RESEARCH ARTICLE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Incorporating vital rates and harvest into stochastic population models to forecast elk population dynamics

J. Terrill Paterson[1] | Kelly M. Proffitt[2] | Jay J. Rotella[1]

[1]Montana State University, 310 Lewis Hall, Bozeman, MT 59718, USA

[2]Montana Department of Fish, Wildlife, and Parks, Bozeman, MT 59718, USA

Correspondence
J. Terrill Paterson, Montana State University, 310 Lewis Hall, Bozeman, MT 59718, USA.
Email: terrillpaterson@gmail.com

Abstract

The dynamics of ungulate populations across variable ecosystems and management strategies demonstrate disparate trajectories such that some populations are overabundant, while other populations are subject to recovery efforts. Understanding how variation in vital rates such as pregnancy and survival integrate to shape the trajectories of populations is, therefore, helpful for informed management, particularly given that our understanding of the dynamics of harvested ungulate populations is often limited. Age-related variation in vital rates among elk (*Cervus canadensis*) suggest that suitable population matrix models require age-specific vital rates that can be logistically and analytically challenging to obtain. Our goals were to use a large, long-term data set on elk and hierarchical Bayesian models to estimate age-specific pregnancy and annual survival rates and their process variances, use stochastic population projection matrices to understand the effects of additional mortality from harvest on population dynamics, and identify the influence of different combinations of vital rates on population trajectories. We found that median age-specific pregnancy rates increased with age from yearlings (0.52, 90% credible interval [CrI] = 0.37, 0.65) to a plateau among prime ages (e.g., 9-year-old: 0.91, 90% CrI = 0.87, 0.94), followed by a decline for the oldest ages (e.g., 19-year-old: 0.10, 90% CrI = 0.03, 0.28). Annual survival rates plateaued among prime-aged animals (e.g., 9-year-old: 0.94, 90% CrI = 0.92, 0.96), and declined for the oldest-ages (e.g., 19-year-old: 0.21, 90% CrI = 0.04, 0.56). We found higher process variation in pregnancy

rates than survival rates; annual pregnancy rates for a 7-year-old varied from 0.82 (90% CrI = 0.67, 0.92) to 0.98 (90% CrI = 0.95, 0.99), and annual survival rates varied from 0.94 (90% CrI = 0.85, 0.96) to 0.96 (90% CrI = 0.93, 0.99). Simulated population trajectories indicated that additional mortality due to harvest resulted in a shift in the age structure towards younger animals with lower probabilities of pregnancy. When we held calf survival between 0.48 and 0.50 and specified constant pregnancy rates, changes in age structure alone resulted in variation of the recruitment of female calves from 0.20 to 0.16. We found that populations with a low mean value of calf survival (0.25) and no additional mortality due to harvest had marginal demographic performance ($\overline{\lambda_{geo}}$ = 1.02) and could sustain no additional mortality from harvest and still increase. In contrast, productive populations with a high mean value of calf survival (0.75) required high harvests to abate population growth (e.g., harvest rate = 0.20, $\overline{\lambda_{geo}}$ = 0.94). Finally, we found a temporally lagged effect of harvest on age structure such that a shift towards younger animals could persist for multiple years following a reduction in harvest, suggesting that harvest may have multi-year lagged depressive effects on population growth rates above and beyond the direct effects on survival rates. Our work highlights the importance of considering the effect of varying age-structure on population dynamics, suggests minimum combinations of vital rates required for increasing or decreasing elk population growth rates to general management objectives, and provides the framework required for future management-specific recommendations using stochastic population projection matrices.

Populations of elk (*Cervus canadensis*) in the species' historical range in the Rocky Mountain West have largely recovered from overexploitation following European colonization, which led to the near extirpation of the species (O'Gara and Dundas 2002). Patterns of population growth are substantially different among populations due to variation in predation pressure from recovering carnivore populations, land management, harvest history, and environmental conditions (Eberhardt et al. 1996, White et al. 2010, Brodie et al. 2013, Proffitt et al. 2014, Simpson et al. 2020). There are concerns for the conservation of some elk populations in light of declining recruitment rates amid variation in predation and environmental pressure (Middleton et al. 2013, Christianson and Creel 2014, Hebblewhite et al. 2018, Lukacs et al. 2018). Given the important role of ungulates in ecosystem function

(Persson 2003, Parsons et al. 2013), and the substantial economic and cultural benefits derived from their exploitation (Gordon et al. 2004, Peterson et al. 2011), understanding the limiting and regulatory factors associated with elk population dynamics has received considerable attention (Raithel et al. 2007, Eacker et al. 2016).

In contrast to conservation concerns for some populations, elk populations are overabundant in other areas and present a risk to ecosystem function and stress social tolerance (Bradford and Hobbs 2008, Hegel et al. 2009, Walter et al. 2011). Overabundant populations of ungulates can have substantial, negative effects on plant communities, serve as reservoirs of disease, and challenge the recovery of other species (Garrott et al. 1993, Côté et al. 2004, Bradford and Hobbs 2008, Wittmer et al. 2010, Cotterill et al. 2018, Valente et al. 2020). Moreover, these impacts extend to agriculture, where crop damage, disease, and pathogen transmission threaten the economic viability of livestock producers and lead to social conflict between stakeholders (Walter et al. 2011, Bleier et al. 2012, Roberts et al. 2012).

The differences in management challenges for elk populations (i.e., conservation and population recovery for some, reduction for others) typify a dichotomy of modern population management as a key component of ecosystem dynamics (Naiman 1988, Brussard et al. 1998, Allen et al. 2011, Chapron et al. 2014, Apollonio et al. 2017). For the recovery of populations, studies seek to identify which combinations of vital rates yield positive population trajectories. When population reduction is the goal for overabundant populations, the focus shifts to identifying combinations of vital rates that will yield negative population growth (Barlow et al. 1997, McShea et al. 1997, Carey et al. 2012). Given some vital rates are harder to manipulate than others through management and that some contribute more to population growth than others, much effort has been expended on identifying combinations of vital rates that can be expected to result in increasing or decreasing population trajectories (Gaillard et al. 1998, Saether and Bakke 2000, Wisdom et al. 2000).

One common method of manipulating vital rates to affect changes in population trajectories is through harvest (Apollonio et al. 2017, Festa-Bianchet et al. 2017). But exploiting a population through harvest complicates the understanding of how vital rates integrate to shape population trajectories, given the accumulating evidence for harvested populations to display complex population dynamics (Glaser et al. 2014, Hastings et al. 2018, Krebs et al. 2018), and counter-intuitive patterns arising from both intrinsic and extrinsic drivers (Bonenfant et al. 2009; Bowyer et al. 2014, 2020; Koons et al. 2014). The dominant paradigm of ungulate population dynamics suggests little variation in adult survival in non-harvested populations coupled to substantial variation in offspring recruitment (Gaillard et al. 1998); however, adult survival in exploited populations of ungulates can vary substantially and affect population growth if the harvest mortality is additional to other sources of mortality (Brodie et al. 2013). An unaddressed question in elk population dynamics is if there are consequences of harvest to the population trajectories of elk beyond the reduction in adult survival if some fraction of the harvest is additive. There is ample evidence that pregnancy rates of elk demonstrate age-related variation characterized by lower pregnancy rates for younger animals, higher rates for middle-aged animals, and senescence-related lower rates for older animals (Raithel et al. 2007, Proffitt et al. 2014, Bender and Piasecke 2019). Such variation can set the stage for impacts to population-level recruitment rates from a shifted age structure, although the significance of the effects on population dynamics are not well understood (Langvatn and Loison 1999, Coulson et al. 2001, 2004, Shelton et al. 2015, Bender and Piasecke 2019).

The primary tool used to understand how vital rates integrate to shape the trajectories of populations are population projection matrices (Caswell 2013), which have been used to inform management decisions for a variety of species (Crowder et al. 1994, Heppell et al. 1996, Johnson et al. 2010). Although projection matrices are commonly used to understand the asymptotic behavior of populations (e.g., stable age or stage structure, population growth rate), for populations subject to a high degree of environmental or demographic stochasticity, conclusions from an asymptotic analysis may be misleading (Merrill et al. 2003; Koons et al. 2005, 2006). Both of these sources of stochasticity are relevant to populations of ungulates (Lande 1993, Johnson et al. 2010). An asymptotic analysis of population dynamics can also be inappropriate given the comparatively shorter time scale over which management actions are taken. Under such circumstances, a population will experience temporal variation in vital

rates, age-structure, and size such that transient population dynamics will be of particular interest for management (Yearsley 2004, Koons et al. 2005). Despite the drawbacks of asymptotic analyses, the use of stochastic population models focused on shorter-term dynamics is still rare, and we are aware of no published studies on elk that incorporated stochastic population projections to characterize uncertainty in population trajectories over time with a focus on transient dynamics.

The lack of stochastic population projections for elk is understandable given the data requirements for using stochastic population projection matrices with a fully age-dependent structure (Tuljapurkar 1989, Caswell 2013). Estimating age-specific vital rates is a challenging task for elk given the expense and logistical challenges involved, and such challenges have led to the use of age classes (e.g., young, prime, old, senescent) to aggregate data for estimation (Raithel et al. 2007, Proffitt et al. 2014). Yet this aggregation of age classes can mask important transient dynamics that depend on finer age-specific detail present among individuals that compose the real population (Tenhumberg et al. 2009, Stott et al. 2011). Moreover, stochastic population projection matrices require estimates of the biological variability in each rate (i.e., the process variation; Burnham 2012) to parameterize the distributions of vital rates (Tuljapurkar 1989, Caswell 2013), which adds to the already-difficult challenge of estimating age-specific vital rates. Combined, these challenges have limited the ability of previous research to evaluate the impacts of harvest on elk population dynamics using fully age-structured, stochastic population projection matrices. As a consequence, we have a poor understanding of how variation in vital rates due to environmental drivers, age structure, and harvest integrate to define population trajectories and, in turn, the combinations of vital rates that support either the recovery or reduction of a population.

Our objective was to fill in gaps in our understanding of the dynamics of harvested elk populations by achieving 3 goals: 1) estimate age-specific vital rates and their variances to parameterize stochastic population projection matrices, 2) use stochastic population projections to assess the impacts on population trajectories of harvest and varying vital rates using simulations, and 3) identify the possible effects of different combinations of vital rates on population trajectories. For our second and third goals, we considered 3 simulation scenarios that addressed 1) the most general consequences of harvest on age structure and population dynamics, 2) the combinations of vital rates and harvest required for a population to grow, and 3) the levels of harvest required to reduce a growing population. If simulated harvest resulted in a shift of the age structure of a population towards younger animals with lower probabilities of pregnancy and survival, we would predict a negative impact on population growth rates. We then further explored the potential consequences of this shift in age structure in the context of 2 clear management questions (2 and 3, above).

