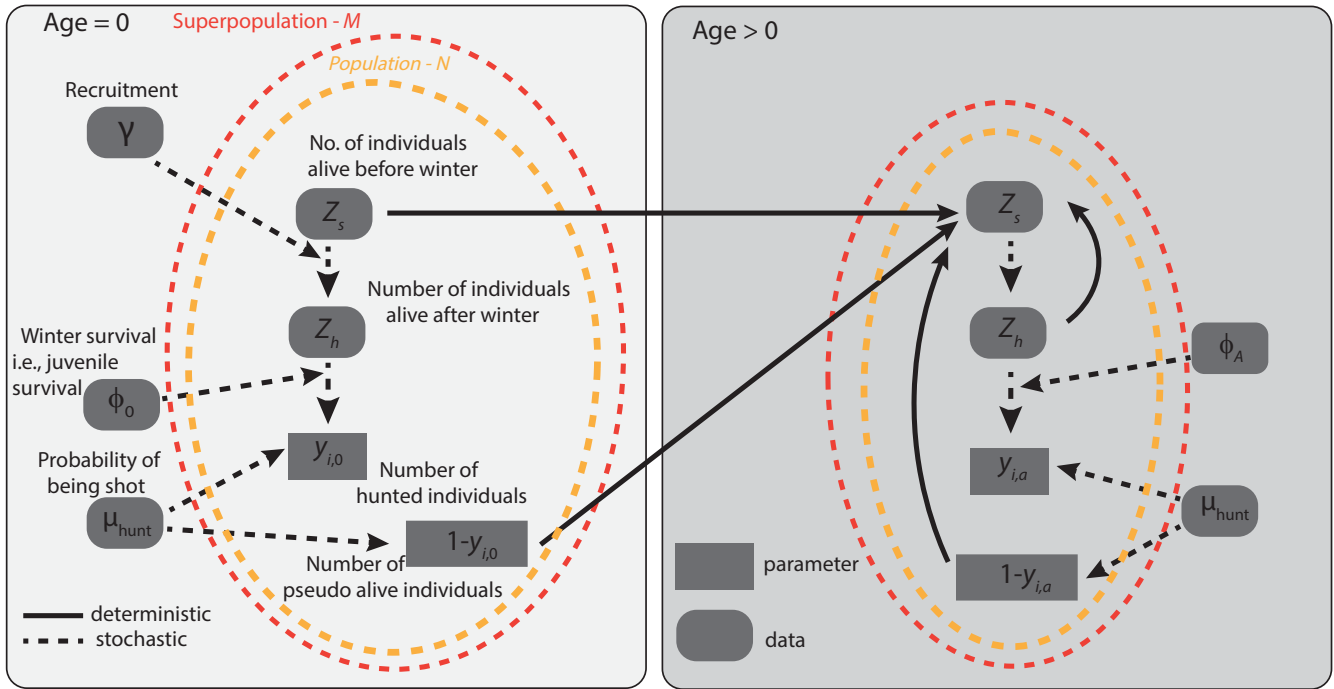


FIGURE 1 Schematic representation of the statistical reconstruction population model (Equations 1–6). Rounded rectangles represent model parameters and square rectangles represent data. Deterministic processes are represented by plain arrows, while stochastic processes are represented by dotted arrows. We decompose the life cycle of the population, where the latent number of individuals alive before winter z_s are recruited with recruitment rate γ at year 1 and age 0 (see Equation 1). The individuals that survive through winter z_h according to a juvenile survival probability ϕ_0 and then are harvested through the autumn with probability μ_{hunt} provide information on the population through the age-at-harvest data. As we do not have direct information on the living population, we augmented the observed age-at-harvest data by adding pseudo-individuals to the population N and created a superpopulation M from which the sampling is drawn. For subsequent years, the individuals continue the life cycle with an adult survival ϕ_A until they are harvested $y_{i,t,a}$ or do not survive $1 - y_{i,t,a}$.

$$z_s(i, 0, a) \sim \text{Bern}(\gamma_t). \quad (1)$$

$$z_h(i, t, a + 1) \sim \text{Bern}(\phi_A z_s(i, t, a + 1)), \quad (5)$$

Individuals z_h of age 0 can survive after winter with a probability of survival ϕ_0 (i.e., juvenile survival) as

$$z_h(i, 0, a) \sim \text{Bern}(\phi_0 z_s(i, 0, a)). \quad (2)$$

Observed harvested individuals at age 0 are defined as

$$y(i, 0, a) \sim \text{Bern}(\mu_{\text{hunt}}), \quad (3)$$

where the mean harvest probability $\mu_{\text{hunt}} = z_h(i, 1) \times h$ and h is the harvest probability which is constant over individuals. If the harvest effort f at year t is available, it can be included in Equation (3) such as $\mu_{\text{hunt}} = z_h(i, t, a) \times h \times f_t$. When $a > 0$, the individuals z_s alive after harvest and before winter survival are defined as

$$z_s(i, t, a + 1) = (1 - y(i, 1)) z_h(i, t, a + 1). \quad (4)$$

An individual alive in summer conditionally that they survived to winter is defined as

where ϕ_A is the adult survival probability for all ages greater than ($a > 0$), $z_h(i, t, a + 1)$ describes the status of an individual i and takes on values (0, 1), “0” signifies that the individual of the superpopulation M was not harvested, and “1” signifies that an individual of the superpopulation M has been harvested. Following the life history of many long-lived mammals, adult survival is expected to be less variable than juvenile survival (Fowler & Smith, 1981); therefore, we considered adult survival (i.e., $a > 0$). Then, an harvested individual is expressed as

$$y(i, t, a + 1) \sim \text{Bern}(\mu_{\text{hunt}}), \quad (6)$$

where μ_{hunt} is the mean hunting probability. As there is no information about juvenile survival in the upper diagonals of the age-at-harvest matrix, the individuals alive in summer, z_s , were defined as $z_s(i, t, 0) \sim \text{Bern}(z_s \times \phi_0 \times \phi_A^n)$ where n is the index number of the upper diagonal and ϕ_0 is the juvenile survival probability (Gove et al., 2002).

Under this model, we define $N_s(t, a)$ as the age-specific population alive in summer, such that $N_s(t, a) = \sum_{i=1}^{M-1} z_s(i, t, a)$. The age-specific population alive after winter survival is $N_h(t, a) = \sum_{i=1}^{M-1} z_h(i, t, a)$, and the estimated age-specific harvested population is $P_h(t, a) = \sum_{i=1}^{M-1} \mu_{\text{hunt}} z_h(i, t, a)$.

