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Aligning population models with data: Adaptive management for big game harvests

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ABSTRACT

Models of population dynamics are a central piece for harvest management, allowing managers to evaluate alternative strategies and to identify uncertainty. Here we present a density-dependent population dynamics model that can be used in conjunction with adaptive management to optimize big game management, designed to use data commonly collected by state and provincial wildlife agencies. We review a case study for white-tailed deer (*Odocoileus virginianus*) in North Dakota, USA, where we evaluate how harvest composition and monitoring frequency affect the maximum sustainable yield (MSY). Data were obtained from winter aerial surveys and hunter questionnaires over six years between 2009 and 2019. Harvest composition moderately skewed towards antlered individuals (37.5% antlerless deer and 62.5% antlered deer, i.e., antlerless:antlered harvest ratio = 0.6) resulted in a harvest rate of 0.2, which translates to a long-term harvest that is more than double that obtained if the harvest composition matched the population composition. However, given environmental uncertainty, we recommend that managers adopt a harvest strategy that is at least 10−15% lower than the maximum sustainable yield to buffer against environmental variability. Despite the fact that contrasting monitoring schemes resulted in similar optimal harvest rates, we illustrated how adopting an adaptive harvest strategy (i.e., where harvests change with population size) affords lower risks of overexploitation than a static strategy in which populations are assessed only occasionally. An adaptive harvest strategy features resilience allowing harvested populations to return to equilibrium even after substantial perturbation events.

1. Introduction

Uncertainty associated with decision making is a recurring challenge for wildlife agencies and managers (Sit and Taylor 1998). Reducing uncertainty over time can be achieved using adaptive management, which allows resource managers to simultaneously manage and learn about natural resources through an iterative process (Walters 1986). Despite the potential

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advantages of adaptive management and its applications in fisheries, forestry, and waterfowl management (Walters 1986; Holling 1978; Nichols et al. 1995, 2007; Williams 2011), this approach seldom has been applied to big game populations (Varley and Boyce 2006). Population models are a crucial piece of the adaptive management process because they help to identify alternative management strategies and reduce structural uncertainty. Uncertainty typically is associated with limited ecological understanding of population responses to alternative management actions (Williams 2011). Another essential step in active adaptive management is monitoring the population of interest, which brings key information for adjusting policies as part of the interactive learning process (White 2001; Williams 2011).

Although ecological processes that generate population dynamics typically include stage-class demographic rates, density dependence, and environmental or demographic stochasticity, there have been few attempts to combine them into a single model (Coulson et al., 2008). Incorporating age class into population models can be done by adopting a Leslie matrix model (Caswell 2001) but this model does not take into account resource constraints (i.e., density dependence), and cannot yield harvest optimization (Mendelssohn 1976). Age-specific vital rates are seldom available for each age as required for an age-structured model (Gross 1969; Gross et al., 1973; Conn et al., 2008) although classification of animals into adult males, adult females, and young are more easily obtained (Boyce et al., 2012). Likewise, other deer harvest models exist that require check-station data that are not available in most jurisdictions (Millspaugh et al., 2009). Also, ungulate vital rates are typically nonlinear stage-structured functions of population density (Fowler 1987; Eberhardt 2002; Owen-Smith 2006). Among ungulates, density dependence most strongly affects juvenile survival, then the age at which females first reproduce (i.e., fecundity), and lastly adult survival (Gaillard et al., 1998; Eberhardt 2002). Density dependence in ungulate populations, in many circumstances, can be a more important driver of population dynamics than age-structured variation or climate (Getz and Haight 1989; Coulson et al., 2008).

Here we present a stage-structured model with density dependence that can be used to model big game population management. More specifically, in this case study, we tested the hypothesis that monitoring frequency and harvest composition affect the maximum sustainable yield (MSY) of white-tailed deer (*Odocoileus virginianus*) in North Dakota. We predicted that (1) a higher monitoring frequency (e.g., reassessing populations and harvest strategies annually) would result in a higher MSY than a more sporadic monitoring scheme (e.g., every 5 or 10 years); and that (2) a harvest composition moderately skewed towards antlered individuals (i.e., more bucks than does and fawns in harvest) would result in a higher MSY. We also evaluated population resilience to pulse perturbations to infer optimal harvest strategies for populations under severe winter conditions and demonstrated the advantages of implementing population models in an adaptive harvest framework for big game species.