STUDY AREA

We used information from multiple populations of elk across Montana, USA (~147,000 km^2), information that was unbalanced among populations and years (2003–2020; Figure 1). Populations were defined based on wintering distributions and predominately located in west-central and southwestern Montana, areas with mixed physiography generally defined by mountainous terrain and intermontane valleys, elevations across populations from 636 m to 3,173 m, and climate conditions ranging from hot summers (30-year average [1981–2010] Jul temperatures: 13.0°C to 21.9°C) to cool winters (30-year average [1981–2010] Jan temperatures: −7.7°C to −2.3°C) and wide variation in annual precipitation (30-year average [1981–2010]: 307.9 mm to 871.7 mm; PRISM Climate Group 2012). These populations are generally sympatric with a variety of other ungulate species including pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). In the past 2 decades, portions of this area have also seen the recovery of large carnivore species such that it now hosts the intact suite of native predators including wolves (*Canis lupus*), mountain lions (*Felis concolor*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*). Two populations were located in north-central Montana, an area with physiography defined by prairie breaks adjacent to
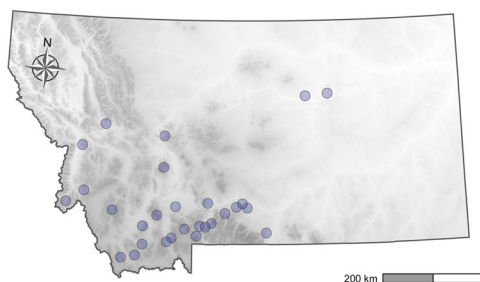
POPULATION DYNAMICS AND HARVEST

THE JOURNAL OF
WILDLIFE
MANAGEMENT

THE
WILDLIFE
SOCIETY

5

FIGURE 1 Approximate locations of wintering elk populations in Montana, USA, that we used to estimate age-specific survival (2003–2019) and pregnancy (2005–2020) rates. Shading indicates elevation with darker areas of higher elevation

the Missouri River. These populations generally share the suite of sympatric ungulates with the west-central and southwestern Montana populations (with the exception of mountain goats) but are not subject to predation from wolves and grizzly bears. The predominate vegetation groups varied across the western, south-western, and south-central portions of the state from a mix of montane forest (e.g., lodgepole pine [*Pinus contorta*], Douglas fir [*Pseudotsuga menziesii*], and aspen [*Populus tremuloides*]), open sage-grassland (e.g., big sagebrush [*Artemesia tridentata*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], and Idaho fescue [*Festuca idahoensis*]), upland grass-lands, and alpine areas. The vegetation in the north-central region of Montana was dominated by big sagebrush and mixed-grass prairie, riparian areas dominated by prairie cottonwood (*Populus sargentii*) and willow (*Salix* spp.), and steep coulees dominated by Rocky Mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*).

METHODS

Our analytical approach required 2 steps: first, estimating age-specific vital rates and process variances, and second, using the distributions of vital rates to construct population models to understand the effects of harvests on populations through simulations. We focused on only the female component of the population, under the assumption that males were not a limiting factor.

Estimating age-specific vital rates and process variances

To estimate pregnancy and survival rates, we used a large data set from the Montana Department of Fish, Wildlife, and Parks that included pregnancy tests and known-fate survival information from the monitoring of global positioning system (GPS)-collared elk from multiple populations and years. Researchers captured animals during December–March using a combination of helicopter net-gunning and chemical immobilization. They assessed pregnancy using pregnancy-specific protein B assays (Noyes et al. 1997). Crews estimated the age of each animal at the time of capture either from an extracted tooth and subsequent aging based on cementum annuli counts, or from eruption and wear patterns (Keiss 1969, Hamlin et al. 2000). We used the GPS collar data to monitor survival and determine date of death and censored any records that had <7 days of monitoring to remove any capture-related mortalities.

We estimated age-specific pregnancy and annual survival rates and their process variances using a single, flexible model. In the model for each vital rate, the probabilities of pregnancy or survival had an expected, age-specific value that we modeled using a penalized thin-plate spline approach with a parsimonious *a priori* definition

of 3 knots (ages 6, 11, and 16) to provide a simple, flexible model form (Crainiceanu et al. 2005). We chose this approach given our primary goal was estimating age-related patterns of variation in vital rates, rather than testing *a priori* hypotheses about such variation from life-history theory using defined model forms (e.g., a quadratic form to test for evidence of actuarial senescence). We acknowledge splines may suffer from poor fit near the boundaries of data; however, their overall flexibility in the face of the technical challenges of selecting the best model in a mixed-modeling framework (i.e., choosing which model form inference should be based on) outweighs their drawbacks for our purposes. To assess the degree of model-induced smoothing and the robustness of our results to our approach, we also fit a version of the model with independent, age-specific vital rates for comparison (i.e., no smoothing). We used a random-effects interpretation of process variance (White 2000, Burnham and White 2002): for every population-year, we allowed age-specific vital rates to deviate from the expected value using an additive random effect across ages, we interpreted the variance of the random effect as process variance incorporating both temporal and spatial variation.

Pregnancy

We used a logistic-regression approach in a Bayesian framework to estimate age-specific probabilities of pregnancy and process variance. We modeled the result of a pregnancy test ($\text{Preg}_{i,t}$: 0 = no, 1 = yes) for individual i in year t as a Bernoulli random variable:

$$\text{Preg}_{i,t} \sim \text{Bernoulli}\left(P^{\text{age}_{i,t}}_{\text{popyear}_{i,t}}\right).$$

The probability of pregnancy ($P^{\text{age}_{i,t}}_{\text{popyear}_{i,t}}$) was a function of the age of individual i in year t with an additive random effect for the population year, and modeled using the logit link:

$$\text{logit}\left(P^{\text{age}_{i,t}}_{\text{popyear}_{i,t}}\right) = \alpha + \mathbf{b}\mathbf{Z}_{\text{age}_{i,t}} + \epsilon_{\text{popyear}_{i,t}},$$

where α was an overall intercept, $\mathbf{b}$ was the vector of coefficients corresponding to the spline component of the model, $\mathbf{Z}_{\text{age}_{i,t}}$ was the component of the spline basis corresponding to age of individual i in year t, and $\epsilon_{\text{popyear}_{i,t}}$ was the additive random effect for the population-year. The following priors complete the model specification:

$$\alpha \sim \text{Logistic}(0, 1)$$
$$b_n \sim \text{Normal}(0, \sigma), n = 1, 2, 3$$
$$\sigma \sim \text{Uniform}(0, 10)$$
$$\epsilon_{\text{popyear}} \sim \text{Normal}\left(0, \sigma^P_{\text{pv}}\right)$$
$$\sigma^P_{\text{pv}} \sim \text{Uniform}(0, 10).$$

Under this model definition, we interpreted σ^P_{pv} as the process variance for pregnancy rates. Our model formulation conflates process variation in this vital rate across populations and through time (i.e., the combination of spatial and temporal process variances). Finally, our model for the probabilities of pregnancy made 2 simplifying assumptions: the probability of pregnancy for calves was 0, and multiple years of pregnancy tests on individuals were treated as entirely independent sampling events.

Annual female survival

To accommodate the staggered entry and exit of individuals in the known-fate data set, we used the ragged telemetry approach in a Bayesian framework previously used to model known-fate nest survival in birds to estimate

annual adult female survival (Schmidt et al. 2010). Here, we modeled the fate of individual i in year t ($Alive_{i,t}$: 1 = survived, 0 = died) as a Bernoulli random variable:

$$Alive_{i,t} \sim Bernoulli\left(\left(S^{age_{i,t}}_{popyear_{i,t}}\right)^{\frac{days_{i,t}}{365}}\right),$$

with the probability of survival modeled as a function of the age-specific annual survival rate (S) for that population-year factored into a daily survival rate ($\frac{1}{365}$) and then raised to the value of the number of days in that individual's monitoring record in that year ($days_{i,t}$). We modeled the age-specific probabilities of annual survival using the logit link:

$$logit\left(S^{age_{i,t}}_{popyear_{i,t}}\right) = \alpha + \mathbf{b}\mathbf{Z}_{age_{i,t}} + \epsilon_{popyear_{i,t}},$$

where α was an overall intercept, $\mathbf{b}$ was the vector of coefficients corresponding to the spline component of the model, $\mathbf{Z}_{age_{i,t}}$ was the component of the spline basis corresponding to age of individual i in year t, and $\epsilon_{popyear_{i,t}}$ was the additive random effect for the population-year. The following priors complete the model specification:

$$\alpha \sim Logistic(0, 1)$$
$$b_n \sim Normal(0, \sigma), n = 1, 2, 3$$
$$\sigma \sim Uniform(0, 10)$$
$$\epsilon_{popyear} \sim Normal\left(0, \sigma^{S^{adult}}_{pv}\right)$$
$$\sigma^{S^{adult}}_{pv} \sim Uniform(0, 10).$$

Under this model definition, we interpreted $\sigma^{S^{adult}}_{pv}$ as the process variance for survival rates. Our model for the probability of annual survival was specifically for non-harvest mortality, and we truncated monitoring records at the day prior to death for those individuals that were harvested. Notably, this conflates all other sources of mortality aside from reported hunting offtake into a single category of natural mortality.

We did not have the information required to directly estimate the probability of calf survival and to estimate its process variance. Therefore, we searched the scientific literature to curate a list of sources that estimated annual calf survival for multiple years and that included either the standard error for each estimate or the sample size each estimate was based on. We then estimated the process variance within each study across the years by separating the sampling variance from the total variance (White 2000; available in Supporting Information). We used the approximate mean value of these estimated process variances in our simulations ($\sigma^{S^0}_{pv}$).

Model fitting and evaluation

We fit all models using the runjags package (Denwood 2016) as an interface to the JAGS program for Markov chain Monte Carlo sampling (Plummer 2003) in the R programming environment (R Core Team 2020). We ran pregnancy models for 20,000 iterations with the first 10,000 discarded as burn-in, and survival models for 30,000 iterations with the first 10,000 discarded as burn-in (the higher number of iterations for survival was suggested by initial model runs for adequate convergence). We graphically assessed convergence of each model using traceplots.

Because aging of animals by eruption and wear patterns may be unreliable for older-aged elk, we treated all ages >12 years estimated from eruption and wear patterns as missing data. We assigned a vague prior to these ages using a categorial distribution with an equal probability of ages from 12–21 years. We assumed that all assigned ages <12 years based on both cementum annuli and eruption or wear patterns were accurate. To ensure that our

results were robust to the inclusion of data from animals whose ages were based upon eruption or wear patterns and the cementum annuli method, we ran an additional version of the pregnancy and survival models that used only ages based on cementum annuli. We then compared results of the models that used the entire dataset and the cementum annuli-only data set using a simple graphical comparison of the age-specific estimated vital rates.

Population modeling to understand the effects of harvest

Our second major goal was to understand the consequences of harvest for elk population dynamics. We used a fully age-structured (0–21 yr), female-specific population based on a pre-birth pulse census design as the basis for our simulated population trajectories to match the manner in which most elk populations are surveyed (i.e., in late winter and early spring when the population is composed of calves [<1 yr; N_0], yearlings [1–2 yr; N_1)], …). We used the binomial distribution to incorporate demographic stochasticity in our population projections.

To keep track of the different components of calf recruitment, we modeled the production of calves in year t with a multi-step process. At the beginning of biological year t (i.e., the birth-pulse), we modeled the total number of female calves born (Total Calves$_t$) as the sum of female calves born to all ages of adult females from the previous year:

$$\text{Total Calves}_t = \sum_{\text{age}=1}^{21} \text{Calves}_t^{\text{age}}$$

$$\text{Calves}_t^{\text{age}} \sim \text{Binomial}(0.5 \times P_{t-1}^{\text{age}}, N_{t-1}^{\text{age}}),$$

where Calves$_t^1$ would represent the number of female calves born at the start of year t (assuming an equal sex ratio at birth) to females that became pregnant as yearlings in year $t - 1$ (N_{t-1}^1). This assumed a litter size of 1, a reasonable assumption given the rarity of a female elk producing >1 offspring (Bubenik 1982).