Simulation study

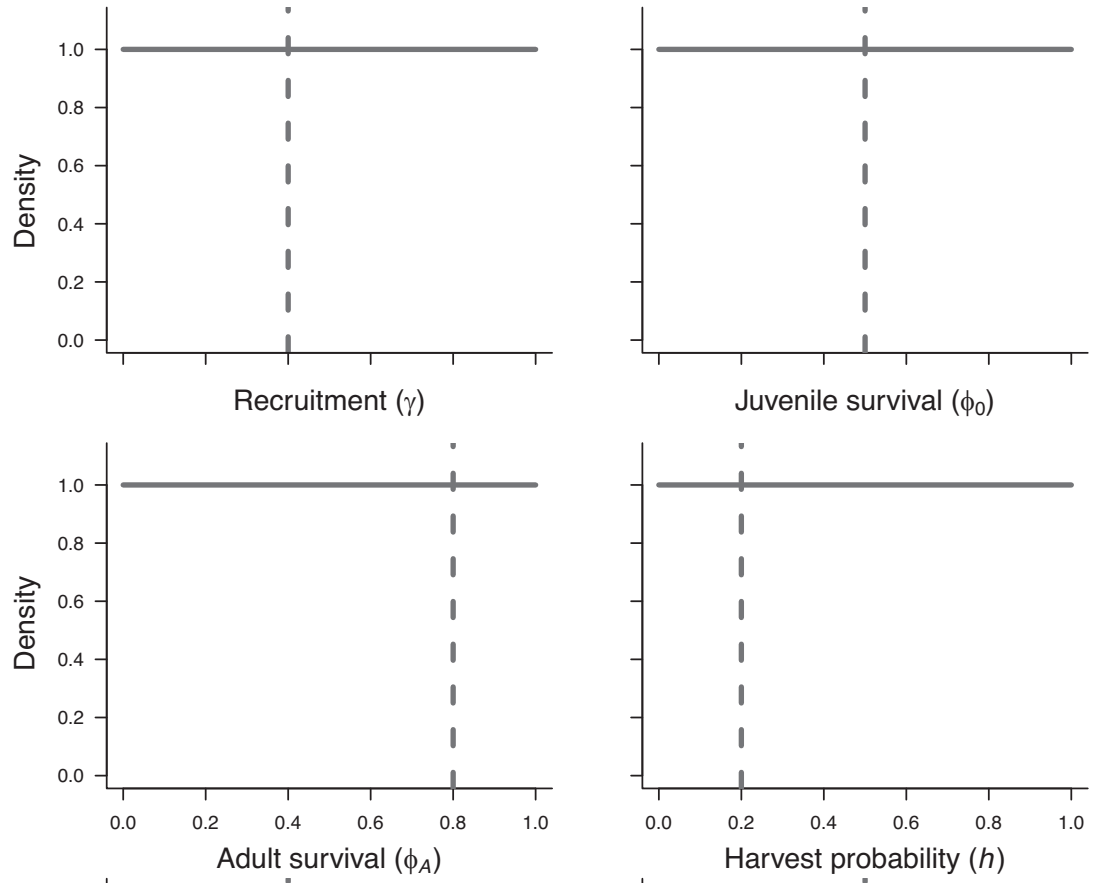
We simulated the age-at-harvest data under the statistical population reconstruction model (Equations 1–6), choosing demographic parameters according to the knowledge of the life history of long-lived mammals (Caughley, 1977). We defined six scenarios to evaluate the performance of our model (Table 1). We considered our model performance by varying age, temporal structure, superpopulation size, harvest probability, the incorporation of the upper diagonal or not, and prior information (Table 1 and Figure 2). We varied these different characteristics because it can affect the performance of our model. In scenario 1 and scenarios 4–6, we did not include the age-at-harvest matrix's upper diagonals because of computation time limitations. In addition, there is no information about the juvenile survival in the upper triangle of the age-at-harvest matrix. We expect that including prior information should improve the accuracy of the posterior mean estimates. We integrated the prior information from knowledge of the characteristics of the life history of a long-lived mammal by defining informative priors through the beta distribution (see Figure 2 and Appendix S2). For scenarios 1–5, the age-at-harvest matrix was composed as five age classes for five years. The scenarios were defined as follows: Scenario 1—We varied the superpopulation size with uninformative priors (Figure 2 and Appendix S2), and the superpopulation sizes were set at $M = 400$ and 700 . Scenario 2—We investigated the effect of integrating the upper diagonals on the parameter estimation, as the upper diagonals of the age-at-harvest matrix contain

only information about the adult survival. The priors were informative and the superpopulation size was set at $M = 400$. Scenario 3—We integrated the upper diagonals, the priors were informative (Figure 2 and Appendix S2), and the superpopulation size was set at $M = 400$. Scenario 4—We varied the harvest probability, and the priors were uninformative. We set the harvest probability at $h = 0.4$, $h = 0.3$, and $h = 0.1$, and the superpopulation size was set at $M = 400$. Scenario 5—It is the same as scenario 4, but the priors were informative (Figure 2 and Appendix S2). Scenario 6—We varied the number of age classes and years of the age-at-harvest matrix with informative priors (Figure 2 and Appendix S2). We varied the number of age classes to be two, four, and eight and the number of years to be five and ten. The superpopulation size was set at $M = 400$. For all scenarios (see Table 1), the recruitment γ was defined at 0.45, the juvenile survival ϕ_0 at 0.5, and the adult survival ϕ_A at 0.8. For scenarios 1, 2, 3, 5, and 6, the harvest probability h was fixed at 0.2. The prior central tendency was on the true parameter. Over the six scenarios, we defined 13 simulation cases, which were simulated one hundred times each. For each simulated case, we fitted the Bayesian population statistical reconstruction model (Equations 1–6). We estimated the posterior medians to evaluate accuracy (difference from truth) and precision (variation around the median). We used Markov chain Monte Carlo (MCMC) to estimate parameters via the software JAGS (Plummer, 2003) in R (R Core Team, 2021) via the R packages rjags (Plummer, 2022) and R2jags (Su & Yajima, 2021). We checked for convergence using the Gelman–Rubin statistics, R (Gelman et al., 2004), where the model was assumed to have converged when $\hat{R} \leq 1.1$. As running an extensive number of simulation scenarios can take a relative long time, we run the simulation on a high computing server, Linux CentOS7, with a Dell PowerEdge R730xd Server and Dual Xeon E5-2683 v4 processors, with 32 cores total (64 threads total) and 64 GB RAM. The R code for simulating an age-at-harvest matrix and fitting the model is

TABLE 1 Characteristics of each simulated scenario (see *Simulation study*).