2. Methods

2.1. Study area

We focused a case study on white-tailed deer populations in northwestern North Dakota, USA. These populations are managed primarily through the allocation of hunting licenses. We used data from the deer hunting unit (DHU) with the most data (DHU 3A1), a unit in the Northwest Coteau, an area characterized by rolling, mixed-grass prairie and numerous glacial pothole wetlands (Seabloom 2011). Terrain in North Dakota is relatively flat and the climate is cool, sub-humid or semi-arid continental interior (Seabloom 2011). Mean annual temperature is 3−6 °C, annual precipitation is 36−51 cm, and average total snowfall is 69−130 cm (Seabloom 2011, National Oceanic and Atmospheric Administration [NOAA], 2018).

In North Dakota, white-tailed deer populations are managed mainly through lottery deer-gun season, which regular deer-gun and landowner-gratis hunters are restricted to one of 38 hunting units. Lottery license types are any-species antlered, any-species antlerless, white-tailed deer antlered, white-tailed deer antlerless, mule deer antlered and mule deer antlerless; DHU 3A1 lottery is for an any-species antlered or antlerless license. White-tailed deer also can be harvested during an archery season, youth deer season, and muzzleloader-gun season, which all combined represent a relatively small portion of the harvest and are not restricted to a hunting unit. For instance, in 2018 it was estimated that 80% of the antlered and 75% of the antlerless white-tailed deer harvest in DHU 3A1 were harvested during the regular deer-gun season by gratis and lottery license holders. For the reasons mentioned above, here we included lottery deer-gun season only.

Deer management in North Dakota currently relies only on relative changes in deer populations, which are translated in adjustments in historical hunting regulations. Population trends (from aerial surveys and hunter questionnaires - see details below) and public opinion are used to inform management goals (e.g., increase, decrease, or maintain the deer population size), which are then used to guide whether the number of licenses and their antlerless:antlered ratio should increase, decrease, or be kept constant from one year to the next. For example, in years that the management goal is to decrease the deer population, the number and the antlerless:antlered ratio of licenses are increased; whereas the opposite strategy is adopted when the management goal is to increase the population size. By convention and state century code, the regular deer-gun season starts at noon the Friday before Veterans Day, November 11, and continues for 16 ½ days. This hunting season occurs during the peak of the rut (Michel et al., 2017).

2.2. Deer population data

Population estimates (minimum counts) of white-tailed deer in the hunting unit were obtained from winter aerial surveys. Standardized surveys were conducted in a monitoring block (3263 km^2) centrally located that occupies 33% of DHU 3A1. The monitoring block has similar habitats to the rest of the area and is assumed to be a representative sample of DHU 3A1. Surveys were conducted from 2009 to 2011 and from 2017 to 2019 between 1 January and 15 March of each year when conditions provided continuous snow cover; conditions were not met during the winters of 2012−2016. Surveys consisted of intense searches by a pilot and one observer (100% coverage census per survey unit) from fixed-wing light aircraft at altitudes 76−107 m and at flight speeds below 130 kph. Previous sightability trials in this region revealed that up to 87% of the deer are typically counted by aerial observers (Schaffer 2013; Sternhagen 2015). Therefore, we assumed sightability bias to be negligible (similar to previous studies in the region; Christie et al., 2015; Nagy-Reis et al., 2019). Deer density was estimated by dividing deer minimum count by survey unit area. We then estimated deer population by extrapolating the survey-unit density to the entire hunting unit (9790 km^2).

Population composition (proportion of fawns, does, and bucks) was estimated using hunter observation data from questionnaires. Based on comparison tests conducted in North Dakota (Stillings et al., 2016), hunter observation data are assumed to provide a good approximation of herd composition.

2.3. Harvest data

Total estimated harvest and harvest composition for the deer-gun season in DHU 3A1 were obtained from hunter questionnaires. Deer-gun season in DHU 3A1 is estimated to represent about 80% of the antlered and 75% of the antlerless white-tailed deer harvest (data from 2018; unpublished data, W.F. Jensen). Each year questionnaires were sent to a stratified random sample of up to 150 individual hunters, of each license type in each DHU, who purchased a current-year deer hunting license. In 2018 a total of 18,470 and 8144 questionnaires were delivered to regular-gun and gratis license holders statewide, respectively (Stillings et al., 2019). The long-term average questionnaire response rate was 60%, which along with the deployed sampling effort, is likely to result in precise harvest estimates. Periodically, all hunters in selected DHUs have been surveyed by phone to check for non-response bias.