To incorporate harvest in the survival process, we used a simple mortality model where animals of each age (1–21) were removed in proportion to their representation in the total population. First, to incorporate randomness in the harvest process and acknowledge the real-world disjunction between a specified and achieved harvest rate, we simply drew a random value of annual harvest (h_t) from a truncated normal distribution (truncated to between 0 and 1) parameterized by the mean equal to the specified harvest rate and a standard deviation of 0.02. For example, an annual harvest rate with an expected value 0.10 would be drawn from a Normal(0.10, 0.02) distribution, which yields a distribution of random harvest rates with a mean of 0.10 and 1% and 99% quantiles of 0.05 and 0.15:

$$h_t \sim \text{Truncated Normal(harvest rate, 0.02)}.$$

The total number of animals removed was then a function of h_t and the size of the population in the previous year:

$$\text{Total Harvest}_t = h_t \times \left(N_0^{t-1} + N_1^{t-1} + N_2^{t-1} + \cdots + N_{21}^{t-1} \right).$$

We apportioned the total number of animals harvested (Total Harvest$_t$) into age-specific harvests (Harvest$_t^{\text{age}}$) using a multinomial distribution:

$$\left[\text{Harvest}_t^0, \text{Harvest}_t^1, \ldots, \text{Harvest}_t^{21} \right] \sim \text{Multinomial}(\boldsymbol{\pi}_t, \text{Total Harvest}_t).$$

We accounted for the fact that calves born in year t are represented in annual harvests by assuming that 2% of the harvested total of females in each year was composed of female calves (Appendix A, available in Supporting Information), and assumed the remainder was proportional:

$$\boldsymbol{\pi}_t = \left[0.02, 0.98 \times \frac{N_{t-1}^0}{N_{t-1}^0 + \cdots + N_{t-1}^{21}}, \ldots, 0.98 \times \frac{N_{t-1}^{21}}{N_{t-1}^0 + \cdots + N_{t-1}^{21}}\right],$$

where the number of yearlings harvested in year t was a function of the total harvest and the proportion of calves at the end of year $t - 1\left(\frac{N_{t-1}^0}{N_{t-1}^0 + \cdots + N_{t-1}^{21}}\right)$. We then constrained harvest to be zero for any age class that had an abundance of zero. Finally, we incorporated the number harvested in each age in population projections by subtracting the harvest from the relevant age group prior to the survival process in year t:

$$N_t^{\text{age}} \sim \text{Binomial}(S_t^{\text{age}}, N_{t-1}^{\text{age}-1} - \text{Harvest}_t^{\text{age}}).$$

We recycled the estimated survival rate for 21-year-olds, creating a ≥21 age class in the model: $N_t^{21} \sim \text{Binomial}(S_t^{21}, N_{t-1}^{20} + N_{t-1}^{21} - (\text{Harvest}_t^{20} + \text{Harvest}_t^{21}))$. There are 3 substantial assumptions made by this model. First, it is a simplification of the actual biological year wherein all animals are exposed to potential natural mortality from spring to late summer, subject to harvest in addition to natural mortality in the late summer to late fall, and then exposed to natural mortality in the winter and late spring (i.e., fall harvest is assumed to occur before any other mortality sources act on the population, including wounding loss and summer mortality). Second, it assumes complete additive harvest mortality. Third, it ignores density dependence. We did not incorporate density dependence in our model, which would be unlikely for the simulated populations under consideration: either small and recovering populations or large and currently growing populations not under apparent resource limitation.

To incorporate environmental stochasticity in age-specific probabilities of pregnancy and survival, we used a framework identical to the model used for vital rate estimation: we drew a year-specific random effect (pregnancy: ξ^P, survival: ξ^S) from a mean-zero normal distribution defined by the estimated process variance on the logit scale and then added that to expected age-specific vital rate (i.e., an additive structure in which a year that was good or bad applied to all age classes). For calf survival, we drew a random value from a beta distribution that was parameterized using the mean and variance form. Each random draw of either the random effect on the logit scale (pregnancy and survival) or calf survival was independent and no covariation between rates was incorporated. For example, at each time step we made the following draws:

$$\text{Pregnancy: } \xi^P \sim \text{Normal}\left(0, \sigma_{pv}^P\right)$$
$$\text{Adult survival: } \xi^S \sim \text{Normal}\left(0, \sigma_{pv}^{S^{\text{adult}}}\right), \text{age} = 1, 2, \ldots, 21$$
$$\text{Calf survival: } S^0 \sim \text{Beta}\left(\text{mean} = S^*, \text{variance} = \sigma_{pv}^{S^{\text{calf}}}\right)$$

and calculated vital rates as:

$$\text{Pregnancy: logit}(P^{\text{age}}) = E(P^{\text{age}}) + \xi^P$$
$$\text{Adult survival: logit}(S^{\text{age}}) = E(S^{\text{age}}) + \xi^{S}{'}$$

where S^* was a specified mean value of calf survival. We calculated the expected values for age-specific pregnancy and survival, $E(P^{\text{age}})$ and $E(S^{\text{age}})$, using the results from the spline formulation from the models for vital rate estimates using the median value of the **b** coefficients from the approximate posterior distribution. Similarly, we

used the median of the approximate posterior distribution of σ_{pv}^{P} and $\sigma_{pv}^{S^{adult}}$ to characterize the distributions (we did not include uncertainty in coefficient estimation).

Simulation space

Simulations based on this model required specifying a modest set of parameters: mean calf survival, initial population size, and harvest rate. Our 3 key questions related to elk population dynamics required 3 separate scenarios to address (Table 1). To evaluate the most general effects of how harvest affects the age distribution of a population (scenario 1), we chose an initial population size of 1,000 females and a mean calf survival rate of 0.5. To allocate the initial 1,000 females into each age at the first time step, we made an initial draw of all vital rates and

TABLE 1 Definition of simulation scenarios used to understand how harvest was related to elk population dynamics based on elk survival and pregnancy rate data collected in Montana, USA, 2003–2020. We used scenario 1 to generally understand how harvest affects population dynamics, scenario 2 to assess how different combinations of vital rates could result in positive population trajectories for a population with poor demographic performance, and scenario 3 to assess the harvest rates required to abate the growth of a rapidly growing population, and any temporally lagged effects of harvest. We defined each simulation scenario by the initial population size, the mean value of annual calf survival (S^*), and the expected harvest rates over 3 intervals: 0–10 years, 11–20 years, and 21–30 years

	Starting population	S^*	Expected harvest from 0–10 years	Expected harvest from 11–20 years	Expected harvest from 21–30 years
Scenario 1	1,000	0.50	0.00	0.10	0.10
			0.00	0.20	0.20
			0.00	0.30	0.30
Scenario 2	500	0.25	0.00	0.00	0.00
			0.10	0.10	0.10
			0.20	0.20	0.20
		0.40	0.00	0.00	0.00
			0.10	0.10	0.10
			0.20	0.20	0.20
		0.55	0.00	0.00	0.00
			0.10	0.10	0.10
			0.20	0.20	0.20
		0.70	0.00	0.00	0.00
			0.10	0.10	0.10
			0.20	0.20	0.20
Scenario 3	5,000	0.75	0.10	0.00	0.10
			0.10	0.10	0.10
			0.10	0.20	0.10
			0.10	0.30	0.10

constructed a population projection matrix using those values. We then used the stable age distribution for that single draw of vital rates to allocate the initial total into ages, the integrated result of which was stochasticity in initial age distributions for the simulations. To understand the dynamics of populations based on our vital rates in the absence of harvest, we allowed every simulation to run for 10 time steps (years) with no harvest (harvest rate = 0). To characterize the impact of harvest on populations, we then followed that initial 10-year period by a 20-year period wherein the specified harvest rate in every year was 0.10, 0.20, or 0.30.

To address our second scenario regarding how the dynamics of a struggling population with low mean calf survival that has already been exposed to harvest can be affected by combinations of varying calf survival and harvest rates (scenario 2), we simulated a small population (initial size of 500 females) with a lower mean calf survival rate of 0.25. To allocate the 500 females into each age at the first time step, we used the age distributions at the final step of the first simulation scenario (i.e., a population that had been exposed to steady harvest for 20 years at a harvest rate of 0.10). We allowed every simulated population to run for an initial period of 10 years at a modest harvest rate of 0.10 with the low mean calf survival rate of 0.25, and then defined a set of simulation sub-scenarios based on manipulating mean overall calf survival (values of 0.25, 0.40, 0.55, or 0.75) and harvest rates (0, 0.10, and 0.20) for the next 20 years, resulting in 12 total sub-scenarios (4 values of calf survival and 3 values of harvest rates).

To address our third scenario regarding how harvest can arrest or reverse the population growth of large, productive populations (scenario 3), we simulated a large (5,000 females), productive (mean calf survival = 0.75) population. To allocate the initial 5,000 females into each age at the first time step, we used the same strategy as our first simulation scenario (using the stable age distribution from a random population projection matrix). To understand the population dynamics of such populations in response to harvest, we allowed every simulation to run for an initial period of 10 years at a modest harvest rate of 0.10 and then defined our simulation sub-scenarios based on the harvest rate in the next 10 years (0.10, 0.20, and 0.30) for 3 total sub-scenarios. Finally, to assess any longer-term impacts on population dynamics from higher harvest rates, we ran all population projections for the simulations for the final 10 years at the reduced, initial harvest rate of 0.10.

Our simulated population trajectories were the integrated result of multiple sources of variation, including age-specific vital rates and process variance in vital rates. To help reduce the dimensionality of the results, we define 2 metrics of the structure of a population to help visualize the impact that these multiple sources of variation have on population trajectories: the ratio of female calves born at the beginning of year t to the number of adult females in year $t-1$ (Calf ratio$_t$ = $\frac{\text{Total Calves}_t}{N_{t-1}^1 + \cdots + N_{t-1}^{21}}$ just after the birth pulse), and the ratio of calves that survived year t to the number of adult females in year $t-1$ (i.e., a recruitment ratio: Recruitment ratio$_t$ = $\frac{N_t^0}{N_{t-1}^1 + \cdots + N_{t-1}^{21}}$ at the end of the biological year). Finally, we define the population growth rate in year t, λ_t, as $\lambda_t = \frac{N_{t+1}^{Total}}{N_t^{Total}}$, where N_t^{Total} is the total number of animals across all age classes in year t.

RESULTS

The pregnancy data set included 1,005 individual records, with 23 yearlings aged by tooth eruption patterns, 604 adults aged by eruption or wear patterns, and 340 aged by cementum annuli (Appendix B, available in Supporting Information). Ages ranged from 1–19 years (Appendix B, Table B1). There were 38 individuals with missing ages. These data were from 25 populations sampled in 15 years, for a combined total of 41 population-years (Appendix B, Figure B1). The survival data set included 912 individual records with 18 yearlings at the time of collaring aged by eruption patterns, 468 adults aged by eruption or wear patterns, and 386 aged by cementum annuli (Appendix B). Ages ranged from 1–19 years of age. There were 40 individuals with missing ages. These data were from 27 populations sampled in 18 years at the time of collaring, for a combined total of 100 population-years of monitoring

(Appendix B, Table B2). Finally, there were 78 non-harvest-related mortalities broadly distributed across ages and years (Appendix B, Figure B2), and 70 harvest mortalities that were censored to the day prior to harvest.

Estimating age-specific vital rates and process variances

We found evidence for age-related patterns of variation in both pregnancy and survival (Figure 2; details in Appendix C, available in Supporting Information). Yearlings had an estimated probability of pregnancy that was lower than values for all but the oldest-aged elk (median of approximate posterior distribution = 0.52, 90% highest posterior density credible interval [CrI] = 0.37, 0.65). There was a plateau of pregnancy probabilities across ages for adult elk (Figure 2). Age-related variation in survival rates showed a similar plateau (Figure 2). In contrast to the results for pregnancy rates, we found no evidence for overall lower survival for yearlings (0.98, 90% CrI = 0.90, 1.00); however, because of the timing of collaring, yearlings were only monitored for a few months in the late winter and early spring and, as a result, these survival rates are likely biased high.