	Uninformative priors	Informative priors	Superpopulation size	Harvest probability	Composition age-at-harvest matrix	Upper diagonal
Scenario 1	×		×			
Scenario 2	×	×				×
Scenario 3		×				×
Scenario 4	×			×		
Scenario 5		×		×		
Scenario 6		×			×	

Uninformative priors



Informative priors

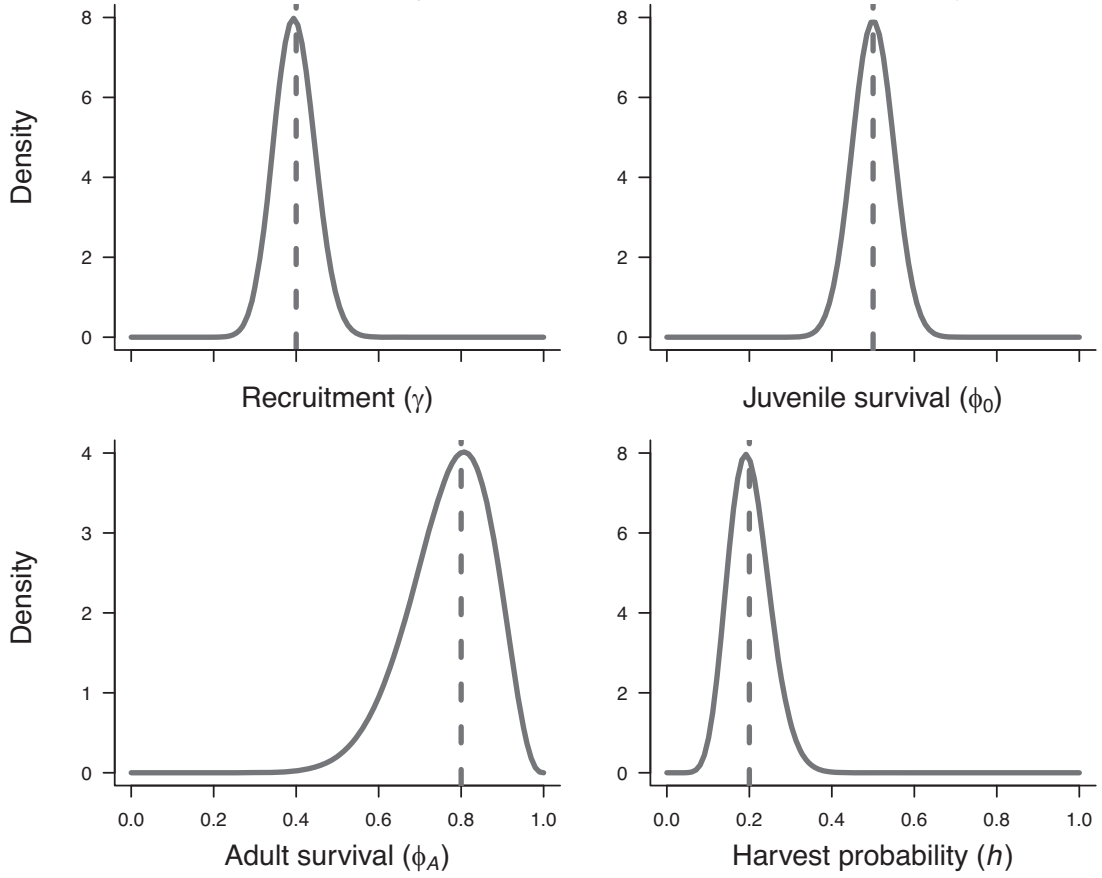


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accessible at <https://doi.org/10.6084/m9.figshare.22894874.v2> (Bellier et al., 2024).

White-tailed deer and fisher as case studies

White-tailed deer (hereafter, “deer”) are a common species in Rhode Island (3147 km²), as well as throughout the Northeastern United States (Appendix S3: Figure S1). Their characteristic habitat are a mixed successional type of forest (McShea, 2012). They can also be found in suburban areas with mixed forest, shrubs, and lawns. Deer in Rhode Island are hunted from mid-September to the end of February. The data collected at deer check stations during the hunting season included age, sex, antler points, weight, antler beam measurements, and disease surveillance (see Appendix S3 for more details on the data collection). In total, we had information on individuals harvested from 2012 to 2021 (Appendix S3: Figure S2). The overall number of deer harvested was 21,704 (11,427 males, 10,676 females) from 2012 to 2022 (Appendix S3: Figure S2). Three age classes were defined as age class 0.5, age class 1.5, and age class 2.5+ (Appendix S3: Figures S3 and S4). We estimated harvest effort as the total annual harvest for all age classes divided by the average annual harvest over the period analyzed (ten years; Appendix S3: Figure S5) (Skalski et al., 2007). We carried out the statistical population reconstruction analyses separately for the males and the females, as natural survival and harvest probability are expected to differ for males and females (Van Deelen et al., 1997). The definition of the priors of the vital rates and harvest probability was based on the literature and expert knowledge (Van Deelen et al., 1997; Whitlaw et al., 1998), as specific survival rates data were absent in Rhode Island (Appendix S2: Figure S3). The juvenile survival, that is, fawn survival has been estimated at 14%–87% across eastern North America (Dion et al., 2020). Adult survival varied widely in the literature. In Michigan’s upper peninsula, survival rates were estimated at 0.81 (SE, 0.09) for adult females, 1.0 (SE, 0.05) for adult males and yearling females, and 0.84 (SE, 0.07) for yearling males (Van Deelen et al., 1997). In Oklahoma, adult male survival was estimated at 0.86 (SE, 0.07) (Ditchkoff et al., 2001) and in New Brunswick, adults were estimated at 0.66 for males and 0.89 for females (Whitlaw et al., 1998). Therefore, we defined the priors by

integrating life history of deer. Male harvest probability were estimated to range between 0.1 and 0.5, and for female, it varies from 0.1 to 0.3 (Ditchkoff et al., 2001; Van Deelen et al., 1997; Whitlaw et al., 1998). We specified beta distributions for each vital rate and harvest probability (Figure 3 and Appendix S2).

