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The Utility of Transient Sensitivity for Wildlife Management and Conservation: Bison as a Case Study

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Abstract

Developing effective management strategies is essential to conservation biology. Population models and sensitivity analyses on model parameters have provided a means to quantitatively compare different management strategies, allowing managers to objectively assess the resulting impacts. Inference from traditional sensitivity analyses (i.e., eigenvalue sensitivity methods) is only valid for a population at its stable age distribution, while more recent methods have relaxed this assumption and instead focused on transient population dynamics. However, very few case studies, especially in long-lived vertebrates where transient dynamics are potentially most relevant, have applied these transient sensitivity methods and compared them to eigenvalue sensitivity methods. We use bison (*Bison bison*) at Badlands National Park as a case study to demonstrate the benefits of transient methods in a practical management scenario involving culling strategies. Using an age and stage-structured population model that incorporates culling decisions, we find that culling strategies over short time-scales (e.g., 1–5 years) are driven largely by the standing population distribution. However, over longer time-scales (e.g., 25 years), culling strategies are governed by reproductive output. In addition, after 25 years, the strategies predicted by transient methods qualitatively coincide with those predicted by traditional eigenvalue sensitivity. Thus, transient sensitivity analyses provide managers with information over multiple time-scales in contrast to the long time-scales associated with eigenvalue sensitivity analyses. This flexibility is ideal for adaptive management schemes and allows managers to balance short-term goals with long-term viability.

Keywords

Badlands National Park, Bison, Eigenvalue, Population matrix model, Sensitivity analyses, Transient dynamics, Wildlife management

1. Introduction

Population models and sensitivity analyses of summary demographic statistics (e.g., population growth) to changes in model parameters are central to many population biology studies. Indeed, sensitivity analyses have been used to explore evolutionary questions (e.g., Gaillard et al., 1998, Pfister, 1998) as well as to inform management and conservation actions (e.g., Clark et al., 2008, Crowder et al., 1994, Mills and Lindberg, 2002). One of the most common approaches in each of these settings is to employ population matrix models and sensitivity analyses that focus on dominant eigenvalues and calculations based on a stable age distribution (Caswell, 2001; hereafter referred to as eigenvalue sensitivity, see Section 2.4.1). Because the calculation and, consequently, inference is based on a stable age distribution, this method is often limited to long-term persistence questions after populations have had a chance to converge to their stable age distribution. However, the relatively short time-scales over which many management actions are taken appear to be at odds

with the long-term nature of these methods (Ezard et al., 2010). Long-term growth in a population can be preceded by drastic declines in the short-term, especially when demographic stochasticity is taken into account (Koons et al., 2007). In such cases, populations may be driven to extinction before converging to the stable age distribution that inference from eigenvalue sensitivities is based on. Additionally, changing environmental conditions may alter population demographic parameters before inference based on eigenvalue sensitivities is valid necessitating the evaluation of management strategies over shorter time-scales (Ezard et al., 2010, Koons et al., 2005, Mertens et al., 2006).

The aforementioned concerns led to several approaches of incorporating transient dynamics into sensitivity analyses (Fox and Gurevitch, 2000, Yearsley, 2004). These approaches give managers the benefit of exploring sensitivity of population growth rate to demographic parameters over short management time-scales (e.g., annual adjusting of hunting and fishing regulations or land acquisition decisions for a species of concern) and thus better reflect the dynamic environmental conditions under which management strategies are implemented. Subsequent to earlier methods that focused on transient sensitivity (e.g., Fox and Gurevitch, 2000, Yearsley, 2004), Caswell (2007) introduced a highly flexible method for calculating sensitivity over short time-scales to the ecological community. This method proposed by Caswell (2007), hereafter referred to simply as transient sensitivity (Section 2.4.2), provides the sensitivity of a variety of model outputs (e.g., total population size or number of individuals in a certain class) to changes in model parameters (e.g., harvest rates, initial age-class sizes, fecundities) across multiple time-scales.