We found evidence for process variation in the probability of pregnancy (σ_{pv}^{preg} = 0.82, 90% CrI = 0.62, 1.00, on the logit scale, Appendix C). This translated into variation in pregnancy rates on the probability scale (Figure 3), although the additive nature of our model on the logit scale implied that variation was attenuated for pregnancy rates that were otherwise high. For example, the probability of pregnancy for yearlings ranged from 0.21 (90% CrI = 0.08, 0.43) to 0.76 (90% CrI = 0.53, 0.91), and only from 0.82 (90% CrI = 0.67, 0.92) to 0.98 (90% CrI = 0.95, 0.99) for a 7-year-old. In contrast, we found comparatively limited evidence for process variation in the probability
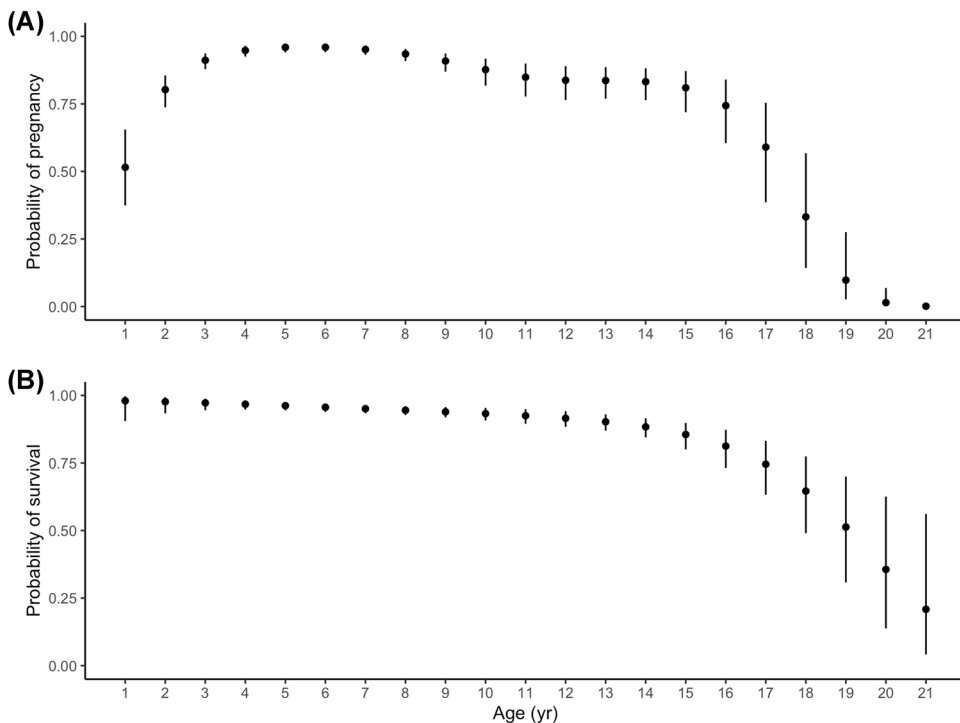

FIGURE 2   Age-specific elk pregnancy (A, from years 2005–2020) and survival (B, from years 2003–2019) rates estimated using a generalized additive modeling approach and data from 25 and 27 populations, respectively, of elk in Montana, USA. The dot indicates the median of the approximate posterior distribution, and the line represents the 90% highest posterior density credible interval. Knots were pre-defined at ages 6, 11, and 16
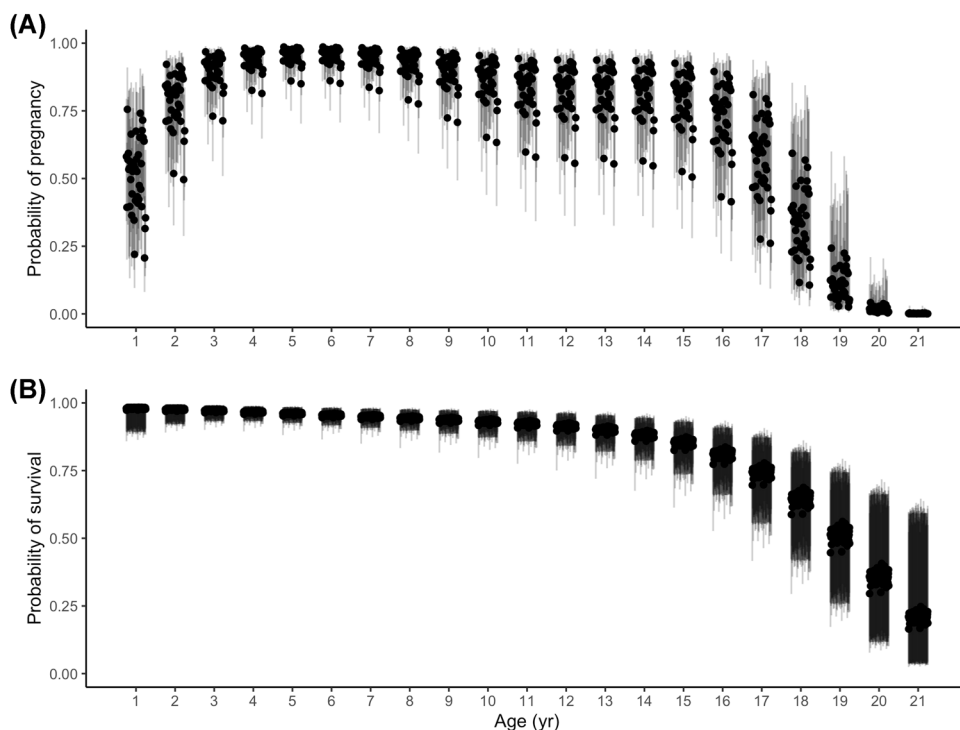
FIGURE 3 Variation in age-specific elk pregnancy (A, from years 2005–2020) and survival (B, from years 2003–2019) rates among populations and years estimated using a generalized additive modeling approach and data from 25 and 27 populations, respectively, of elk in Montana, USA. The dot indicates the median of the approximate posterior distribution for the age-specific vital rate in a population-year, and the line represents the 90% highest posterior density credible interval

of survival (σ_{pv}^S = 0.31, 90% CrI = 0.00, 0.68 on the logit scale) that translated into limited variation on the probability scale. For example, the probabilities of annual survival for a yearling ranged from 0.97 (90% CrI = 0.86, 1.00) to 0.98 (90% CrI = 0.91, 1.00), and from 0.94 (90% CrI = 0.85, 0.96) to 0.96 (90% CrI = 0.93, 0.99) for a 7-year-old. Because of the additive nature of our model on the logit scale, this small value of process variation resulted in more variation for those ages with lower overall survival; for example, estimated survival had a minimum value of 0.16 (90% CrI = 0.02, 0.52) and a maximum value of 0.25 (90% CrI = 0.05, 0.65) for a 21-year-old, even if the wide credible intervals prevented strong inference.

For calf survival, our literature search resulted in 11 sources with the required information to estimate process variance. Across these studies, process variance had an overall approximate mean value of 0.01 and ranged from 0.00 to 0.04 (Appendix C, Figure C1). We used the median value to parameterize the distribution of annual calf survival rates for the population projections.

We combined the age-specific estimates of pregnancy and survival with their process variances and generated the distributions of vital rates used for simulated population projections. To illustrate the magnitude of variation associated with these vital rates, we drew 10,000 samples for each age-specific vital rate from the distribution on the logit scale that was parameterized by the age-specific expected value and the process variance (Appendix C, Figure C2). Our inference on age-related variation in vital rates was robust to 2 key assumptions of our modeling approach: the use of information from animals with ages estimated from eruption or wear patterns (Appendix D, Figure D1), and our use of penalized splines as a smoothing function to estimate age-specific vital rates across an uneven distribution of animal ages at collaring (Appendix D, Figure D2).

Population modeling to understand the effects of harvest

In our first scenario to understand the general consequences of harvest on population dynamics, the additional mortality due to simulated harvest had an impact on population trajectories (scenario 1; Figure 4A), and a modest impact on the age structure of a population (Figure 4B). Across simulations and years, annual population growth rates (λ_t) during the non-harvest period (years 1 to 10) had a median value of 1.12, with a range from the 1st to 99th percentile of values from 1.02 to 1.23 (i.e., the variation in annual growth rates across simulations and years,
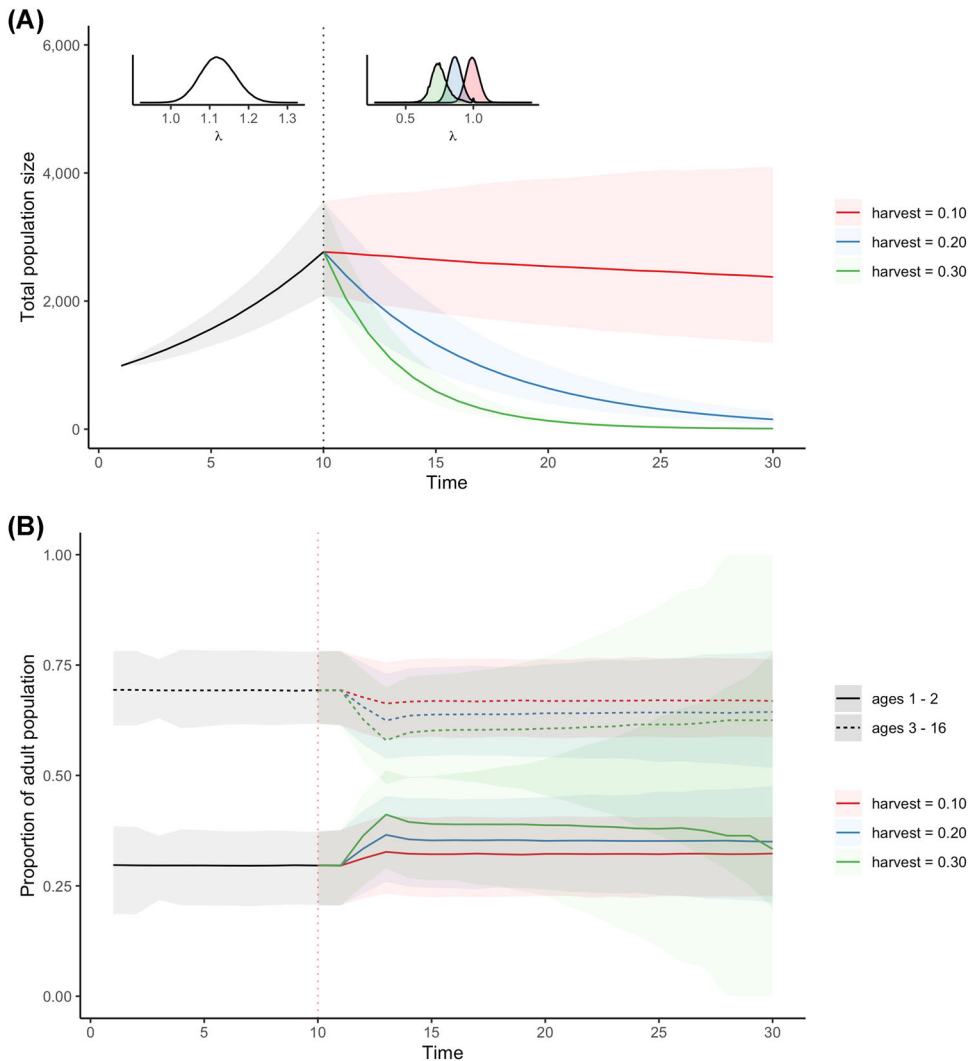