Fisher (*P. pennanti*) are carnivorous mammals of the Mustelidae family, which were extirpated from Rhode Island in the 18th and 19th centuries when forests were being cleared for farmland. Fisher have made a return in recent decades. Populations that persisted in Maine and New Hampshire have been source populations for fisher dispersal into Rhode Island (Buskirk et al., 2012). Fisher can be found in various woodland habitats and tend to avoid large areas without high overhead canopy closure, like agricultural areas (Powell, 1993). Age-at-harvest data of fisher were provided by the Rhode Island Department of Environmental Management, Division of Fish and Wildlife. Details about the data collection can be found in the Appendix S3. The total number of individuals harvested was 503 from 2013 to 2021 (Appendix S3: Figure S6). We determined nine age classes of harvested fisher from 2013 to 2021 (Appendix S3: Figure S7). The harvest effort was estimated in the same way as previously mentioned for white-tailed deer (Appendix S3: Figure S8). The definition of the priors of the vital rates and harvest probability was based on results from empirical studies on life history of fisher (Appendix S3: Figure S4). From estimated survival rates for established fisher populations in North America (Buskirk et al., 2012; Lewis et al., 2012), we defined the mean and levels of uncertainties of the priors (Figure 3 and Appendix S2).

RESULTS

Simulation study

Scenario 1—With uninformative priors, we found that increasing the superpopulation size M from 400 to 700 did not affect the estimation of the parameters (Figure 4, box plots) as the distances between the true value and the medians of the box plots remained the same. The adult abundances, \hat{N}_h , were precisely estimated for both sizes of superpopulation (i.e., $M=400$ and 700) (Appendix S4: Figure S3). Scenarios 2 and 3—Including the upper diagonals did not affect the estimation of the

FIGURE 2 Uninformative priors of the demographic rates represented by uniform distributions: recruitment (γ), juvenile survival (ϕ_0), adult survival (ϕ_A), harvest probability (h) and prior distributions for the demographic rates that integrates life history of a long-lived mammal for the simulation study: recruitment (γ), juvenile survival (ϕ_0), adult survival (ϕ_A), and harvest probability (h). The dotted line represents the true simulated value. See Appendix S2 for the distributions parameters.

Informative priors

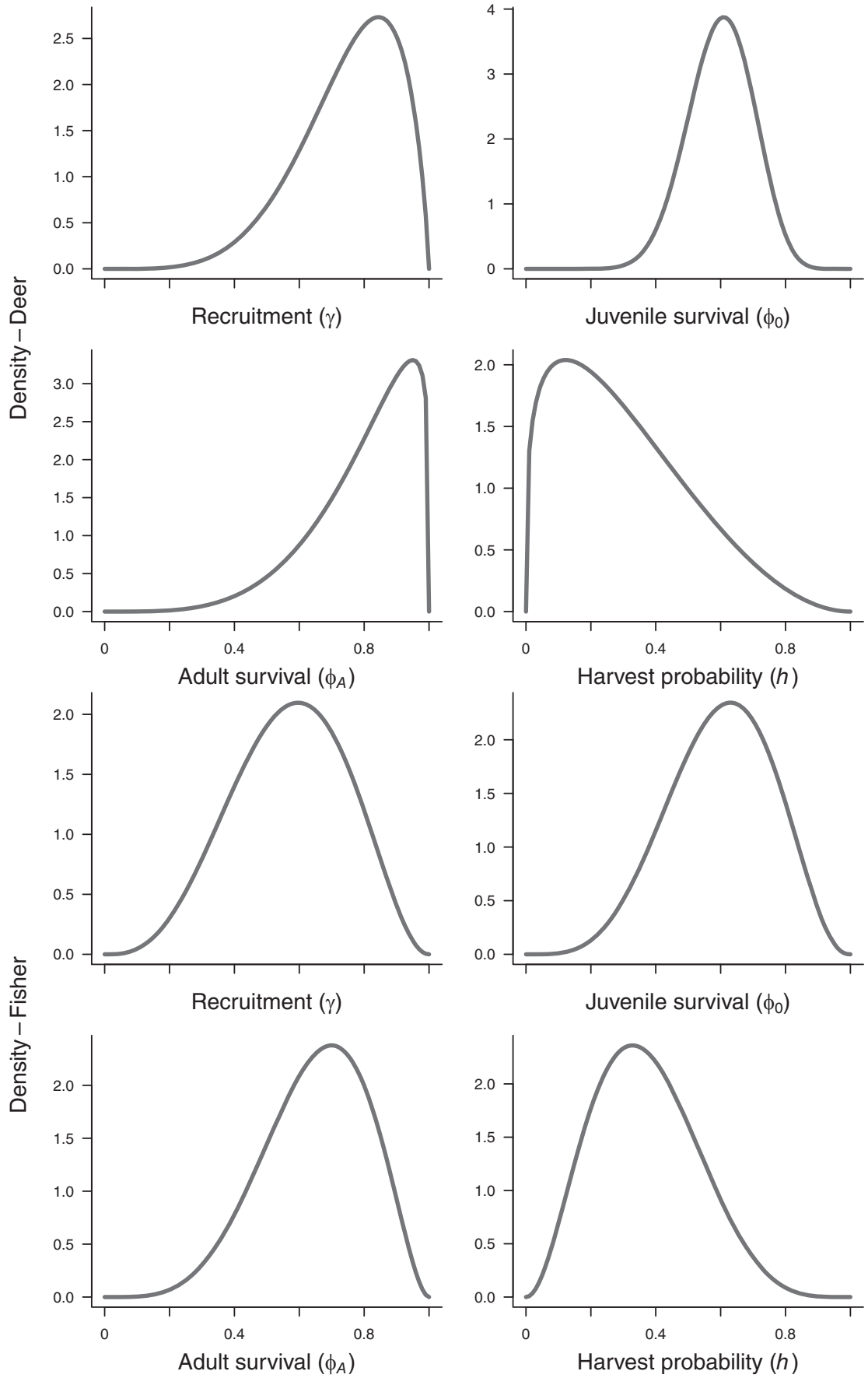


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demographic parameters whatever the information included in the priors (Appendix S4: Figure S4, box plots). Scenario 4—With a superpopulation of $M = 400$, recruitment and juvenile survival estimates were increasingly overestimated when the harvest probability increased from 0.1 to 0.4 using uninformative priors. Differently, the harvest probability, \hat{h} , was overestimated when $h = 0.1$, accurately estimated when $h = 0.3$, and slightly overestimated when $h = 0.4$ (Appendix S4: Figure S5, box plots). Scenario 5—When using informative priors, the variability of the estimates was lower than when the priors were non-informative (Appendix S4: Figures S5 and S6, box plots). The recruitment and juvenile survival parameters were also increasingly overestimated, and the adult survival was underestimated when $h = 0.4$ (Appendix S4: Figure S6, box plots). The harvest probability was slightly overestimated when $h = 0.1$; the precision and accuracy were improved when $h = 0.3$; when $h = 0.4$, the harvest probability was underestimated (Appendix S4: Figure S6, box plots). The precision of the abundance estimates was increased when the harvest probability increased (Appendix S4: Figures S7 and S8). Scenario 6—When using informative priors along with an age-at-harvest matrix composed of two age classes and five years, the recruitment, juvenile survival, and harvest probability were overestimated (Figure 5), while adult survival was underestimated. Increasing the demographic information (i.e., age from two to eight, years from two to ten) increased the recruitment and juvenile survival accuracy. We obtained an accurate estimation of recruitment and juvenile and adult survival when the age-at-harvest matrix comprised eight age classes and ten years (Figure 5). Increasing the number of years improved the accuracy of the harvest probability. The age class 0 abundance estimates were slightly overestimated, whatever the number of age classes and years (Figure 6). When there were more than two age classes, the abundance estimates for ages higher than zero were accurately estimated (Figure 6).