Despite these advantages, there are few examples of practical management scenarios that employ transient sensitivity. The applications of transient sensitivity to conservation biology that do exist have focused primarily on reproduction and survival in species with a relatively small number of ages and reproductive states to consider and do not take into account specific management (i.e., culling) actions (McMahon and Metcalf, 2008, Ozgul et al., 2009). Here, we explore transient sensitivity (i.e., Caswell, 2007) along with the traditional eigenvalue approach (i.e., Caswell, 2001) to assess the impact of culling decisions on natural populations composed of a large number of possible ages and reproductive states.

Harvesting/culling/augmentation decisions are some of the most common actions taken in wildlife management. For example, governments and states set harvest regulations for a variety of species (e.g., waterfowl, ungulates, fish); make decisions on augmenting reintroduced populations (Schaub et al., 2009); and/or set policies to diminish invasive species populations. As a case study, we explore bison (*Bison bison*) culling at Badlands National Park, USA (BNP). Bison were once numerous in the Great Plains of North America, but by 1903 they were functionally extirpated (Meagher, 1986). Since this near-extinction, small bison populations have been reintroduced and recovered in parks due largely to the pioneering efforts of the American Bison Society (Berger and Cunningham, 1994). Most places with bison herds do not support populations of native predators (e.g., wolves, *Canis lupus*), and as a result, culling is required to manage bison population sizes in order to maintain adequate forage for the herds, general herd health, and limit negative bison-park visitor interactions (Millspaugh et al., 2008). Annually, the decision to cull or not and subsequent decisions about the age and sex of culled bison are currently made based on the current population size and age distribution of the herd, expert opinion about the effect of herd structure on population dynamics, and economic limitations to animal shipment.

We present the first quantitative analysis of culling decisions made on the bison herd in BNP. To do this, we first provide an age- and state-structured population model that incorporates culling to describe population dynamics in the BNP herd. We then compare the sensitivity of the dominant eigenvalue to culling parameters using methods reviewed by Caswell (2001) to the sensitivity of total population size using methods that incorporate transient dynamics proposed by Caswell (2007). Our goal is to investigate the use of transient sensitivity to guide culling strategies in order to meet management goals and to elucidate how strategies

suggested from transient sensitivity compare to those predicted using eigenvalue sensitivity. Additionally, our comparison of methods, coupled with our illustrative example of these methods in a real-world management scenario, has wide applicability to other managed systems.

2. Methods

2.1. Study area and study species

The bison at BNP are restricted by fences and steep cliffs to the 26,000 ha Badlands Wilderness Area (Badlands National Park Bison Management Plan, unpublished report; Berger and Cunningham, 1994). The Wilderness Area consists mainly of uplands dominated by typical northern mixed grass prairie vegetation, riparian corridors dominated by cottonwoods, and prevalent badland formations (Berger and Cunningham, 1994). No natural predators (i.e., wolves or grizzly bears (*Ursus arctos horribilis*)) are present at BNP, and the BNP herd does not have brucellosis, a concern in other bison herds (Bradley and Wilmshurst, 2005, Fuller et al., 2007, Meagher, 1986,).

The National Park Service’s current goal is to maintain the BNP herd at approximately 700 bison (Badlands National Park Bison Management Plan, unpublished report), which is a target based on estimated vegetation productivity values for drought years (Radeke and Cole, 1969). Roundup and culling events are used as needed, usually on an annual basis, occurring in October. Culling decisions are made based on the current status of the herd as well as expert knowledge, but quantitative analyses of culling strategies can help to confirm and/or improve management efforts. These culling strategies are the focus of our investigation; specifically, given a particular state of the bison population, we seek to find the demographic categories that managers should cull from to reach a desired herd size while maintaining a viable herd.