FIGURE 4 Simulation results for scenario 1 (mean calf survival, $S^* = 0.5$) across time (years) for elk population trajectories based on estimated pregnancy (data from 2005–2020) and survival rates (data from 2003–2019) from elk in Montana, USA. Panel A illustrates simulated population trajectories: years 1–10 with harvest rate = 0, and a variety of harvest rates (colors) from years 11–30. The inset graphs show the distribution of population growth rates across simulations and years during each period. Panel B illustrates the impact of harvest on the age structure of a population, indexed by the proportion of the adult population composed of animals aged 1–2 and animals aged 3–16. Lines indicate the median value across simulations and years. The ribbon indicates the 1st and 99th percentile of values

denoted as 98% percentile interval [PI], PI = 1.02, 1.23), with a median geometric mean population growth rate ($\overline{\lambda_{geo}}$) across simulations of 1.12 (98% PI = 1.09, 1.15; i.e., the range in long-term growth rates across simulations). In contrast, across simulations and years 11–30 the distribution of population growth rates declined commensurate with increasing harvest (harvest = 0.1: median λ_t = 0.99 [98% PI = 0.89, 1.11], harvest = 0.2: median λ_t = 0.87 [98% PI = 0.76, 0.98], harvest = 0.3: median λ_t = 0.75 [98% PI = 0.61, 1.00]), as did the geometric mean population growth rates (harvest = 0.1: median $\overline{\lambda_{geo}}$ = 0.99 [98% PI = 0.97, 1.02], harvest = 0.2: median $\overline{\lambda_{geo}}$ = 0.87 [98% PI = 0.84, 0.89], harvest = 0.3: median $\overline{\lambda_{geo}}$ = 0.75 [98% PI = 0.72, 0.77]). These population growth rates are likely overly optimistic given the positive bias we suspect for yearling survival rates. The increased mortality due to harvest had a modest impact on the age structure of the population. Results from vital rate estimates suggested that pregnancy
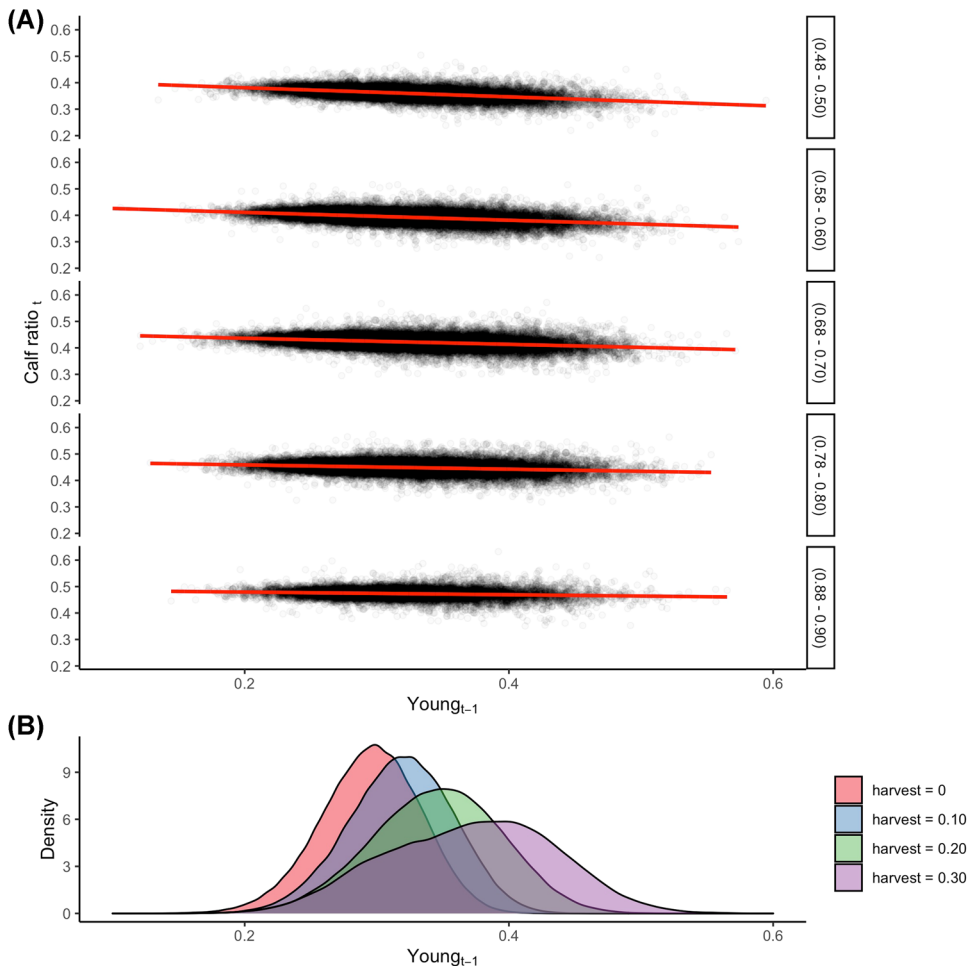

FIGURE 5 The influence of harvest on age structure and reproductive productivity (scenario 1) for simulated elk population trajectories based on estimated pregnancy (data from 2005–2020) and survival rates (data from 2003–2019) from elk in Montana, USA. Panel A illustrates the impact of shifting the age structure towards younger animals in year $t − 1$ (Young$_{t−1}$) on the production of female calves at the beginning of year t (female calves born per adult female) at a series of approximately constant value of mean pregnancy of animals aged 1–2 (e.g., 0.48–0.50, …, 0.88–0.90). Black dots represent individual simulations, and the red line represents a *post hoc*, descriptive linear regression showing the expected relationship. Panel B illustrates the distribution of age structure values at a variety of harvest rates

rates were lower only for animals ages 1–2, and we used this age group as an index for the structure of the population. Across simulations and years, the proportion of the adult female population (ages 1–21) that was composed of young animals (ages 1–2; Young_t) during the first 10 years had a median value of 0.30 (98% PI = 0.20, 0.38), compared to the proportion composed of older animals (ages 3–16; median = 0.69 [98% PI = 0.61, 0.78]). Values of Young_t across simulations and years increased with harvest (harvest = 0.1: median Young_t = 0.32 [98% PI = 0.22, 0.41]), harvest = 0.2: median Young_t = 0.35 [98% PI = 0.23, 0.46]), harvest = 0.3: median Young_t = 0.38 [98% PI = 0.10, 0.63]), although the multiple layers of stochasticity in the simulations resulted in distributions of Young_t that overlapped across harvest rates.

This shift in the age structure towards younger animals had a modest impact on population-level vital rates related to reproduction (Figure 5). The production of female calves at the start of the biological year was a function of the stochastic, age-specific pregnancy rates and the age structure in the prior year when animals became pregnant (i.e., Young_{t-1}). *Post hoc*, we wanted to parse the relative influences of the age-structure and pregnancy rates. Therefore, we binned the average pregnancy rates of 1–2-year-olds and then examined the relationship between the production of female calves at the start of the biological year and the proportion of the population composed of these young animals in year $t - 1$ (i.e., held pregnancy rates for these young animals constant). We found that the influence of age structure on the production of female calves declined as mean pregnancy rates increased (i.e., more closely resembled the pregnancy rates of older animals). *Post hoc*, descriptive linear regressions of female calf production on age structure suggested that when mean pregnancy rates of 1–2-year-olds was low (0.48–0.50), increasing Young_{t-1} over its range was associated with a decline in Calf Ratio$_t$ (defined in Methods) from 0.39 to 0.32. As mean pregnancy values for 1–2-year-olds increased to between 0.88 and 0.98, this ratio declined from 0.48 to 0.46. Later in the biological year, the recruitment of female calves at the end of year t was the product of the size of the female calf cohort and calf survival through the year. To parse the relative influence of age structure on the resulting Recruitment ratio$_t$ (defined in Methods), we similarly binned calf survival values and examined the relationship between the age structure, calf survival, 2 binned values of mean pregnancy rates (0.48–0.50 and 0.88–0.98) and the recruitment ratio of female calves at the end of year t (Recruitment ratio$_t$; Figure 6). We found that the influence of age structure on recruitment was trivial when mean pregnancy rates of 1–2-year-olds were high (0.88–0.90). Again, using *post hoc* descriptive regressions, we found that at calf survival values from 0.48 to 0.50, increasing Young_{t-1} over its range had no effect on Recruitment ratio$_t$. In contrast, we found that when mean pregnancy rates were lower (0.48–0.50) and at calf survival values from 0.48 to 0.50, increasing Young_t over its range was associated with a decline in Recruitment ratio$_t$ from 0.20 to 0.16.

We used the second scenario to understand how combinations of vital rates affected population growth rates of small populations with marginal performance (indexed by population growth rates, scenario 2). Results indicated that the demographic performance of a population with poor mean calf survival (0.25) and modestly diminished productivity due to a shifted age structure could be increased by combinations of reduced harvest and improved calf survival (Figure 7). Decreasing the harvest rate to 0 (Figure 7A) at the same mean value of calf survival of 0.25 resulted in population trajectories with marginal demographic performance: across simulations and years population growth rates had a distribution with an overall median of 1.02 (98% PI = 0.93, 1.15), and a distribution of $\overline{\lambda_{\text{geo}}}$ values across simulations with a median of 1.02 (98% PI = 1.00, 1.05). Increasing calf survival in the absence of harvest improved demographic performance such that an overall mean value of calf survival of 0.75 resulted in a distribution of $\overline{\lambda_{\text{geo}}}$ values with a median of 1.20 (98% PI = 1.18, 1.21). At a harvest rate of 0.10 (Figure 7B), mean calf survival values of 0.25 and 0.4 resulted in declining population trajectories in all cases (e.g., S* = 0.4: median $\overline{\lambda_{\text{geo}}}$ = 0.96 [98% PI = 0.94, 0.98]). Mean calf survival of 0.55 had marginal results for population growth (median $\overline{\lambda_{\text{geo}}}$ = 1.01 [98% PI = 0.99, 1.03]), and only mean calf survival values of 0.75 resulted in consistently high population growth rates (median $\overline{\lambda_{\text{geo}}}$ = 1.07 [98% PI = 1.05, 1.09]). At a harvest rate of 0.20, no value of mean calf survival yielded consistently positive population trajectories (e.g., S* = 0.75: median $\overline{\lambda_{\text{geo}}}$ = 0.94 [98% PI = 0.92, 0.96]; Figure 7C).