Statistical reconstruction of white-tailed deer and fisher populations

The number of harvested male deer decreased from 2012 and 2016 but increased from 2016 to 2021 (Appendix S3: Figure S2). In 2012, 1203 males were harvested, and this

decreased to 936 in 2016. A peak was observed in the number of harvested female deer in 2014, where 1332 females were harvested. After 2014, the number of harvested female deer decreased to 935 in 2018 and stayed stable (Appendix S3: Figure S2). The vital rate estimates of male deer were relatively high, while the juvenile survival was lower than the adult survival, and the harvest probability was also low (Appendix S5: Table S1 and Figure S1). The estimated male deer abundance decreased until 2014, after which the abundance slightly increased again and fluctuated around 10,320 individuals until 2021 (Figure 7a). The number of individuals for age class 0.5 stayed constant over the years. In age class 1.5, abundance decreased from 2012 to 2013, then increased slowly until peaking in 2019 and leveling back out until 2021 (Appendix S5: Figure S2). For the age class 2.5+, the estimated abundance decreased from 2012 to 2014, then increased until 2018 and fluctuated around 3,215 individuals until 2021 (Appendix S5: Figure S2). The estimated number of harvested males decreased until 2018 and increased until 2021 (Appendix S5: Figure S3). The observed and estimated number of harvested males had the same trend. The estimated vital rates of female deer were relatively similar to the males (Appendix S5: Table S1 and Figure S4). The harvest probability was slightly lower for females than for males (Appendix S5: Table S1). The estimated abundance of female deer slightly decreased over time (Figure 7b). The estimated abundance of age class 0.5 and 1.5 was almost constant over the years, and the abundance of age class 2.5+ fluctuated around 3578 deer (Appendix S5: Figure S5). The estimated number of harvested females decreased each year until an increase during 2021 (Appendix S5: Figure S6). As for the males, the observed and estimated number of harvested females had the same trend.

The number of harvested fisher decreased over the study period (2013–2021). In 2014, about 90 individuals were harvested, which declined to 18 by 2021 (Appendix S3: Figure S6). There were nine age classes of harvested individuals (Appendix S3: Figure S7). The most abundant age classes were age class 0 and age class 1. The number of harvested individuals in these classes and in the oldest age classes decreased over time. In the last three years of the study period, no individuals were in the age classes above 4 years of age (Appendix S3: Figure S7). The estimated juvenile survival ϕ_0 was higher than the estimated adult survival ϕ_A

FIGURE 3 Prior distributions for the white-tailed deer population which integrated life history characteristics of the species: recruitment (γ), juvenile survival (ϕ_0), adult survival (ϕ_A), and harvest probability (h) and prior distributions for the demographic rates for the fisher population: recruitment (γ), juvenile survival (ϕ_0), adult survival (ϕ_A), harvest probability (h). See Appendix S2 for the distributions parameters.