2.4. Population model

Our model was adapted from a generalized density-dependent matrix population model (Eqs. (1) and (2); Xu and Boyce 2010) originally developed for moose (*Alces alces*), and was designed to use data typically available to wildlife agencies. Using this model we can estimate the population post-harvest; the model includes 1) stage and sex population structure, 2) estimation of carrying capacity (K) and population composition at (K, 3) stage-structured density dependence, following the general patterns documented in ungulate populations (Eberhardt 2002; Bergman et al., 2015), and 4) environmental stochasticity. We considered three sex-stage classes: 1) young (y; female and male fawns, y_f, y_m, respectively), 2) adult female (f; does), and 3) adult male (m; bucks) (Eq. (2)).

The model structure is that of a nonlinear matrix population model with harvesting,

$$N_{t+1} = A_t N_t - H_t \tag{1}$$

where N_t is a vector containing the number of animals in each stage and sex class at time t, and H_t. is a vector of harvested individuals. This may be written in full detail as

$$\begin{pmatrix} n_{y,t+1} \\ n_{f,t+1} \\ n_{m,t+1} \end{pmatrix} = \begin{pmatrix} 0 & R_t & 0 \\ \delta S_{yf,t} & S_f & 0 \\ (1-\delta)S_{ym,t} & 0 & S_m \end{pmatrix} \begin{pmatrix} n_{y,t} \\ n_{f,t} \\ n_{m,t} \end{pmatrix} - \begin{pmatrix} H_{y,t} \\ H_{f,t} \\ H_{m,t} \end{pmatrix} \tag{2}$$

where R_t is the density-dependent recruitment rate at time t, δ is the proportion of female among young at recruitment, H is harvest mortality (y = young, f = female, and m = male), and S is annual survival, either of adult females or adult males (S_f, S_m) or the density-dependent survival from fawn to female or male adult (S_{yf} and S_{ym}, respectively). The subscript t implies that the value of the variable or parameter varies over time (i.e., years).

We assumed recruitment of young (R) and survival of young females and males (S_{yf} and S_{ym}) to be functions of density (Clutton-Brock et al., 2002; Xu and Boyce 2010, Eqs. (3) and (4)), because density dependence most strongly affects juvenile survival and adult fecundity (Gaillard et al., 1998; Eberhardt 2002). Here,

$$R_t = \alpha_0 \, exp\left(p \left[1 - \left(\frac{N_t}{K} \right)^{\gamma} \right] \right) \tag{3}$$

$$S_{i,t} = S_y \, exp\left(-\alpha_i \left(\frac{N_t}{K}\right)^\gamma \right), \; i \; = \; yf, \; ym \tag{4}$$

where maximum recruitment, $R^* = \alpha_0 \, exp(p)$, occurs at low population numbers (i.e., $N_t \approx 0$). S_y is the survival probability of young deer at low population densities (assumed to be the same for young females and males). N_t is the total population size (the sum of the vector components of N), K is the carrying capacity, i.e., N where $dN/dt = 0$; γ is the density-dependence exponent in recruitment and survival, and α_i ($i = 0, y_f, y_m$) are coefficients relating to the relative abundance of three stages at carrying capacity (Xu and Boyce 2010).

We parameterized our model using data from DHU 3A1. When necessary, parameters were obtained from literature on studies conducted in North Dakota or adjacent areas. We focused our model fitting on estimating parameters for which estimates in the literature did not exist (Table 1).

Carrying capacity (K) and group composition at carrying capacity (o_{yf} and o_{ym}) were estimated by conditional least squares. We restricted K to be $\geq$ the maximum observed population size during the period for which data were available because it seems unlikely that the observed population was over K given constant harvest pressure in the region. The recruitment coefficient (p) was estimated from the maximum recruitment equation ($R^* = \alpha_0 \, exp(p)$). Coefficients regulating relative abundance of different stages at carrying capacity ($\alpha_0, \alpha_{yf}, \alpha_{ym}$) were calculated from S2–S4 of Xu and Boyce (2010), where full details are available. We fitted models with density-dependence exponents (γ) of 1, 2, and 3, and evaluated model fit by visually comparing model predictions to observed data.

2.5. Harvest optimization and model simulation

We first built a deterministic model to project deer populations in DHU 3A1 and compared model predictions to observed data. We then built a stochastic model and plotted the mean population size and the 5th and 95th percentiles of the one-year ahead predictions, taken from 10,000 model runs, to evaluate model performance. Stochasticity was added to the models using equations S8–S10 of Xu and Boyce (2010), which assume log-normal environmental noise. For each simulation, we generated a random noise vector ε (each component corresponds to the noise affecting each stage and sex class) from a multivariate normal distribution with a mean of 0 and variance-covariance matrix Σ estimated from the error terms during model fitting (Table 1).