POPULATION DYNAMICS AND HARVEST

THE JOURNAL OF
WILDLIFE
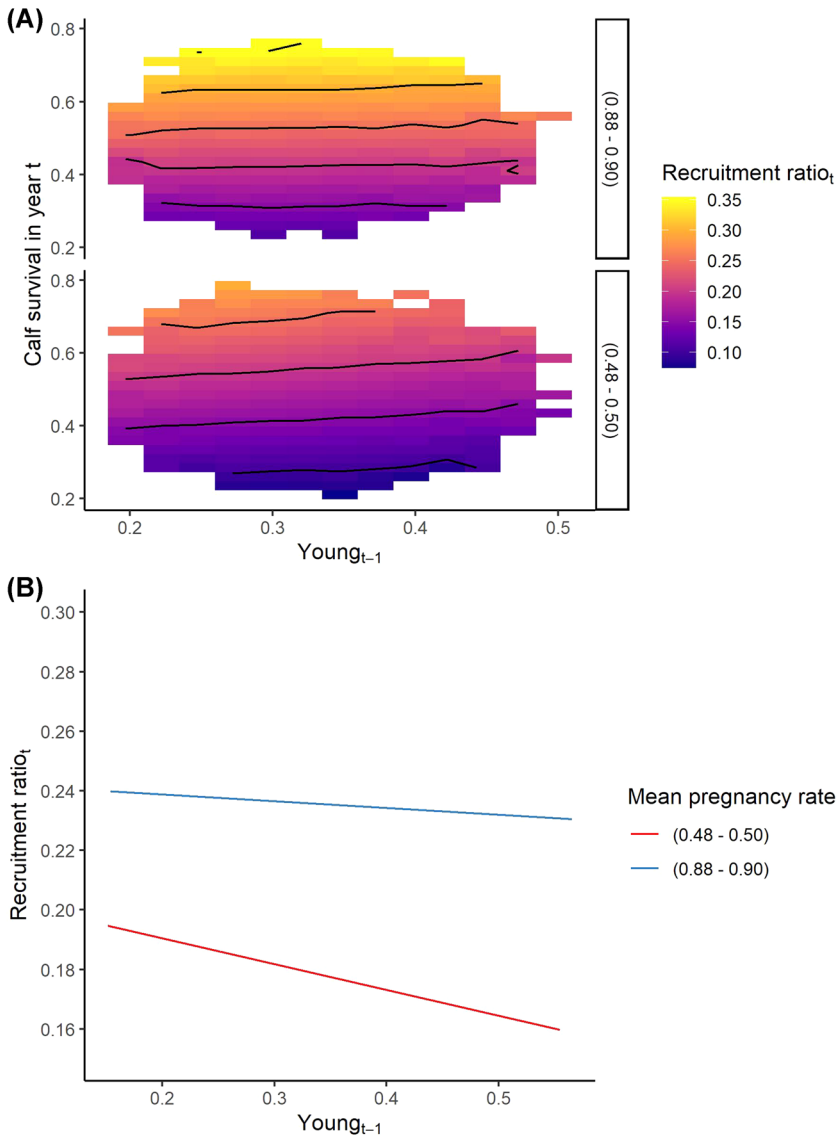MANAGEMENT

THE
WILDLIFE
SOCIETY

17

FIGURE 6 The impact of shifting the age structure on the recruitment of female calves (scenario 1) for simulated elk population trajectories based on estimated pregnancy (data from 2005–2020) and survival rates (data from 2003–2019) from elk in Montana, USA. Panel A illustrates the effects of increasing the proportion of young (aged 1–2) animals in year $t-1$ and calf survival in year t on recruitment (values of which are indicated by tile colors). In our simple model, recruitment was the product of 3 terms: the probabilities of pregnancy for young animals, the proportion of young animals in the population (Young$_{t-1}$), and calf survival. To facilitate interpretation of the results from the multidimensional simulation space, we present values of recruitment across the proportion of young animals and calf survival at 2 approximately constant values of mean pregnancy rates for animals aged 1–2 (0.48–0.50 and 0.88–0.90). Panel B illustrates the effect of increasing the proportion of young animals on recruitment at an approximately fixed value of calf survival (0.48–0.50), and 2 approximately constant values of mean pregnancy rate for animals aged 1–2 in the previous year (0.48–0.50 and 0.88–0.90).
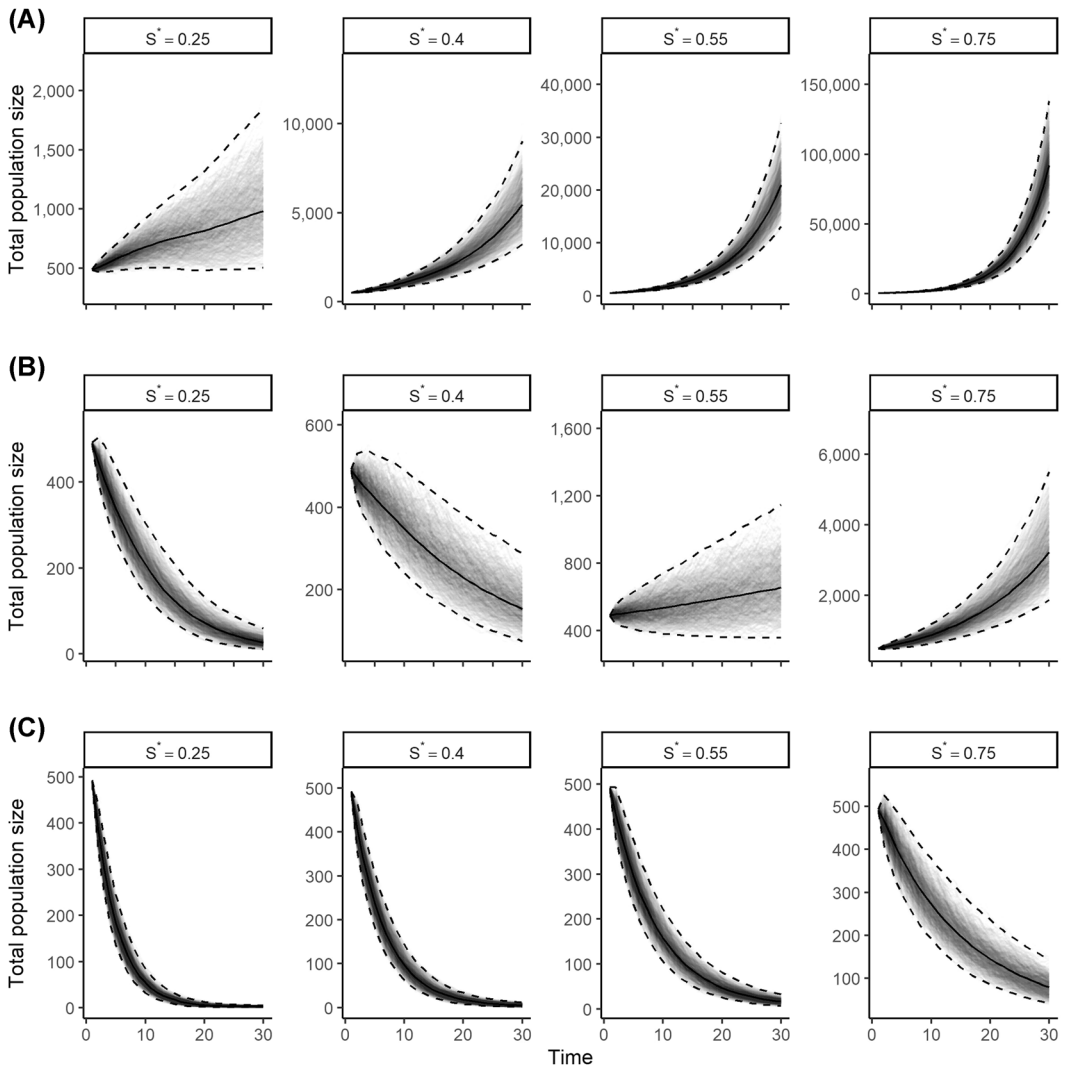
THE WILDLIFE SOCIETY

THE JOURNAL OF WILDLIFE MANAGEMENT

FIGURE 7 Simulation results (scenario 2) for a population initiated with a shifted age structure due to harvest at a variety of values for mean calf survival (S*) and harvest rates: harvest rate = 0 (A), harvest rate = 0.1 (B), and harvest rate = 0.2 (C) for simulated elk population trajectories based on estimated pregnancy (data from 2005–2020) and survival rates (data from 2003–2019) from elk in Montana, USA. Within each plot, the solid line indicates the median value across simulations, and the dashed lines indicate the 1st and 99th percentile of values across time (years)

In our third scenario to understand how combinations of vital rates influence demographic performance for a rapidly growing population (scenario 3), we found that for a population with a moderate harvest (harvest rate = 0.10) and high calf survival (S* = 0.75), increases in harvest rate were required to decrease population growth rates (Figure 8A). For comparison, a consistent harvest rate of 0.10 from years 1–30 resulted in population growth rates across simulations and years with a median value of 1.07 (98% PI = 0.95, 1.18), and distribution of $\overline{\lambda_{geo}}$ values with a median of 1.07 (98% PI = 1.03, 1.10). Increasing the harvest rate to 0.20 from years 11–20 resulted in diminished population growth rates with a median across simulations and years of 0.94 (98% PI = 0.83, 1.04), and a distribution of $\overline{\lambda_{geo}}$ values with a median of 0.94 (98% PI = 0.90, 0.97), distributions that further decreased at a higher harvest
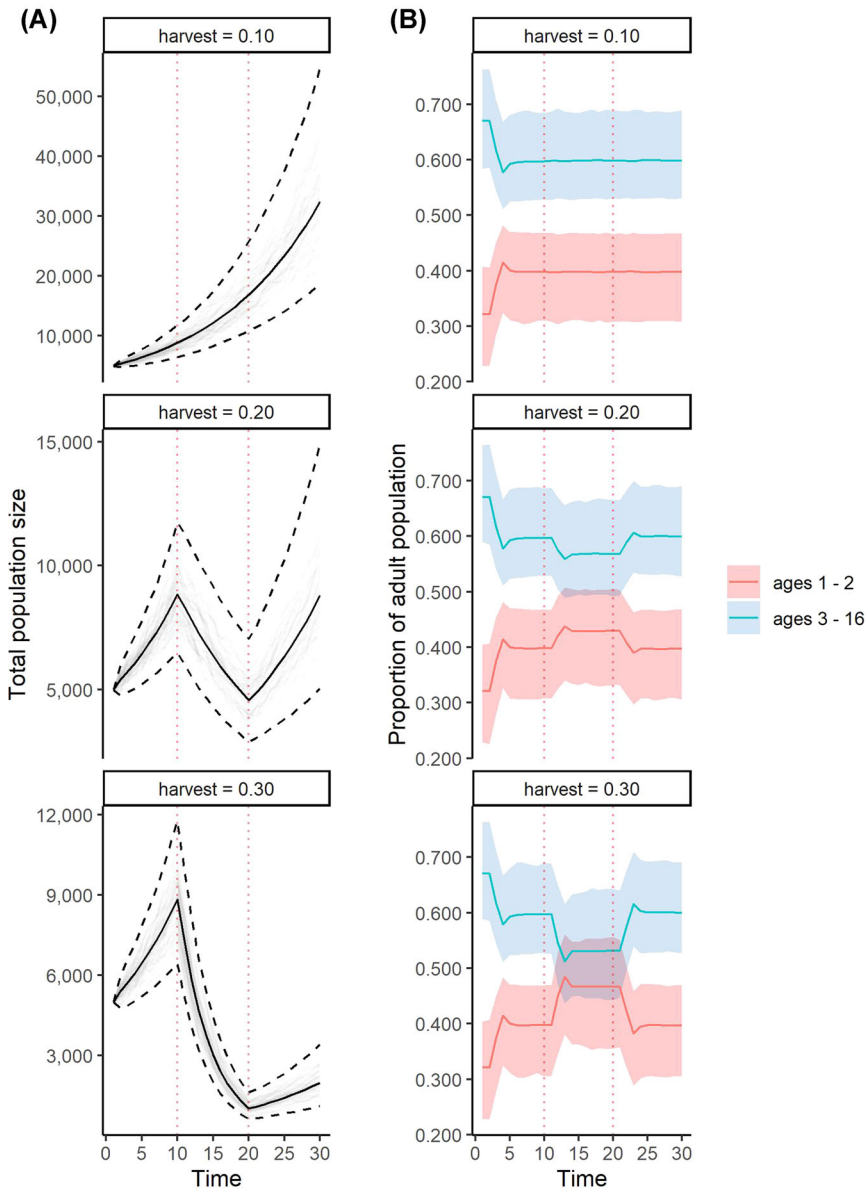
POPULATION DYNAMICS AND HARVEST

THE JOURNAL OF
WILDLIFE
MANAGEMENT

THE
WILDLIFE
SOCIETY

19

FIGURE 8 Simulation results (scenario 3) for population trajectories from a productive population (mean calf survival, S* = 0.75) for simulated elk population trajectories based on estimated pregnancy (data from 2005–2020) and survival rates (data from 2003–2019) from elk in Montana, USA. Panel A illustrates simulated population trajectories at a variety of harvest rates from year 11 to year 20 (harvest rates were fixed at 0.1 from years 1–10 and years 21–30). The solid line indicates the median across simulations, and the dashed lines indicate the 1st and 99th percentile of values. Panel B illustrates the age structure of the population through time, with the proportion of the adults in the population composed of animals aged 1–2 and aged 3–16. The solid line indicates the median across simulations, and the ribbon the 1st and 99th percentile of values. Vertical dotted lines indicate a change in harvest rate at year 10 and year 20

rate of 0.30 (distribution across simulations and years: median λ_t = 0.81 [98% PI = 0.71, 0.91], median $\overline{\lambda_{geo}}$ = 0.81 [98% PI = 0.78, 0.84]). In each case of higher harvest, reducing the harvest rate back to 0.10 beginning in year 21 yielded distributions of population growth rates indistinguishable from the initial period (years 1–10; i.e., distribution across simulations and years: median λ_t = 1.07 [98% PI = 0.95, 1.19], median $\overline{\lambda_{geo}}$ = 1.07 [98% PI = 1.03, 1.10]). The age structure of the population responded to increased harvest rates in years 11–20. Following an approximately 4-year unstable period (years 11–14), the distribution of the proportion of the population composed of individuals aged 1–2 stabilized with a median value of 0.43 (98% PI = 0.33, 0.50) for a harvest rate of 0.20 and 0.47 (98% PI = 0.35, 0.55) for a harvest rate of 0.30 (Figure 8B). Similarly, reducing the harvest rate back to 0.10 in year 21 induced an approximately 4-year period of instability in the age structure before stabilizing with a distribution of the proportion of individuals aged 1–2 with a median of 0.40 (98% PI = 0.31, 0.47).

DISCUSSION

We found evidence for age-related variation in elk pregnancy and survival rates that had population-level implications when simulated harvest shifted the age structure towards younger animals. The effects of shifts in age structure due to harvest on population trajectories were modest in comparison to the effects of annual variation in calf and adult survival. Our results provide minimum thresholds of calf survival and harvest rates to meet population recovery or reduction objectives and suggest the impact on the age structure from harvest may have lagged effects in the population. Additionally, our results provide context for variation in annual population growth rates in the presence of multiple sources of variation in vital rates.