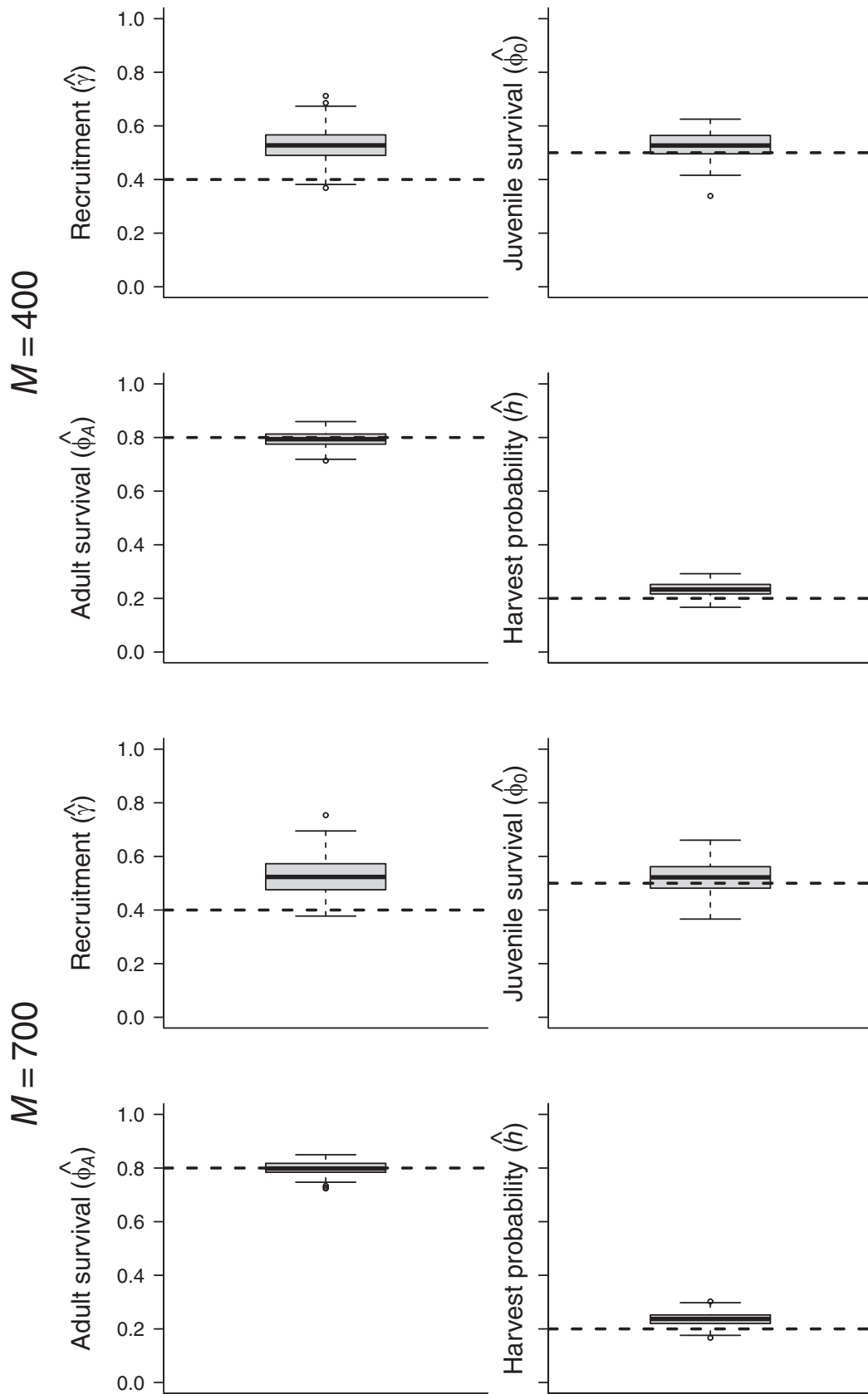


FIGURE 4 Box plots of one hundred estimated means of recruitment $\hat{\gamma}$, juvenile survival $\hat{\phi}_0$, adult survival $\hat{\phi}_A$, and harvest probability \hat{h} when the priors were uninformative with an age-at-harvest matrix with five age classes and over five years, and a superpopulation of $M = 400$ and 700 . The plain black line indicates the median of the estimated mean values across one hundred simulations. The box represents the lower quartile (0.25) and the upper quartile (0.75). The dashed line is the true value of the simulated parameters.

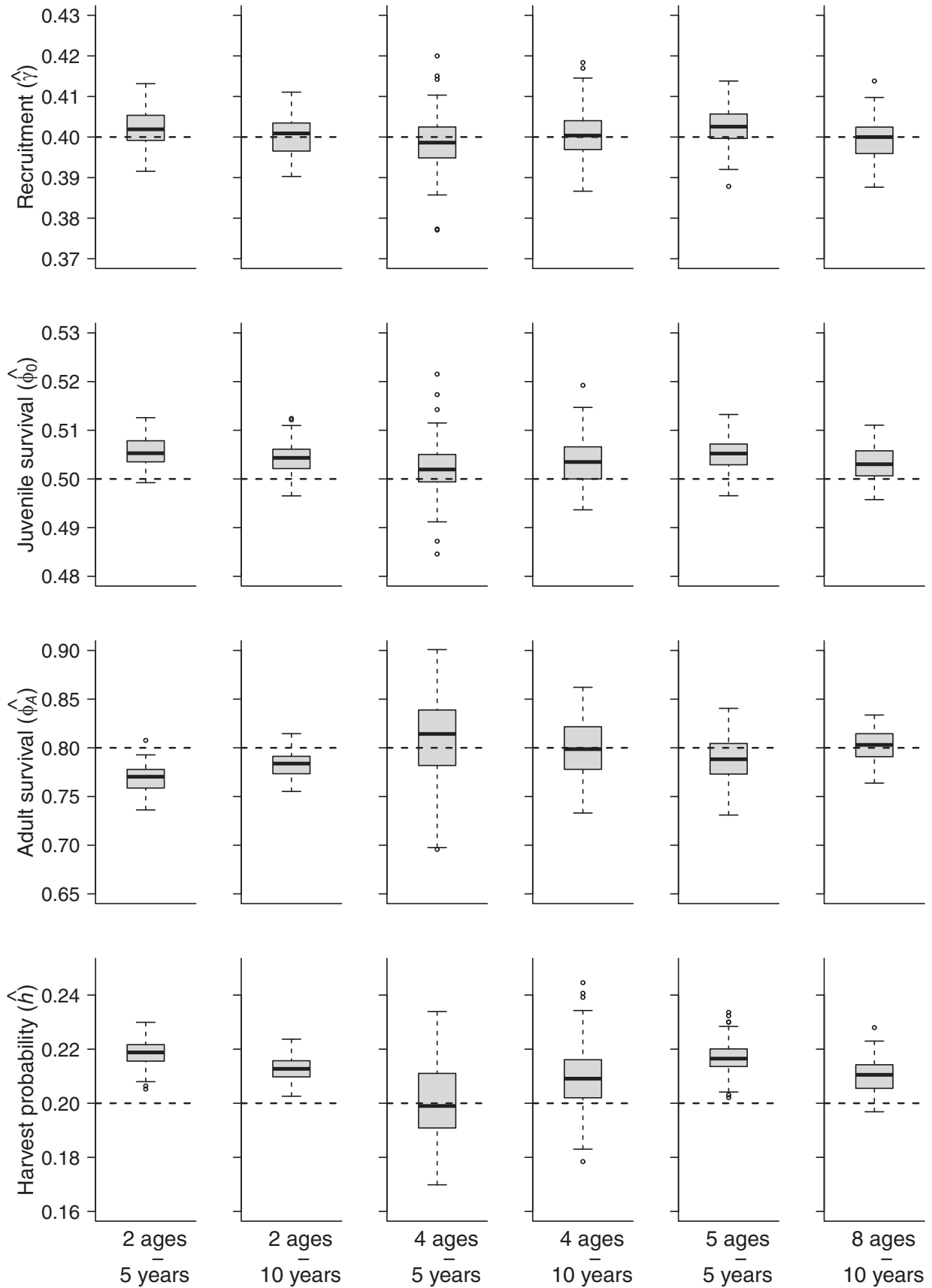


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(Appendix S5: Table S1 and Figure S7). The estimated number of individuals decreased in the first seven years (Figure 7c). After 2019, the estimated abundance slightly increased. The estimated number of individuals in age class 0 decreased from 2013 to 2017 (Appendix S5: Figure S8). For the age class 1, the estimated abundance slightly reduced until 2017. The abundance remained constant after 2017. In age class 2, a peak was observed in 2014, then abundance decreased and fluctuated around 20 individuals. In age class 3, the estimated abundance slightly decreased over the study period. The estimated number of harvested individuals peaked in 2014, then declined the rest of the study period (Appendix S5: Figure S9). The observed and estimated number of harvested individuals had the same decreasing trend (Appendix S5: Figure S9).

DISCUSSION

In this study, we propose a novel Bayesian model to statistically reconstruct wildlife populations from age-at-harvest data. From an extensive simulation study, we demonstrated that our model provides a robust estimation of the vital rates and abundances estimates. The age-at-harvest matrix with the most age classes and years (i.e., eight age classes and ten years) provided the most accurate estimates of demographic rates, while the harvest probabilities were slightly overestimated. We found that increasing the demographic information by increasing the number of age classes and the number of years of the study period increased the accuracy of the parameter estimates. We showed that integrating life history characteristics via prior information increased the parameter estimates' accuracy, demonstrating this modeling framework's reliability and utility. We make evident that defining model from expert knowledge and empirical studies is useful to improve precision and accuracy of demographic parameters and population size. Thereby, we demonstrate that integrating empirical results and expert knowledge within Bayesian model can be helpful to inform natural resource management and conservation (Dorazio & Johnson, 2003; Kuhnert et al., 2010).