We determined the optimal harvest for white-tailed deer by evaluating the yield (i.e., deer harvested) and the population trajectory under a range of harvest rates. We first ran our model assuming harvest composition to be proportional to population composition and evaluated how the frequency that harvest is reassessed affects harvest optimization. Then, we investigated optimal harvest composition by considering a range of antlerless:antlered kill ratios, determining the optimal harvest rate for each given harvest composition considered. Note that we assumed the ratio of fawns:does in the antlerless kills was the same as the ratio in the population, thus assuming no selection against fawns. Although studies have not found

Table 1
White-tailed deer population model parameters. Parameters were either estimated by model fitting (using data from deer hunting unit 3A1, North Dakota, USA) or published estimates from other populations in the Northern Great Plains.

Parameters		Estimated from model fitting	Value from literature
Recruitment rate at low population density = neonate survival × fecundity (litter size) × proportion of R* breeding females			1.19[a,b] (0.65 × 1.9 × 0.96)
Survival probability** of fawns at low population density	S_y		0.95[a,c,d]
Survival probability** of adult females	S_f		0.90[a,c]
Survival probability** of adult males	S_m		0.82[c]
Geometric rate of increase	λ_0	1.28	
Carrying capacity	K	11500[†]	
Number of females per fawn at carrying capacity	o_{yf}	1.95[†]	
Number of males per fawn at carrying capacity	o_{ym}	1.47[†]	
Coefficients regulating relative abundance of different stages at carrying capacity	α_0	0.51[†]	
	α_{yf}[e]	0.75[†]	
	α_{ym}[e]	0.61[†]	
Recruitment coefficient	P	0.84[†]	
Variance-covariance matrix of error vectors	Σ	Σ[†]	
Proportion of female fawns at recruitment	δ		0.46[b]
Density dependence exponent	γ		1–3

*Using density dependence exponent $\gamma = 1$. $\Sigma^† = (0.27, -0.18, 0.04, -0.18, 0.13, -0.05, 0.04, -0.05, 0.25)$.
**Natural survival probabilities (i.e., excluding harvest mortality).
[a] Schaffer 2013, Sternhagen 2015, Moratz 2016.
[b] Jensen unpublished data.
[c] Hewitt 2011, Jensen unpublished data.
[d] Smith et al., 2007.
[e] Calculated from O_{fy} and O_{my}.

evidence of a sex ratio threshold wherein drastic short-term deleterious effects occur in white-tailed deer populations (Ozoga and Verme 1985; White et al., 2001), it is known that highly skewed sex ratios can result in negative effects on ungulate reproduction (Rausch et al., 1974; Keech et al., 2000; Ginsberg and Milner-Gulland 1994). Therefore, we adopted a precautionary approach and discarded any harvest strategies that resulted in buck to doe ratios lower than 1:20 at any time in the simulations.

We then conducted a perturbation analysis to evaluate the rate of return to equilibrium following a pulse perturbation. This was done through the following numerical experiment: first, we fixed all parameters and the harvest rate and let the population converge to equilibrium ($N*$); we then perturbed the stage-specific population values by 10% (without changing the population composition) and observed the trajectory after perturbation, assessing how quickly the population returned to the equilibrium. The population was perturbed at census time (i.e., post-harvest). We recorded the time it took for the population to recover to within 1% of the equilibrium value. Perturbations were done for both a 10% increase in population size and, in a second experiment, with a 10% decrease. We performed a perturbation analysis for the proportional harvest model and another using the optimal harvest composition. All models were built in R software (R Development Core Team, 2014) and all code is available online in Supporting Information.

3. Results

Predictions from our deterministic models provided a reasonable match to observed data (Tab. S1). For the stochastic model, only the model fit using a density dependence exponent (γ) of 1 had a reasonable fit (Tab. S1). Considering model fit and limitations of data, we set $\gamma = 1$ in all subsequent models.

Under a harvest rate model in which harvest composition is assumed to be the same as population composition, the harvest rate that leads to the highest sustainable yield is 0.13 (Fig. 1a). This means that 13% of the white-tailed deer population can be harvested each year under an "any white-tailed deer" type of license, which corresponds to an equilibrium annual yield of 630 deer in the hunting unit 3A1 (Fig. 1). An adaptive harvest strategy in which population size and harvest rates are reassessed either annually (Fig. 1a) or every 5 years (Fig. 1b) leads to a lower risk of overexploitation than using a harvest quota that is updated only once a decade (Fig. 1c).