Bison generally have high survival and calving rates. Female bison begin reproducing between the ages of two and four (Berger and Cunningham, 1994, Meagher, 1986) and are thought to be at peak fertility until age 13 (Shaw and Carter, 1989). In a given year, a reproducing cow usually only produces a single calf (Meagher, 1986). Male bison may copulate with females as early as three, but tend not to breed until age six when they have attained their full size (Meagher, 1986). Bison in the wild typically live to the age of 20, although there are records of bison that have reached 30 years and older (Meagher, 1986). Old male bison are less likely to be rounded up or handled as these animals are dangerous in the pens and few of this age class are thought to exist within the park. These old animals are not the target of management.

Our modeling efforts are based on data collected during the yearly roundups between 2002 and 2007. During these years each bison was marked individually, allowing for the estimation of various parameters (i.e., survival and breeding-state transition probabilities) using mark-recapture analytical methods (Williams et al., 2002) – details of which can be found in Pyne et al. (2010). We used the estimates of Pyne et al. (2010) to parameterize our matrix population model.

2.2. Bison population model

We propose the following pre-breeding Leslie matrix population model:

(1)

$$\mathbf{n}(t + 1) = \mathbf{H}[\boldsymbol{\theta}]\mathbf{R}[\boldsymbol{\theta}]\mathbf{S}[\boldsymbol{\theta}]\mathbf{n}(t), t = 0, 1, 2, \dots,$$

where $\mathbf{n}(t)$ is the population vector, and $\mathbf{H}[\boldsymbol{\theta}]$, $\mathbf{R}[\boldsymbol{\theta}]$, and $\mathbf{S}[\boldsymbol{\theta}]$ are the harvest, reproduction, and survival matrices that depend on $\boldsymbol{\theta}$, a vector of lower-level parameters (i.e., age and state-specific harvesting, survival, and reproduction parameters). The initial population vector is given by the vector $\mathbf{n}(0)$. The projection matrix, \mathbf{A} , is then given by $\mathbf{H}[\boldsymbol{\theta}]\mathbf{R}[\boldsymbol{\theta}]\mathbf{S}[\boldsymbol{\theta}]$.

Additionally, we define three states within our population vector related to reproductive status. Wet females (w) are lactating, or nursing a calf, at the time of the roundup whereas dry females (d) are those not lactating. A female could be dry for several reasons, including that she did not reproduce that year, the calf did not survive to the roundup, or the calf was weaned early. The transitions from dry to wet and wet to wet represent both reproduction and survival of the calf from birth to the roundup. Thus, we choose a model structure that mirrors the reproductive information contained in the mark-recapture data (Pyne et al., 2010). The final state is males (m), which do not contribute to reproduction in our model. Bison are harem breeders, and we assume males are sufficiently abundant for breeding purposes. This assumption is only valid as long as breeding age males do not experience increased mortality due to over-harvesting or other sources or extrinsic mortality. We include males in the model to investigate culling strategies that may differ between males and females. Because our initial conditions always contain females (see Section 2.3), reducibility in the model is not an issue and analytical results on \mathbf{A} are valid.

We denote these states as follows:

$$\mathbf{n}(t) = \begin{bmatrix} \mathbf{d}(t) \\ \mathbf{w}(t) \\ \mathbf{m}(t) \end{bmatrix},$$

where $\mathbf{d}(t)$, $\mathbf{w}(t)$, and $\mathbf{m}(t)$ are column vectors containing the number of individuals in each age class. Due to the small number of tagged and recorded bison over the age of 20 at BNP, we only model bison to live to the age of 19.5 (i.e., after this age their survival is assumed to be zero, and they are removed from the model). We define i (for $i = 1, 2, \dots, 20$) as the age class of the bison. Since field data are collected in the autumn, but breeding takes place in the spring, the age of bison in age class is $i - 0.5$ (e.g., individuals entering age class 1 are 0.5 years old) such that:

$d_i(t)$ = the number of dry females in age class i .

$w_i(t)$ = the number of wet females in age class i .

$m_i(t)$ = the number of males in age class i .