To our knowledge, our study is the first demonstrating that developing a statistical reconstruction model within a Bayesian framework which does not depend on the inclusion of auxiliary data is possible. Likelihood

models for age-at-harvest data are estimable but need strong assumptions or auxiliary data information about vital parameters. Our Bayesian model provides flexibility in how the data are integrated and allows us to account for demographic stochasticity. Additionally, an added benefit to choosing more informative priors is that it reduces computational time by limiting the parameter space an MCMC algorithm needs to explore (Banner et al., 2020). A few other studies have used a Bayesian approach to fit age-at-harvest data, but a bit differently. For example, Allen et al. (2018) developed a Bayesian state-space model using age-at-harvest data to estimate abundances of black bears (*Ursus americanus*) in Wisconsin, USA. Their model does not include a probabilistic and hierarchical definition of the latent variables, which allowed us to estimate the harvest probability directly. Their model also relies strongly on only prior information for many parameters. Conn et al. (2008) developed a Bayesian model for wildlife age-at-harvest data applied to black bears, which integrated mark-recovery data to provide accurate estimates of abundance and vital rates. Lastly, Skelly et al. (2023) developed a Bayesian model to estimate survival by age classes from age-at-harvest data, but the model does not estimate abundance or other demographic parameters.

We found the estimates of vital rates of the white-tailed deer were consistent with estimates obtained for black-tailed deer (*Odocoileus hemionus columbianus*) in western Cascades of Washington, USA, for which the survival was 0.72 and harvest probability 0.16 (Skalski et al., 2012). We found that the total abundance of deer in Rhode Island averaged $\mu_{\bar{N}} = 21,200$. Specifically, we found that males and females were similar at an average of $\mu_{\bar{N}} = 10,362$ and 10,387. Overall, we estimated the deer density over Rhode Island land to be 8.20 deer/km² (7.93–8.29, 95% credible interval) (Appendix S5: Table S4). This result is consistent with a study that estimated deer density between 7 and 11 deer/km² in Rhode Island in 2008 (Walters et al., 2016). This density is above the recommended deer density of 4–7 deer/km² (DeCalesta, 2017). Above this density, deer can adversely affect the forest ecosystems by influencing their plant composition and abundances (Hanberry & Abrams, 2019). For the fisher, our estimated vital rates were in line with results from telemetry studies in Maine, USA, where the adult female survival was estimated to be 0.65 (Paragi et al., 1994). Similarly, fisher survival has been estimated to be 0.55 in

FIGURE 5 Box plots of one hundred estimated means of recruitment $\hat{\gamma}$, juvenile survival $\hat{\phi}_0$, adult survival $\hat{\phi}_A$, and harvest probability \hat{h} when the priors were informative with different age-at-harvest matrix compositions. The age-at-harvest matrices were composed of two ages, four ages, and eight ages classes with five and over ten years. The plain black line indicates the median of the estimated mean values across one hundred simulations. The dashed line is the true value of the simulated parameters.