Of those antlerless:antlered harvest ratios considered, a ratio of 0.6 obtained the highest yield at equilibrium (Table 2). This corresponds to a harvest composition of 37.5% antlerless deer and 62.5% antlered deer. The annual yield for this harvest ratio at equilibrium increases to 1393 deer and the optimal harvest rate increases to 0.2 (Table 2). These results for a harvest ratio of 0.6 are more than double the sustainable harvest size of the model assuming a proportional harvest composition (1393 harvested deer versus 630).

Our perturbation analysis showed that the convergence time to equilibrium increases with harvest (Fig. 2). Following a pulse perturbation of 10% (we considered perturbations both up and down), a population under an optimal harvest rate (0.2 for the antlerless:antlered kill ratio of 0.6, with the harvest amount updated annually) may take over 20 years to recover to within 1% of its equilibrium value (Fig. 2).

4. Discussion

Population models can assist in decision-making processes by identifying optimal strategies under uncertainty, a recurring challenge for wildlife agencies and managers (Sit and Taylor 1998). Here we presented a population model that uses available data and can be incorporated into an adaptive management framework to evaluate alternative hypotheses related to harvest strategies for white-tailed deer (*Odocoileus virginianus*).

Contrary to our first prediction, the optimal harvest rate for white-tailed deer was not affected by how frequently population and harvest strategies were reassessed. However, shorter intervals between assessments decreased the chances of population overexploitation. Due to high costs associated with population monitoring, many game species are currently managed using surveys as sparse as every 10 years (Boyce et al., 2012). Because this approach cannot readily adapt to changes in population size, it might impose higher risks of under harvest, leading to crop depredation problems for farmers and ranchers. In fact, in many American states, deer populations exceed social carrying capacity despite being below or at biological carrying capacity (Krausman et al., 2014). Alternatively, sparse monitoring might lead to overexploitation, which can be seen by considering Fig. 1. Observe that if a harvest rate higher than the optimal is used but the population is frequently monitored and rates are readjusted, the population still reaches a stable equilibrium size, and the only consequence is that there is a slightly reduced annual sustainable harvest. In contrast, if we accidently set the harvest rate higher than its optimal size and do not reassess it frequently as the population changes, the population eventually crashes. A harvest strategy such as this is theoretically acceptable as long as the harvest level is set correctly and the population is stable, but often this is an unrealistic scenario (Sutherland 2001). Alternatively, managers can adopt an adaptive harvest strategy, in which harvest is reassessed more often and regularly adjusted to reflect population changes. Nonetheless, this can be implemented only if changes in population size are regularly monitored and evaluated, which might be difficult due to budget constraints (White 2001) and environmental conditions (e.g., climate and terrain).

Corroborating our second prediction, a harvest composition moderately skewed towards antlered individuals resulted in a higher MSY. Previous findings suggested that males-only harvesting shifts sex ratios resulting in female-dominated populations and white-tailed deer population abundances near the carrying capacity (Jensen 2000). A number of females that
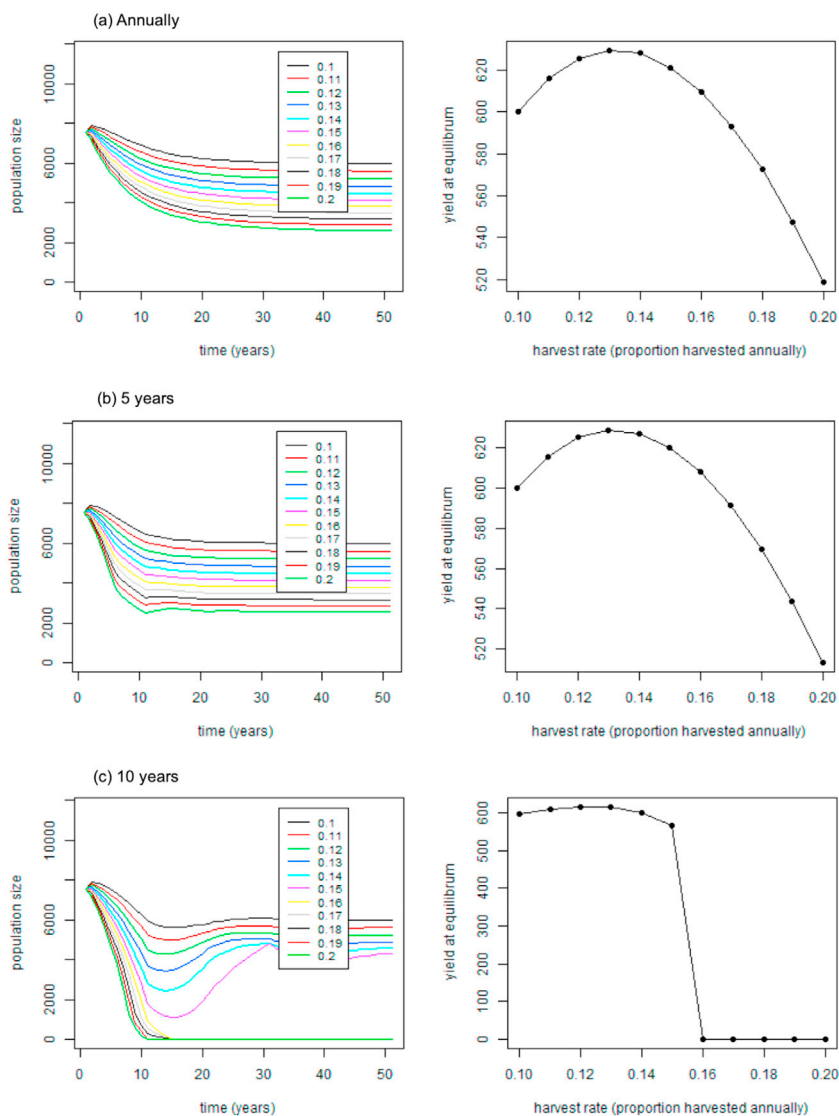
Fig. 1. Simulation of white-tailed deer population size (left) and yield at equilibrium (right) over 50 years under various harvest rates, with varying frequency of population monitoring and subsequent adjustment of the harvest (e.g., in (a), the harvest changes yearly, while in (c), it is only updated every 10 years). Here harvest composition is the same as the population composition. Models parameterized using data from North Dakota, USA (deer hunting unit 3A1).