To model the reproductive process of the population, we use the convention that a bison coming into the roundup wet must have become pregnant the year before. This is consistent with the birthing period usually occurring in early spring and the fact that young bison are usually weaned in the first 7 or 8 months after birth (Meagher, 1986). Using this convention, we assume that females transition from dry to wet (or vice versa) immediately following the roundup. We denote these transition probabilities (for $i = 1, 2, \dots, 19$) with:

$\psi_i^{dw}(t)$ = the probability of a female transitioning from dry to wet in age class i .

$\psi_i^{wd}(t)$ = the probability of a female transitioning from wet to dry in age class i .

After this transition occurs, we introduce the probabilities that a bison survives the following calendar year (for $i = 1, 2, \dots, 19$):

$\varphi_i^d(t)$ = the probability of a dry female surviving from age class i to age class $i + 1$.

$\varphi_i^w(t)$ = the probability of a wet female surviving from age class i to age class $i + 1$.

$\varphi_i^m(t)$ = the probability of a male surviving from age class i to age class $i + 1$.

The matrix $\mathbf{S}[\mathbf{A}]$ is obtained by combining survival probabilities with the possible state transition probabilities (Eq. (A.1)).

The roundup data indicated that our use of wet, or lactating, females as a proxy for births yielded a consistent underestimate of the total number of new births (e.g., a newborn calf could wean early and therefore the calf's mother would not present as 'wet'). Thus, we introduce a correction for this bias,

$$\gamma = \frac{\#calves}{\#wet\ females},$$

Though γ likely depends on multiple covariates, we estimate γ to be 0.924 by taking the average of the 6 yearly γ 's. Thus, assuming it is equally likely for a bison to produce a male or female, a wet cow adds $0.5/\gamma$ bison to both the newborn population of dry females and the newborn population of males. This leads to our reproduction matrix, $\mathbf{R}[\boldsymbol{\theta}]$ (Eq. (A.2)).

In addition, there are several biological constraints on our parameters. First, we assume that female bison cannot give birth to a calf until age two and thus cannot become pregnant until after their first birthday, which implies ψ_1^{dw} . Similar reasoning yields $\psi_1^{wd} = \psi_2^{wd} = \phi_1^w = \phi_2^w = 0$.

Fig. 1 summarizes the life cycle of the bison in the model.

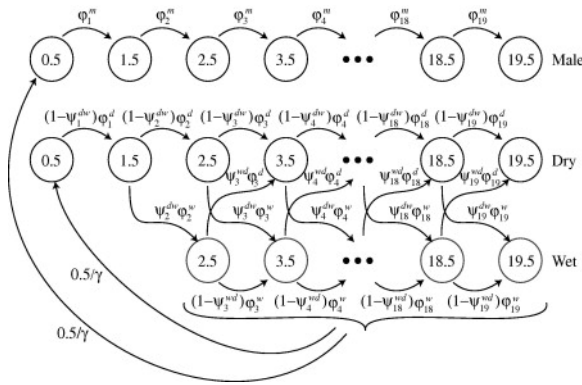


Fig. 1. Life cycle diagram for the bison population model. Field data upon which the model is based are collected in the fall when calves are 0.5 years old and twenty age classes are represented (ages 0.5–19.5) in the model. Three stages (dry – empty udder – female, d ; wet – full udder – female, w ; males, m) are modeled. Transition rates are modeled as a function of survival ($\phi_{age\ class}^{stage}$) and as a function of transition between stages ($\psi_{age\ class}^{stage\ to\ stage}$). Offspring are assumed to be produced in a 50:50 sex ratio. Number of calves produced is corrected ($0.5/\gamma$) for under representation of wet-females γ compared to calves in the data.

To model the culling procedure employed by BNP, we introduce the harvesting parameters (for $i = 1, 2, \dots, 20$):

- $h_i^d(t)$ = the proportion of dry females harvested from age class i .
- $h_i^w(t)$ = the proportion of wet females harvested from age class i .
- $h_i^m(t)$ = the proportion of males harvested from age class i .

The diagonal entries of the harvest matrix, $\mathbf{H}[\boldsymbol{\theta}]$, are these parameters subtracted from one (Eq. (A.3)).