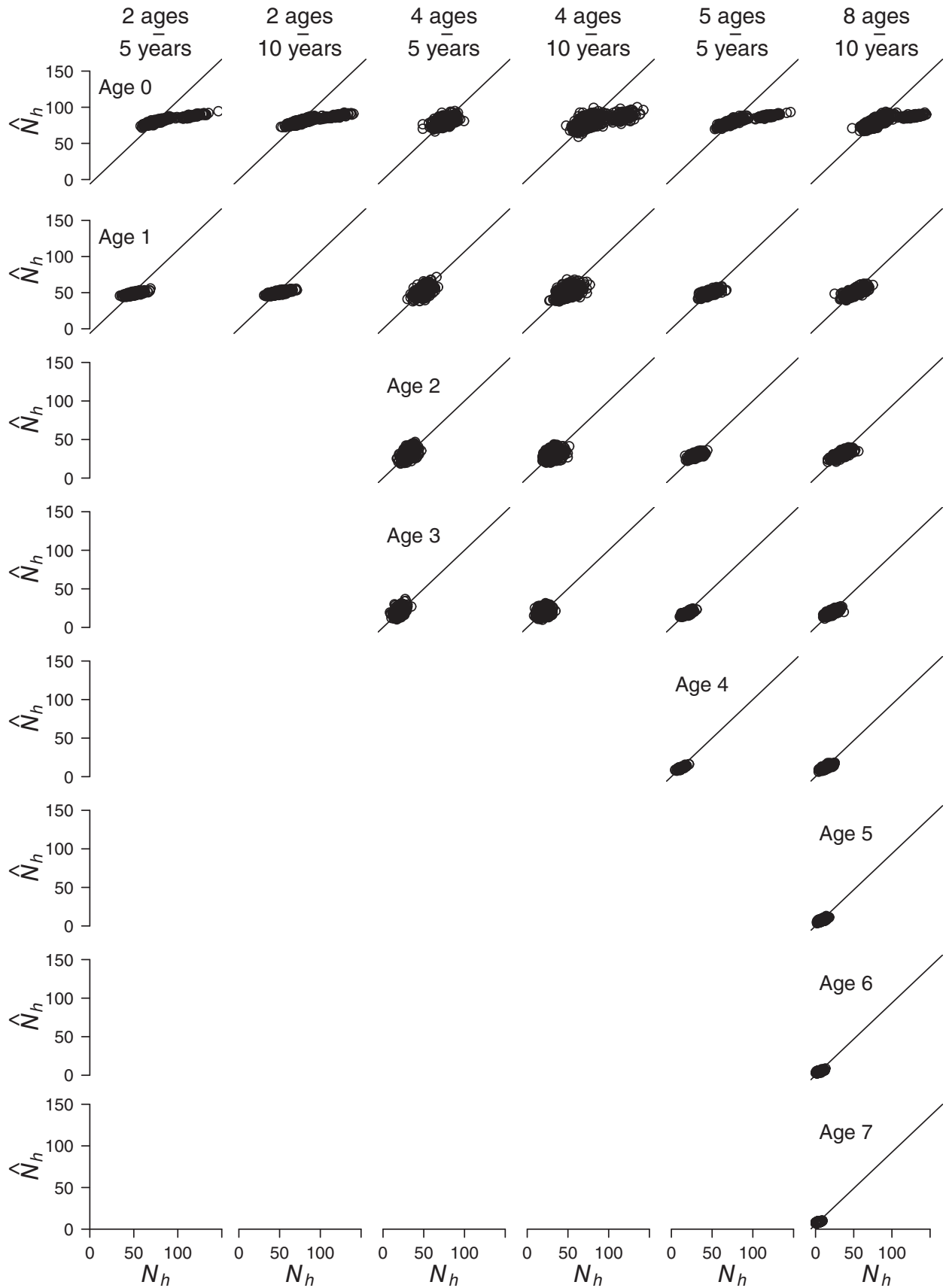


FIGURE 6 Estimated abundances \hat{N}_h as function of the simulated abundances N_h with different age-at-harvest matrix composition and informative priors. The age-at-harvest matrices were composed of two ages, four ages, and eight ages classes with five and ten years. The plain line represents the equality between the estimated and simulated values. Associated estimated vital rates are represented in Figure 5.

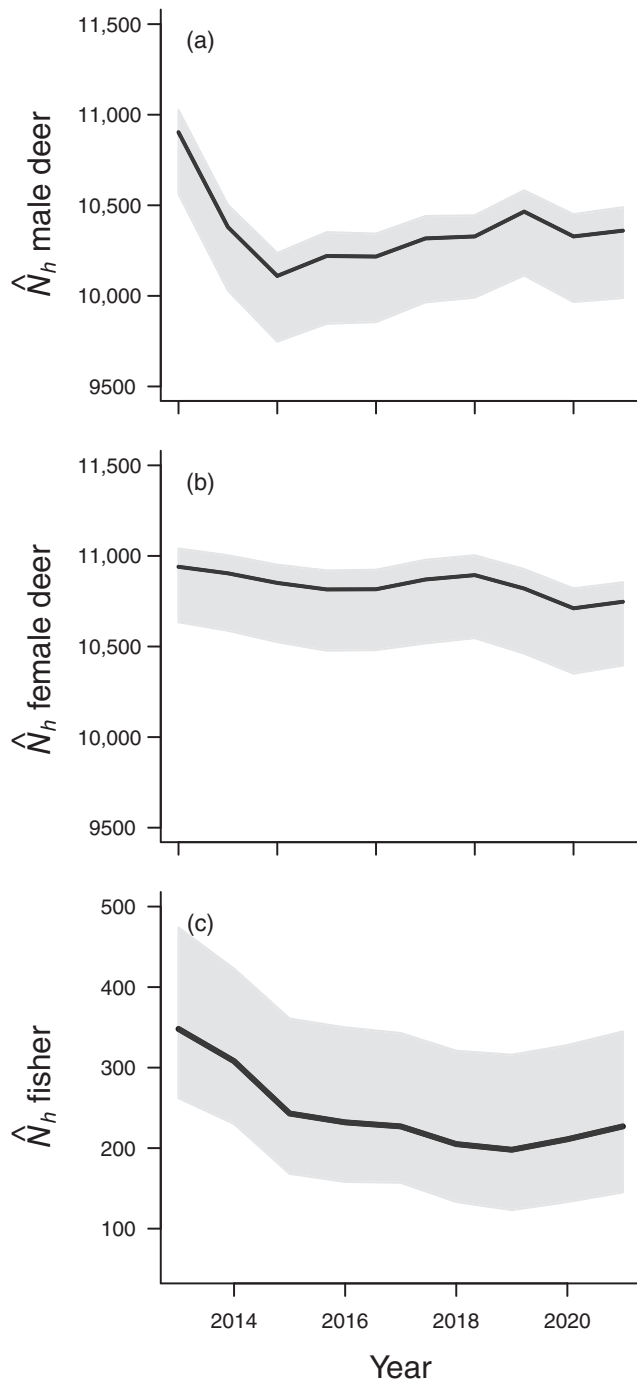


FIGURE 7 Estimated abundances of (a) male and (b) female deer using the statistical reconstruction model (Equations 1–6) and informative priors (Figure 3). (c) Estimated total abundances of fisher from the statistical reconstruction model (Equations 1–6) and informative priors (Figure 3).

Olympic National Park, Washington, and 0.61 in Sequoia national forest, California, USA (Buskirk et al., 2012). The overall mean abundance of fisher over the study period was 244 individuals, making a density of 0.094 km² individuals over land of Rhode Island (Appendix S5: Table S4). This result is consistent with studies on fisher

in California and Oregon, USA, where the density is estimated to be between 0.079 km² individuals and 0.124 km² individuals in Southern Sierra (Sweitzer et al., 2015). Posterior predictive distributions suggested that the fisher model led to a better fit of the data than the deer model. These differences in age structure and posterior predictive distribution may be because the composition of the age-at-harvest data may not represent the living population of deer. Indeed, the number of individuals in each age class might reflect hunter selectivity, age- and sex-specific vulnerabilities to harvest, or the effect of harvest regulations rather than population trends (Rosenberry et al., 2004). Since trapping is a less selective harvest technique than hunting, this may be why the fisher model fit the data better.

Through an extensive simulation study, we demonstrate that our model provides reliable estimations of vital rates and population size. In addition, our framework enabled us to estimate demographic rates and population size of two species with different life history characteristics, which constitute evidence of its robustness. Our approach considers the species' life cycle and history without requiring auxiliary data. Such an approach adds flexibility to tracking population abundance through time and could help evaluate population trends and the impact of policy change. An unstable population age structure can result in varying short-term dynamics that can increase or decrease population size (Koons et al., 2007). Further, analyses of the short-term dynamics of harvested populations can be critical for understanding the effect of harvest on population growth and projecting trajectories of age-structured populations better under different harvest scenarios (Hauser et al., 2006). Such analyses are essential to understanding the impacts of transient dynamics (Hastings, 2004). We hope our approach contributes to a better understanding of population dynamics, which is critical in managing harvested wildlife.

AUTHOR CONTRIBUTIONS

Edwige Bellier developed the model. Edwige Bellier and Brian D. Gerber designed the study with contributions of David M. Kalb. Dylan C. Ferreira and David M. Kalb provided the white-tailed deer age-at-harvest data. Amy E. Mayer and Laken S. Ganoe provided the fisher age-at-harvest data. Edwige Bellier performed the statistical analyses with contributions of Brian D. Gerber, Dylan C. Ferreira and Laken S. Ganoe. Edwige Bellier wrote the manuscript with comments of all the authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data (Bellier et al., 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.22894874.v2>.

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SUPPORTING INFORMATION

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

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