Understanding age-related variation in the vital rates of iteroparous, long-lived vertebrates such as elk has received considerable attention from life-history theory and empirical studies, and our estimates of age-specific probabilities of pregnancy and survival are largely confirmatory (Gaillard et al. 1998, Festa-Bianchet et al. 2017, Lemaître and Gaillard 2017, Bender and Piasecke 2019). Young animals frequently improve reproductive performance with age because of a combination of increased experience with successive reproductive events and the continued somatic investment after age at first reproduction, a pattern consistent with increasing pregnancy rates with age for young elk documented here (Forslund and Pärt 1995, Gaillard et al. 1998, Blas et al. 2009). Similarly, the decline in pregnancy rates for older animals estimated here is consistent with senescence-related processes diminishing the ability to meet and recover from the demands of annual reproduction (Lemaître and Gaillard 2017, Bender and Piasecke 2019). In contrast, survival is expected to decrease with age from the age at first reproduction as residual reproductive value declines with age and a trade-off between survival and reproduction reduces the energetic reserves dedicated to somatic maintenance each year (Kirkwood and Rose 1991, Nussey et al. 2013). Finally, our finding of much higher process variation in pregnancy rates compared to survival rates is consistent with the latter rate being demographically buffered against substantial process variation (Gaillard et al. 1998); however, we acknowledge that our modeling approach based on splines could not formally assess evidence for predictions about age-related variation in vital rates. Future work using these same data could rigorously assess these hypotheses in a model-selection framework using a set of *a priori* functional forms, although there are technical challenges to model selection in mixed-effects models (i.e., those incorporating fixed and random effects; Harrison et al. 2018).

In addition to the well-established importance of variation in adult survival and recruitment (predominately calf survival) on asymptotic population growth rates of elk (Gaillard et al. 1998, Raithel et al. 2007, Harris et al. 2008, Eacker et al. 2016), variation in the age structure due to harvest and simple stochasticity combined with age-related variation in pregnancy rates can play a modest role in shaping population trajectories (Gerber and Kendall 2016). Although our work was specific to the female component of the population, the assumption of an equal sex ratio at birth combined with our results broadly indicate that recruitment ratios of all calves (female and male) can vary up to 0.08 calves recruited per female because of variation in the age structure alone. We suggest that these results

are most likely conservative (i.e., an underestimate of the influence of age structure on population dynamics) for 3 reasons. First, we lacked any empirical information on age-based bias in harvest and assumed animals were harvested in proportion to their representation in the population. If there is any bias in harvest away from younger animals due to either hunter selection or animal behavior (Wright et al. 2006), the impact of harvest on age structure would be more pronounced with an exaggerated proportion of the population composed of younger animals. Second, our results were based on age-related variation in pregnancy rates alone. But a relationship between offspring survival and maternal age has been demonstrated in a variety of species, thought to be related to maternal experience or body condition (Ozoga and Verme 1986, Côté and Festa-Bianchet 2001, Proffitt et al. 2010, Severud et al. 2019, Dion et al. 2020). If elk calves born to younger mothers have lower annual survival rates, then the impact of variation in the age structure would be amplified. Third, our model specification treated harvest mortality as essentially instantaneously removed (i.e., non-harvest mortality acting on the portion of the population removed immediately after harvest rather than harvest and non-harvest mortality acting simultaneously). This is a substantial assumption in our model, and future work is required to better understand how seasonal survival integrates with harvest; given this assumption, we would expect our results to suffer from a positive bias in population projections.

The simulation space that we used to understand how varying vital rates and harvest can be used to achieve management goals of recovery or reduction was modest, yet it is a step forward for informed management of 2 realistic types of populations because of our use of a more complicated age structure, stochastic vital rates, and the direct incorporation of a harvest model (DeCesare et al. 2012). For a recovering population with a low mean value of calf survival (0.25), our results suggest that the population cannot sustain any additional adult mortality due to harvest. Such low values of offspring survival have been reported in elk calves and juveniles of similar species owing to combinations of disease, predation, and environmental effects (Festa-Bianchet 1988, Myers et al. 1998, Portier et al. 1998, Douglas 2001, Zager et al. 2005, Raithel et al. 2007). To the extent that these factors can be manipulated through management to increase in calf survival, harvest can co-exist with a recovering population; however, if the limiting factors of calf survival cannot be controlled by management, eliminating harvest may be the sole remaining option for population recovery. A limitation of our simulation space for such populations was our assumption that 2% of the specified harvest was composed of calves each year. This may be unrealistic if a very large proportion of the population is composed of calves in any given year (under-specifying the likely harvest of calves), and a more rigorous treatment of this component of our harvest model could expand on this point to assess the impact of episodic high calf harvest on population trajectories.

Alternatively, we demonstrated a key relationship between calf survival, harvest rates, and population growth rates that has management implications for large, growing populations that have a management goal for reduction. For populations with higher mean calf survival (0.55 and 0.75), harvest rates of 0.10 were insufficient to abate or reverse population growth; only at high harvest rates of 0.20 were population growth rates reliably less than 1. This has consequences for the management of populations that are exceeding objectives given that such high harvests are not always achievable (Garrott et al. 1993, Valente et al. 2020). Where harvest rates are disconnected from hunter opportunity (i.e., an increase in licenses fails to translate into an increase in harvest) because of combinations of land ownership patterns, physiography, and hunter pressure, required harvest rates may be practically unattainable, suggesting alternative management strategies such as direct management removals or manipulating reproduction via contraception would be required to limit or reduce population growth (McShea et al. 1997, Brown et al. 2000, Merrill et al. 2003, Nugent and Choquenot 2004, Bradford and Hobbs 2008). Compounding this problem is the structure of our simple mortality model where harvest was additional to other sources of mortality; to the extent that any of the additional harvest is compensatory, even higher harvest rates would be required to achieve the same result. Moreover, our assumption of simple additional harvest mortality overlooked a potentially substantial source of mortality on hunted populations; where legally reported harvests underestimate the impact of hunting because of unreported wounding loss (Slabach et al. 2018), harvest mortality may be a super-additive process.

Our results demonstrate that the effects of varying harvest can have a temporally lagged impact on the age structure of the population. These effects are likely quite modest when compared to the importance of variation in calf and adult survival for population growth rates, and our results show them to be insignificant when the pregnancy rates of young animals more closely resemble those of older animals. We speculate that these effects could become important when changes in harvest rates are due to a broader concern over diminished reproduction or survival of a population in general. For example, when a population is below population objective or social carrying capacity and a decline in reproduction or adult survival prompts regulation changes to reduce harvest, our results suggest that it may take several years for the age structure of the population to recover. If the decline in reproduction affects younger animals, overall recruitment could be depressed by a higher proportion of younger-aged animals, even if calf survival is constant. We stress that our model was density-independent, given our focus on small, recovering populations or large, rapidly growing populations targeted for reduction, and that the role of density dependence in moderating the influence of a variable age structure on population trajectories is poorly understood. This could be particularly relevant if harvest interacts with density-dependent processes to alter age-specific fecundities, rather than simply changing the probability of survival.

Our approach and results have implications for understanding the dynamics of harvested elk populations. We are aware of no other studies that simultaneously estimated the age-specific probabilities of pregnancy and survival along with their process variances in the same modeling framework. Our results allow future work to use a single, coherent structure of vital rate estimates for population projections. Further, our results strongly indicate that aggregating information from various ages into age classes and across populations (particularly for survival) is justified when data limitations prevent fully population- and age-dependent vital-rate estimation. We suggest that future work that considers relatively few age classes for survival and reproduction can provide reliable inferences assuming that estimates for each age class are well estimated. Adult survival was consistently high until the oldest ages (e.g., 17–21), and the probabilities of pregnancy essentially had 3 groups: young (ages 1–2), prime (ages 3–16), and older animals. Future work that uses those 3 levels of aggregation should have improved ability to evaluate process variation in vital rates among years. We acknowledge that there are 4 limitations of our vital rate estimation methods that future work should try to ameliorate. First, the timing of the capture season limited the amount of time yearlings were collared to a few months late winter and spring months at most, which likely resulted in a positive bias in estimated survival rates. This positive bias in survival rates likely resulted in a positive bias in population growth rates such that our results are optimistic. Moreover, the comparatively small sample size of yearlings monitored necessitated some model-based smoothing of age-related vital rates, the estimation of which was potentially influenced by greater data density for other ages. Future work estimating independent yearling annual survival rates with larger sample sizes is required to further refine estimates. Second, our use of generalized additive models induced a smooth relationship between age and vital rates that was difficult to cross-validate with our data set, and future efforts should be directed towards improving our understanding using independent estimates of age-specific vital rates. Third, working with additive random effects across ages to estimate process variance can be challenging because of the relationship between the logit and probability scale (i.e., the same large change on the logit scale can translate into a large change on the probability scale when the probability is close to 0.5, or a small change when the probability is close to 0 or 1). More work is required to be able to assess the evidence for age-specific process variances using a less-confining additive structure, an effort with potentially significant implications for management if some age classes have much higher process variances than others (Gaillard et al. 1998, Proffitt et al. 2014, Festa-Bianchet et al. 2017). Finally, our process variances for adult survival and pregnancy rates conflated variation across both space and time, a necessary simplification given the unbalanced structure of the survival and pregnancy data sets. This likely resulted in an over-estimate of the variation in adult vital rates for any single population, and our results, therefore, over-estimate the variation in population growth rates. More work is required to estimate the within-population process variances of age-specific adult vital rates. Where inference on single populations is required and our estimate of process variance(s) is likely an overestimate, a

practical step for future work is to treat our estimates as a maximum and to discount that value in accordance with expert opinion or the results of small, local pilot studies.

MANAGEMENT IMPLICATIONS

Our results demonstrate that the impact of harvest on the age structure of elk populations may have modest effects on population dynamics, above and beyond the direct effects of harvest on survival. To provide a realistic assessment of how variation in key vital rates, age structure, and harvest integrate to shape population trajectories, and to understand how combinations of manipulating calf survival and adult harvest can be used to meet elk population management objectives, wildlife managers may use our estimated vital rates, process variances, and stochastic population models to inform management recommendations. Our results provide general guidelines for combinations of calf survival and adult harvest to achieve population recovery or reduction objectives. In general, our work suggests that large, growing populations of elk may require substantial harvest rates (0.1–0.2, depending on mean calf survival) to arrest population growth rates but that small populations characterized by low calf survival are unable to sustain any additional mortality due to harvest.

CONFLICT OF INTEREST
The authors declare that there are no conflict of interest.

ETHICS STATEMENT
All elk capture and handling followed Montana Fish, Wildlife and Parks approved Cervidae handling procedures (Montana Fish, Wildlife and Parks 2018).

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon request.

ORCID
Kelly M. Proffitt http://orcid.org/0000-0001-5528-3309
Jay J. Rotella http://orcid.org/0000-0001-7014-7524

REFERENCES
Allen, C. R., G. S. Cumming, A. S. Garmestani, P. D. Taylor, and B. H. Walker. 2011. Managing for resilience. Wildlife Biology 17:337–349.
Apollonio, M., V. V. Belkin, J. Borkowski, O. I. Borodin, T. Borowik, F. Cagnacci, A. A. Danilkin, P. I. Danilov, A. Faybich, F. Ferretti, et al. 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. Mammal Research 62:209–217.
Barlow, N. D., J. M. Kean, and C. J. Briggs. 1997. Modelling the relative efficacy of culling and sterilisation for controlling populations. Wildlife Research 24:129–141.

Bender, L. C., and J. R. Piasecke. 2019. Reproductive senescence in free-ranging North American elk *Cervus elaphus* Cervidae. Mammalia 83:593–600.

Blas, J., F. Sergio, and F. Hiraldo. 2009. Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. Ecography 32:647–657.

Bleier, N., R. Lehoczki, D. Újváry, L. Szemethy, and S. Csányi. 2012. Relationships between wild ungulates density and crop damage in Hungary. Acta Theriologica 57:351–359.

Bonenfant, C., J. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. Advances in Ecological Research 41: 313–357.

Bowyer, R., V. Bleich, K. Stewart, J. Whiting, and K. Monteith. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. California Fish and Game 100:550–572.