Table 2
Simulation of white-tailed deer yield at equilibrium in hunting unit 3A1 (North Dakota, USA) under various harvest compositions (antlerless:antlered kill ratios).

Antlerless:Antlered Kill Ratio	Optimal Harvest Rate	Yield at Equilibrium
0.4	0.15	1296
0.6	0.20	1393
0.8	0.25	1324
1.0	0.30	1097

exceeds the carrying capacity might further result in decreases in the MSY of males, which also can decrease harvest revenue (Clutton-Brock et al., 2002). Despite suggestions from a study in the George Reserve in Michigan, USA, that males-only harvesting could increase yield asymptotically with harvest rate (Jensen 2000), here, with data from the Northern Great Plains, we had evidence that there is an optimal antlerless:antlered kill ratio (0.6) and increasing the proportion of males (i.e., antlered) in harvest beyond that in fact decreases the MSY. Similar results were found in a study with black-tailed deer (*Odocoileus hemionus columbianus*), which suggested that female harvest increases male yield (McCullough 2001). The
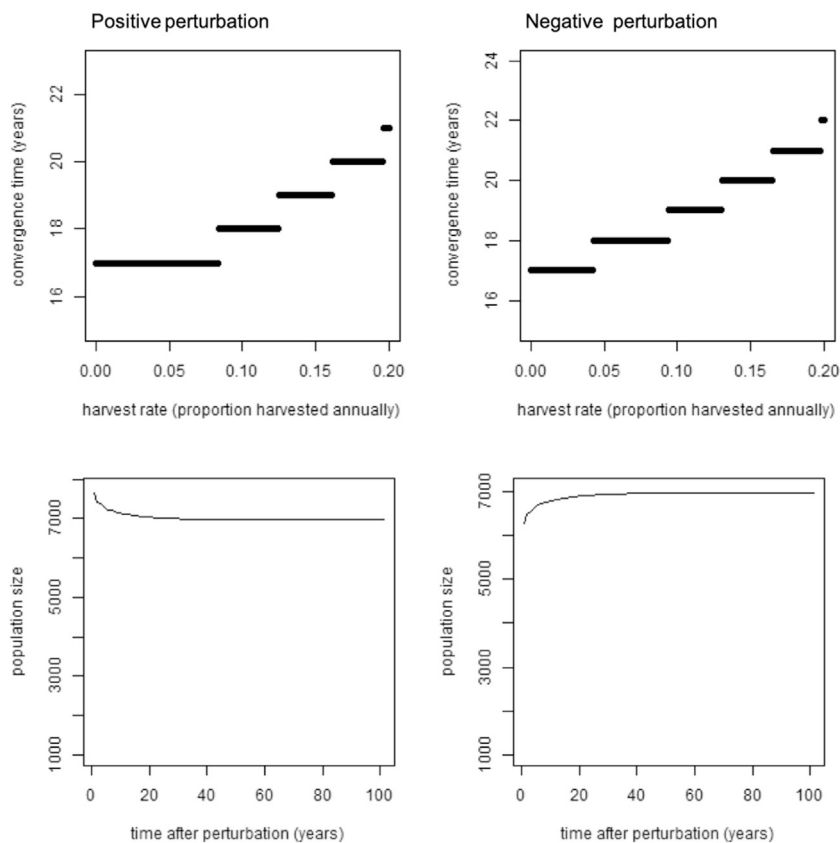
Fig. 2. Perturbation analysis for a white-tailed deer population in North Dakota, USA (deer hunting unit 3A1) under the optimal harvest composition (i.e., antlerless:antlered kill ratio of 0.6) with annual monitoring. Top row: Rate of return to equilibrium (convergence time in years) after a 10% positive perturbation (left) and negative perturbation (right) under various harvest rates. Note that the step-like nature of these results occurs because the convergence time is restricted to discrete time steps. Bottom row: Time series of perturbed population returning to equilibrium. Results for the model with a proportional harvest composition were very similar (Fig. S2, available online in Supporting Information).