We have introduced 156 parameters into the model, given in the 156×1 vector:

$$\boldsymbol{\theta} = (\boldsymbol{\phi}^d \quad \boldsymbol{\phi}^w \quad \boldsymbol{\phi}^m \quad \boldsymbol{\psi}^{dw} \quad \boldsymbol{\psi}^{wd} \quad \gamma \quad \mathbf{h}^d \quad \mathbf{h}^w \quad \mathbf{h}^m)^T.$$

that will be used in our transient sensitivity analyses (see Section 2.4).

2.3. Initial population structure

We use the matrix model presented in Section 2.2 to investigate harvesting strategies on three different initial population structures of 700 bison (see Fig. 2A–C). These population structures were based on BNP roundup data as well as data from Wind Cave National Park (Millspaugh et al., 2008) and reflect the range of possible herd conditions at BNP. The first initial population structure considered has an age structure typical of growing populations, which may arise from a no-culling scenario (Fig. 2A). We also consider a population structure characteristic of an active culling scenario (Fig. 2B). In fact, this structure reflects the current condition of the BNP herd where culling has reduced numbers in older age classes leaving a large proportion of the herd in the youngest age class which is not subject to culling. The final condition represents a population dominated by breeding age bison (Fig. 2C), a scenario that could result from over-harvesting young bison in the past coupled with subsequent low reproductive years, which is a concern to managers at BNP. Using these initial population structures, we compare and contrast culling options suggested from the long-term asymptotic sensitivity (Section 2.4.1) to those from the short-term transient sensitivity (Section 2.4.2) under a variety of potential management scenarios.

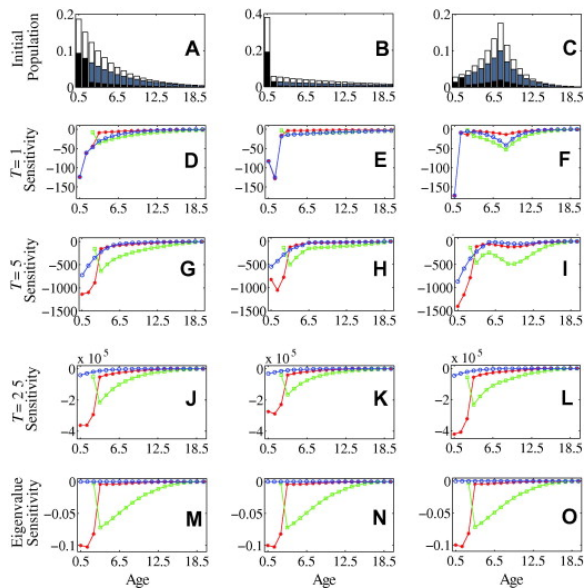


Fig. 2. The top row (Panels A–C) represents the three starting population structures used in the simulations, where the vertical axis is proportion of the population and the horizontal axis is age. The black, gray, and white colors represent dry females, wet females, and males respectively. Panel A is based on a growing population not subjected to culling activities. Panel B represents a population in which most culling activity is focused on 1.5 year olds, the current strategy at Badlands National Park. Panel C represents the population structure that could result from over-harvesting of young bison, combined with a multi-year drought. The second (Panels D–F), third (Panels G–I), and fourth (Panels J–L) rows are the resulting transient sensitivities of total population size to age-specific culling rates for time frames of 1, 5, and 25 years respectively for each of the above initial population structures. The bottom row (Panels M–O) shows asymptotic, eigenvalue sensitivities for the three initial population structures. For each of the sensitivity graphs (Panels D–O), the sensitivity for three stages (male, open blue circles; wet female, open green squares; dry female, red asterisks) of available ages (0.5–19.5) is shown. The sensitivity is the change in total population size or growth rate relative to the change in harvest rate evaluated at an initial harvest rate of zero.