Bowyer, R. T., K. M. Stewart, V. C. Bleich, J. C. Whiting, K. L. Monteith, M. E. Blum, and T. N. LaSharr. 2020. Metrics of harvest for ungulate populations: misconceptions, lurking variables, and prudent management. Alces: A Journal Devoted to the Biology and Management of Moose 56:15–38.

Bradford, J. B., and N. T. Hobbs. 2008. Regulating overabundant ungulate populations: an example for elk in Rocky Mountain National Park, Colorado. Journal of Environmental Management 86:520–528.

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, et al. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Brown, T. L., D. J. Decker, S. J. Riley, J. W. Enck, T. B. Lauber, P. D. Curtis, and G. F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin 28:797–807.

Brussard, P. F., J. M. Reed, and C. R. Tracy. 1998. Ecosystem management: what is it really? Landscape and Urban Planning 40:9–20.

Bubenik, A. B. 1982. Physiology. Pages 125–179 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.

Burnham, K. P. 2012. Variance components and random effects models in MARK. Program MARK: a gentle introduction. http://www.phidot.org/software/mark/docs/book/

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. Journal of Applied Statistics 29:245–264.

Carey, M. P., B. L. Sanderson, K. A. Barnas, and J. D. Olden. 2012. Native invaders—challenges for science, management, policy, and society. Frontiers in Ecology and the Environment 10:373–381.

Caswell, H. 2013. Matrix population models. Volume 1. Sinauer, Sunderland, Massachusetts, USA.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346: 1517–1519.

Christianson, D., and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. PLOS ONE 9:e102330.

Côté, S. D., and M. Festa-Bianchet. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62:173–181.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Cotterill, G. G., P. C. Cross, E. K. Cole, R. K. Fuda, J. D. Rogerson, B. M. Scurlock, and J. T. du Toit. 2018. Winter feeding of elk in the Greater Yellowstone Ecosystem and its effects on disease dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170093.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292: 1528–1531.

Coulson, T., F. Guinness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. Ecology 85:411–422.

Crainiceanu, C., D. Ruppert, and M. P. Wand. 2005. Bayesian analysis for penalized spline regression using WinBUGS. Journal of Statistical Software 14(14):1–24.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4:437–445.

DeCesare, N. J., M. Hebblewhite, M. Bradley, K. G. Smith, D. Hervieux, and L. Neufeld. 2012. Estimating ungulate recruitment and growth rates using age ratios. Journal of Wildlife Management 76:144–153.

Denwood, M. J. 2016. runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. Journal of Statistical Software 71:1–25.

Dion, J. R., J. M. Haus, J. E. Rogerson, and J. L. Bowman. 2020. White-tailed deer neonate survival in the absence of predators. Ecosphere 11:e03122.

Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 297–305.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system. Journal of Wildlife Management 80:1345–1359.

Eberhardt, L. E., L. L. Eberhardt, B. L. Tiller, and L. L. Cadwell. 1996. Growth of an isolated elk population. Journal of Wildlife Management 60:369–373.

Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). Journal of Zoology 214:653–661.

Festa-Bianchet, M., M. Douhard, J.-M. Gaillard, and F. Pelletier. 2017. Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy 98:612–620.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypotheses and tests. Trends in Ecology & Evolution 10: 374–378.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Garrott, R. A., P. J. White, and C. A. V. White. 1993. Overabundance: an issue for conservation biologists? Conservation Biology 946–949.

Gerber, B. D., and W. L. Kendall. 2016. Considering transient population dynamics in the conservation of slow life-history species: an application to the sandhill crane. Biological Conservation 200:228–239.

Glaser, S. M., M. J. Fogarty, H. Liu, I. Altman, C.-H. Hsieh, L. Kaufman, A. D. MacCall, A. A. Rosenberg, H. Ye, and G. Sugihara. 2014. Complex dynamics may limit prediction in marine fisheries. Fish and Fisheries 15:616–633.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.

Harris, N. C., M. J. Kauffman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management 72:1143–1151.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794.

Hastings, A., K. C. Abbott, K. Cuddington, T. Francis, G. Gellner, Y.-C. Lai, A. Morozov, S. Petrovskii, K. Scranton, and M. L. Zeeman. 2018. Transient phenomena in ecology. Science 361(6406):aat6412.

Hebblewhite, M., D. R. Eacker, S. Eggeman, H. Bohm, and E. H. Merrill. 2018. Density-independent predation affects migrants and residents equally in a declining partially migratory elk population. Oikos 127:1304–1318.

Hegel, T. M., C. C. Gates, and D. Eslinger. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222–235.

Heppell, S. S., L. B. Crowder, and D. T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications 6:556–565.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

Keiss, R. E. 1969. Comparison of eruption-wear patterns and cementum annuli as age criteria in elk. Journal of Wildlife Management 33:175–180.

Kirkwood, T. B., and M. R. Rose. 1991. Evolution of senescence: late survival sacrificed for reproduction. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 332:15–24.

Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. Ecological Modelling 185:283–297.

Koons, D. N., R. F. Rockwell, and L. M. Aubry. 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. Journal of Animal Ecology 83:365–374.

Koons, D. N., R. F. Rockwell, and J. B. Grand. 2006. Population momentum: implications for wildlife management. Journal of Wildlife Management 70:19–26.

Krebs, C. J., R. Boonstra, and S. Boutin. 2018. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. Journal of Animal Ecology 87:87–100.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. Wildlife Biology 5:213–223.

Lemaître, J.-F., and J.-M. Gaillard. 2017. Reproductive senescence: new perspectives in the wild. Biological Reviews 92: 2182–2199.

Lukacs, P. M., M. S. Mitchell, M. Hebblewhite, B. K. Johnson, H. Johnson, M. Kauffman, K. M. Proffitt, P. Zager, J. Brodie, and K. Hersey. 2018. Factors influencing elk recruitment across ecotypes in the Western United States. Journal of Wildlife Management 82:698–710.

McShea, W. J., S. L. Monfort, S. Hakim, J. Kirkpatrick, I. Liu, J. W. Turner, L. Chassy, and L. Munson. 1997. The effect of immunocontraception on the behavior and reproduction of white-tailed deer. Journal of Wildlife Management 61:560–569.

Merrill, J. A., E. G. Cooch, and P. D. Curtis. 2003. Time to reduction: factors influencing management efficacy in sterilizing overabundant white-tailed deer. Journal of Wildlife Management 67:267–279.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

Montana Fish, Wildlife and Parks. 2018. Biomedical protocol for free-ranging Cervidae in Montana: capture, anesthesia, tagging, sampling and necropsy procedures. Montana Fish, Wildlife and Parks, Helena, USA.

Myers, W. L., B. Lyndaker, P. E. Fowler, and W. Moore. 1998. Investigations of calf elk mortalities in southwest Washington. Progress report 1992–1998. Washington Department of Fish and Wildlife, Olympia, USA.

Naiman, R. J. 1988. Animal influences on ecosystem dynamics. BioScience 38:750–752.

Noyes, J. H., R. G. Sasser, B. K. Johnson, L. D. Bryant, and B. Alexander. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. Wildlife Society Bulletin 25:695–698.

Nugent, G., and D. Choquenot. 2004. Comparing cost-effectiveness of commercial harvesting, state-funded culling, and recreational deer hunting in New Zealand. Wildlife Society Bulletin 32:481–492.

Nussey, D. H., H. Froy, J.-F. Lemaitre, J.-M. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Research Reviews 12:214–225.

O'Gara, B. W., and R. G. Dundas. 2002. Distribution: past and present. Pages 67–119 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Ozoga, J. J., and L. J. Verme. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. Journal of Wildlife Management 50:480–486.

Parsons, E. W. R., J. L. Maron, and T. E. Martin. 2013. Elk herbivory alters small mammal assemblages in high-elevation drainages. Journal of Animal Ecology 82:459–467.

Persson, I.-L. 2003. Moose population density and habitat productivity as drivers of ecosystem processes in northern Boreal forests. Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Peterson, M. N., H. P. Hansen, M. J. Peterson, and T. R. Peterson. 2011. How hunting strengthens social awareness of coupled human-natural systems. Wildlife Biology in Practice 6:127–143.

Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (Ovis canadensis). Journal of Zoology 245:271–278.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing 124(125.10):1–10.

PRISM Climate Group. 2012. PRISM climate data. https://prism.oregonstate.edu. Accessed 18 Nov 2021.

Proffitt, K. M., J. A. Cunningham, K. L. Hamlin, and R. A. Garrott. 2014. Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk. Journal of Wildlife Management 78:1383–1393.

Proffitt, K. M., J. J. Rotella, and R. A. Garrott. 2010. Effects of pup age, maternal age, and birth date on pre-weaning survival rates of Weddell seals in Erebus Bay, Antarctica. Oikos 119:1255–1264.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

Roberts, T. W., D. E. Peck, and J. P. Ritten. 2012. Cattle producers' economic incentives for preventing bovine brucellosis under uncertainty. Preventive Veterinary Medicine 107:187–203.

Saether, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Schmidt, J. H., J. A. Walker, M. S. Lindberg, D. S. Johnson, and S. E. Stephens. 2010. A general Bayesian hierarchical model for estimating survival of nests and young. Auk 127:379–386.

Severud, W. J., T. R. Obermoller, G. D. Delgiudice, and J. R. Fieberg. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. Journal of Wildlife Management 83:1131–1142.

Shelton, A. O., J. A. Hutchings, R. S. Waples, D. M. Keith, H. R. Akçakaya, and N. K. Dulvy. 2015. Maternal age effects on Atlantic cod recruitment and implications for future population trajectories. ICES Journal of Marine Science 72:1769–1778.

Simpson, B. D., J. B. Smith, and J. A. Jenks. 2020. Survival and cause-specific mortality of neonate elk in a unique predator environment in the Black Hills of South Dakota and Wyoming, U.S.A. American Midland Naturalist 183:194–209.

Slabach, B. L., J. T. Hast, S. M. Murphy, W. E. Bowling, R. D. Crank, G. Jenkins, K. L. Johannsen, and J. J. Cox. 2018. Survival and cause-specific mortality of elk *Cervus canadensis* in Kentucky, USA. Wildlife Biology 2018:wlb.00459.

Stott, I., S. Townley, and D. J. Hodgson. 2011. A framework for studying transient dynamics of population projection matrix models. Ecology Letters 14:959–970.

Tenhumberg, B., A. J. Tyre, and R. Rebarber. 2009. Model complexity affects transient population dynamics following a dispersal event: a case study with pea aphids. Ecology 90:1878–1890.

Tuljapurkar, S. 1989. An uncertain life: demography in random environments. Theoretical Population Biology 35:227–294.

Valente, A. M., P. Acevedo, A. M. Figueiredo, C. Fonseca, and R. T. Torres. 2020. Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mammal Review 50:353–366.

Walter, W. D., M. J. Lavelle, J. W. Fischer, T. L. Johnson, S. E. Hygnstrom, and K. C. VerCauteren. 2011. Management of damage by elk (*Cervus elaphus*) in North America: a review. Wildlife Research 37:630–646.

White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74:355–369.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 *in* L. Boitani and T. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

Wittmer, H. U., R. N. M. Ahrens, and B. N. McLellan. 2010. Viability of mountain caribou in British Columbia, Canada: effects of habitat change and population density. Biological Conservation 143:86–93.

Wright, G. J., R. O. Peterson, D. W. Smith, and T. O. Lemke. 2006. Selection of Northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management 70:1070–1078.

Yearsley, J. M. 2004. Transient population dynamics and short-term sensitivity analysis of matrix population models. Ecological Modelling 177:245–258.

Zager, P., C. White, and M. W. Gratson. 2005. Elk ecology. Study IV. Factors influencing elk calf recruitment. Job numbers 1–3. Pregnancy rates and condition of cow elk. Calf mortality causes and rates. Predation effects on elk calf recruitment. Idaho Department of Fish and Game Federal Aid in Wildlife Restoration Job Progress Report W-160-R-29, Boise, USA.

Associate Editor: Andrew Norton.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.