observed reduction in the MSY when the antlerless:antlered kill ratio goes beyond 0.6 is likely because a harvest composition highly skewed towards male individuals may drive adaptive responses in ungulates by reducing fitness and female fecundity (see Ginsberg and Milner-Gulland 1994; Proaktor et al., 2007 for a comprehensive review). Note also that within the antlerless kills, we assumed no selection against fawns, which might be a limitation of this modeling exercise. We made this assumption in the absence of data on the proportion of antlerless kills that are composed of fawns vs. does and considering that the hunting season occurs when fawns are morphologically similar to does (about 6 months old). Nonetheless, this assumption could be modified as more data become available.

Our perturbation analysis further suggested that an adaptive harvest strategy is unlikely to drive the population to extinction, because perturbed populations returned toward equilibrium. Perturbation analysis also indicates that populations with higher harvesting rates recover more slowly from a perturbation. Harvested populations, therefore, might have lower resilience, but under a proportional harvest strategy, even in the case of a pulse perturbation that reduces the population by 10%, the population still can be expected to return toward its equilibrium size. Examples of pulse perturbations include severe winter conditions, which can impose variations in deer abundance (Jensen 2002), and disease outbreaks that have the po-tential to reduce population size over a short period of time. If such perturbations do not exceed 10% and population changes are closely tracked (i.e., adaptive harvest strategy), then further adjusting harvest rates might not be necessary; population recovery can be achieved under constant harvest rates. However, because recovery can take several years (more than 20 years in some cases), decreasing harvest rates following such perturbation events can speed up population recovery. Overall, this highlights the importance of monitoring big game and adjusting harvest rates periodically to quickly manage response to downturns in population size. This is particularly important in areas like the Northern Great Plains that are subjected to severe winter conditions.

Although we used a deterministic model to set optimal harvest, populations are subject to many types of variability (e.g., environmental, demographic), and adaptive harvest strategies that account for this stochasticity may result in more con-servative recommendations than strictly deterministic models (Xu et al., 2005; Xu and Boyce 2010). While we obtained estimates of population variability (Σ, the variance-covariance matrix), the entries in this matrix were relatively large (an

order of magnitude larger than those found for moose by Xu and Boyce (2010), likely due to the short duration of the time series used for model fitting. This large variability results in a stochastic population model that fluctuates wildly and ultimately goes extinct within most hundred-year simulations. One way to restrict the variability in the stochastic model would be to separate sampling error from process error, the latter being the type of error of interest for population projections. However, to tease these two types of error apart (see White 2000), it is necessary to have estimates of the process error of the population size estimates, which is typically obtained from replicate measurements. In the absence of such data, given environmental uncertainty and considering that small numbers of white-tailed deer also might be harvested in ways not considered here (see Methods section), we recommend an adaptive harvest strategy that is at least 10−15% lower than the MSY to give a buffer against environmental variability (as by Boyce 2000). If environmental variability is high and the population is not monitored regularly, harvest should be set much lower than MSY.

Aligning models with data requires that model structure include essential components of the population (density dependence) while capturing as much data as are available. A stage-structured model allows us to estimate most parameters and data alignment allowed us to estimate coefficients for density dependence. Limitations of data precluded finding a non-linear term for density dependence but we would expect that a larger dataset is likely to reveal more detail in the structure of density dependence (Fowler 1987; Gaillard et al., 1998).