2.4. Sensitivity analyses

2.4.1. Eigenvalue sensitivity calculation

The classic approach to calculating sensitivity from a matrix population model (Caswell, 2001) is to focus on λ , the asymptotic population growth rate, once the population has reached a stable age distribution. The age/stage-specific survival and wet/dry transition rates are considered invariant over long time periods. To assess sensitivity (s_{ij}) of λ to an absolute change in a parameter (a_{ij}) the partial derivative of λ with respect to a_{ij} can be calculated:

(2)

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}.$$

In Eq. (2), \mathbf{v} and \mathbf{w} represent the left and right eigenvectors, respectively, and $\langle \cdot, \cdot \rangle$ is the inner product of two vectors.

In Eq. (2), s_{ij} is the response to an absolute perturbation in parameters regardless of scale. However, demographic parameters are often measured on different scales (e.g., survival probability is bounded by 0 and 1, but fertility may have a very different upper bound). In these cases elasticity (e_{ij}) is often calculated. Additional scalings of sensitivity have also been considered (e.g., Link and Doherty, 2002). In our bison case study, all parameters of interest are probabilities and thus bounded by 0 and 1. Thus, scale is less of an issue, and we focus on the sensitivity, or the change of a model output with respect to a change in model parameters.

2.4.2. Transient sensitivity calculation

Managers often desire to understand how parameters affect population dynamics over short as well as long time-scales, a question that cannot be answered by calculating these aforementioned quantities that characterize long-term behavior alone. Caswell (2007) introduced a method for incorporating transient dynamics into sensitivity analysis of matrix population models to the ecological community. Following his approach, we differentiate $\mathbf{n}(t+1)$ with respect to $\boldsymbol{\theta}$ to obtain the sensitivity of the population vector $\mathbf{n}(t+1)$ with respect to the parameters,

(3)

$$\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^T} = \mathbf{A} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^T} + (\mathbf{n}(t)^T \otimes \mathbf{I}) \frac{d\text{vec}(\mathbf{A})}{d\boldsymbol{\theta}^T},$$

where \otimes is the Kronecker product, T denotes the transpose of a matrix, and the vec operator is used to stack the columns of a matrix into a column vector. Notice that $\frac{d\text{vec}(\mathbf{A})}{d\boldsymbol{\theta}^T}$ is a matrix of derivatives of the entries of our population projection matrix, \mathbf{A} (as calculated from $\mathbf{H}[\boldsymbol{\theta}]\mathbf{R}[\boldsymbol{\theta}]\mathbf{S}[\boldsymbol{\theta}]$), with respect to our parameters, $\boldsymbol{\theta}$. This calculation produces $\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^T}$, which is a matrix that contains the sensitivities of the elements of the vector $\mathbf{n}(t+1)$ to the parameters found in $\boldsymbol{\theta}$.

Most published examples using this approach (e.g., Caswell, 2007) have relatively simple population structures (e.g., at most a five state matrix population model), while our population consists of 60 unique age and state combinations. The large amount of information for this size model can be condensed by considering a specific Quantity Of Interest (QOFI; see Caswell, 2007 for examples) which allows managers to focus on a particular population statistic, such as total population size or number of females. For our study, we use total population

size at a specific point in time, denoted by the number $N(t)$, as our QOFI. The sensitivity of total population size to each of our parameters is given by:

(4)

$$\frac{dN(t)}{d\theta^T} = \mathbf{1}_{1 \times 60} \frac{d\mathbf{n}(t)}{d\theta^T},$$

where $\mathbf{1}_{1 \times 60}$ is a 1×60 row vector of 1's. This QOFI is closely related to the growth rate defined by the eigenvalue and allows us to make reasonable comparisons between the two methods (McMahon and Metcalf, 2008). More importantly, total population size is readily measured by managers at BNP and is the target of management actions.

With the goal of informing management, we consider the sensitivity of the total population size to parameters of interest (Section 2.4.3) over three time periods, 1, 5, and 25 years (Fig. 2D–L). These time frames coincide with immediate goals, goals over a typical 5-year management plan, and more long-term goals associated with the approximate life-span of the bison.