5. Management implications

Harvest models can be useful tools forming the basis for adaptive management to optimize harvest regulations for big game species. Our model is adapted to use available data while providing a conceptual framework to evaluate big game harvests, and compare current strategies to optimal management strategies (Fig. 3).

As examples of the model applications, the MSY found here for DHU 3A1 is twice the mean annual yield obtained there in the last three years. Similarly, we found that antlerless harvests are necessary, adopting an optimal harvest composition (antlerless:antlered kill ratio of 0.6) can more than double the MSY of the proportional composition harvest strategy (i.e., "any white-tailed deer" type of tag), and regular monitoring can decrease the chances of population overexploitation. These results demonstrate how wildlife agencies could improve big game management by adopting population models adapted to available data, such as the one presented here, and highlight the importance of regularly assessing population size and adjusting harvest rates accordingly. We present ways in which data collection could be improved to refine parameter estimation through active adaptive management.

1) Obtaining a time series of population size estimates without gaps would greatly improve overall parameter estimation as well as population variability estimation, which is essential to properly incorporate stochasticity into the models. Although we showed that an adaptive harvest in which population is monitored every 5 years can result in similar yields as annual
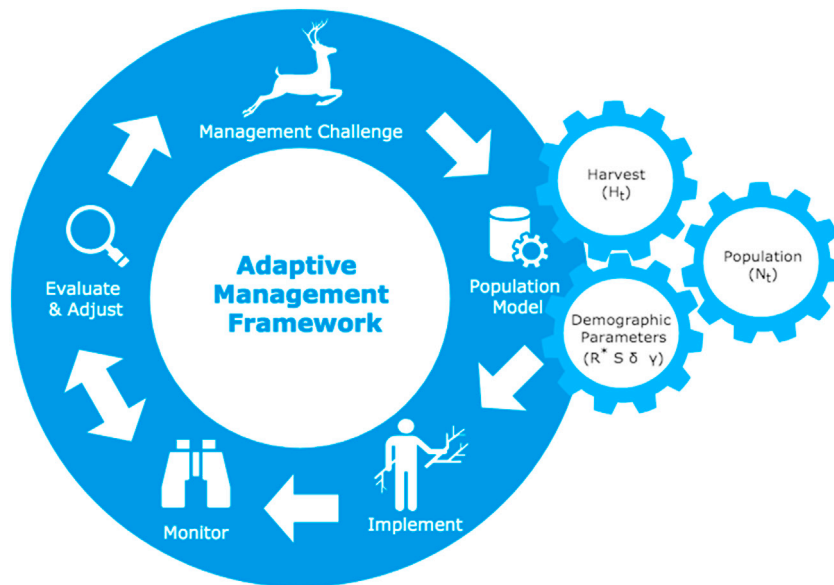

Fig. 3. Conceptual framework linking population dynamics models to big game adaptive management. Data are obtained from multiple sources: harvest data (H_t) from hunter questionnaires, population size and composition (N_t) from winter aerial surveys and hunter observations, respectively, and demographic parameters (recruitment − R^*, survival − S, proportion of female fawns at recruitment − δ, and density dependence exponent − γ) from literature and model fitting. Population models inform optimal harvest strategies (harvest rate/quota) that are then implemented through hunting regulations. Population response is then monitored and evaluated. Strategies and models might be adjusted and monitoring is used to learn more about the system. Built on the adaptive management cycle from Williams and Brown (2014).

monitoring, they do not provide enough information to improve parameter estimation nor to inform population variability. Using the iterative process of manipulating populations, monitoring their response, and comparing it to model predictions, managers would be able to reduce uncertainties associated with parameter estimation, a major component of adaptive management (Williams 2011). Therefore, regardless of the method chosen to improve population estimation, monitoring the population after implementing any management strategy is a crucial step of adaptive management (White 2001).

2) In this study, data on population composition were obtained from field observations by hunters. Given that these observations are done in the fall when fawns are about 6 months old, fawns can be mistakenly classified as does, resulting in recruitment being biased low and adult female survival being biased high. Because our sensitivity analysis suggested that adult female survival is the most sensitive parameter in our projection matrix, this bias could imply that population growth rate is actually lower than our estimates. In this sense, efforts in correcting this bias or, at least, measuring its strength, would be useful. One alternative would be to supplement hunter observation data with ground surveys conducted by qualified field observers, which could then inform a bias-associated correction factor to be applied to the hunter observation data.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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