2.4.3. Parameters of interest

While the sensitivity methods described in Sections 2.4.1 Eigenvalue sensitivity calculation, 2.4.2 Transient sensitivity calculation can be used to compute model sensitivities with respect to all 156 of the model parameters, we focus our analysis on sensitivities with respect to age and state-specific culling rates only. These rates are more readily controlled by managers when compared to other model parameters. We calculate the sensitivity of total population size to age-specific harvesting rates assuming that no culling takes place (i.e., $h^d = h^w = h^m = \mathbf{0}$). We note that age-specific culling is assumed in this population because age is well approximated in this system through tagging of newborns and tooth-wear of adults. In other populations where age is not well established, grouping individuals across a range of ages may be necessary.

3. Results

3.1. General results

Both the eigenvalue and transient sensitivities are interpreted as the change in either the eigenvalue or total population size divided by the change in the harvest parameters (i.e., slopes) evaluated at a particular value of the harvest rate vector (in our case this is assumed to be $\mathbf{0}$). These sensitivities are negative since harvesting decreases population size and growth (Fig. 2D–O). With no harvesting, the projection matrix \mathbf{A} has a dominant eigenvalue of $\lambda = 1.216$, which indicates positive long-term growth and is consistent with growth rates observed in other large herbivores (reviewed in Gaillard et al., 2000). When we implemented a culling strategy similar to one used previously on this herd, culling heavily from individuals in age class 1.5, we found the population growth rate λ decreased to 0.869 indicating a decrease in herd size.

3.2. Eigenvalue sensitivity

Under asymptotic assumptions (Fig. 2M–O), regardless of the starting population structure, the demographic parameters to which the eigenvalue was most sensitive were dry and wet females in young age classes (i.e., ages 0.5–3.5). As females became reproductively mature (approximately age 3.5+), we found that the population growth rate was more sensitive to wet females than to dry females. Also, as bison aged, their contribution to the population growth rate declined, which is seen in the decline in sensitivity with increasing age. Finally, since male bison did not contribute to reproduction in this model, the population growth rate was not sensitive to culling males of any age.

3.3. Transient sensitivity

On a single year time-scale (e.g., when culling decisions are made on an annual basis), we instead calculated the sensitivity of the total population size to age and state-specific harvesting rates (Fig. 2D–F). The total population after 1 year was most sensitive to harvesting male and female calves and yearlings, but the total population was also sensitive to harvesting the most prevalent age classes from the previous year. More specifically, we found, in contrast to the eigenvalue sensitivity results, that population structure had an effect on the transient sensitivities. The trends found in the transient sensitivity results initially reflect the previous year's standing population (Fig. 2D–F). Also, in each case, total population size is most sensitive to culling newborns which reflects the high reproductive output in these populations. However, the magnitude of the effect of culling newborns was highest in the population dominated by breeding age bison (Fig. 1C) indicating that this population structure generated the highest initial reproductive output.

After 5 (Fig. 2G–I) and 25 (Fig. 2J–L) years, the total population was most sensitive to harvesting the younger age classes (ages 0.5–3.5). As the time-scale lengthened, the effect of the initial population structure decreased, but overall reproductive output was still higher from the initial population structure found in Fig. 1C as seen in the higher magnitude sensitivity values. Also, with increased time, total population size became less sensitive to harvesting males. Further, at the 25-year time-scale, we found that the transient sensitivity results had qualitatively come to resemble the eigenvalue sensitivity.

4. Discussion

4.1. Bison management implications

Several management implications emerge from this comprehensive sensitivity analysis that are directly applicable to the BNP bison herd, but similar logic can be applied to other management situations. We see that if a bison herd is not under active management and is consequently larger than set management goals (Fig. 2A), reduction in the short-term, as indicated by the transient sensitivity, is most effectively achieved by culling animals from the most numerous age class, in our case the young age classes. Culling the dominant age class has the largest impact in the short-term due to the fact that the standing population rather than reproduction contributes most to the population in the following year. This observation is related to the recent idea of “seniority” – the probability of being present at a previous time period – and that seniority can be an important consideration in sensitivity analyses (Nichols et al., 2000).

The large sensitivity of total population size to harvesting young bison indicates that culling these young bison can be used to achieve large herd reductions in the short-term. This confirms that the strategy of harvesting primarily 1.5 year old bison practiced by BNP is effective at reducing herd size leading to a population structure dominated by younger bison (Fig. 2B). However, under this strategy, the population is not viable in the long-term due to the population growth rate, λ , being less than one. We also found this in the long-term sensitivities (both transient and eigenvalue methods) as culling 0.5 and 1.5 year old bison had the largest effect on the population, not only under initial conditions similar to those seen in BNP but across all initial population structures considered. Similarly, juvenile survival in other large herbivore species has been found to be the main determinant of population growth rate (Gaillard et al., 2000). Thus, care must be taken when culling young bison for short-term management goals at BNP as this strategy can drastically influence future population numbers if the same culling strategy is naively followed every year. The annual state of the population must be considered.

We also considered a scenario where the BNP population had been previously stressed, a potential result of culling and subsequent reproductive failure in the population (Fig. 2C). Under this scenario, culling is not desirable due to population viability concerns, but roundups may still have economic benefits for the park (e.g., roundups draw visitors to the park) necessitating the sale of some bison to support roundup efforts. In such a

case, managers should target the stages and ages that have little impact on future population size or growth. The transient sensitivity indicates that older bison (age 10.5+) have little effect on the population both in the short-term ($t = 1$, Fig. 2F), as well as in the long-term ($t = 25$ or asymptotic; Fig. 2L and O). Thus, older bison should be targeted for culling when removal is necessary but not desired.

As the time-scale of management goals across all scenarios lengthened, the effect of initial population structure diminished. This occurs until the time frame is long enough (>25 years) that the transient sensitivity yields results that qualitatively resemble its eigenvalue counterpart, and there is little sensitivity to starting conditions due to the increased effect of reproduction through time. Thus, we observed that long-term management strategies predicted by the transient sensitivity are qualitatively similar to those predicted by eigenvalue sensitivity. This fact demonstrates the utility of transient sensitivity to predict long-term strategies under the assumption of constant environmental conditions and vital rates. Previous studies on bison viewed 25 years as an appropriate time frame over which to consider transient dynamics (Millsbaugh et al., 2008), but our results indicate that transient dynamics occur on a much shorter time-scale. We note that the 25-year time frame needed for transient sensitivities to qualitatively resemble asymptotic sensitivities may not apply to all species or populations and may depend on the distance of the initial population to the stable age distribution (Ezard et al., 2010, Keyfitz, 1968, Koons et al., 2005) or the life-span of the study species (Ezard et al., 2010, Koons et al., 2005, Tenhumberg et al., 2009). We also note that if the initial population structure is identical, or approximately identical, to the stable age distribution, there is a quantitative, as well as qualitative, relationship between these two methods of calculating sensitivity.

Our analysis of the BNP bison herd focuses on population growth rate and total population size. However, due to past population bottlenecks and continued low population sizes, preserving the genetic diversity of North American bison herds has become a central concern for bison managers (Freese et al., 2007). Given that culling decisions should be made to maximize the genetic diversity of the remaining herd, future work should incorporate genetic sub-structure into management decisions. Simulation models have been used to calculate the sensitivity of gene diversity to changes in population demographic parameters across long time-spans (i.e., 100 years) in European bison populations (Daleszczyk and Bunevich, 2009). However, we view transient sensitivity as an alternate way to address this problem. Rather than calculating sensitivity of the total population size to age-specific harvesting, effective population size could be used as the QOFI to ensure that culling minimizes genetic loss over a variety of time-scales.

4.2. Utility of transient sensitivity

The methods for calculating sensitivities that incorporate transient dynamics are relatively unused in management and conservation problems. Even though conservation actions must be evaluated by their long-term effects, short-term effects cannot be ignored. Consequently, given that most managers focus on a range of time-scales including short-term decisions (e.g., annual decisions or 5-year management plans), the benefit of these methods to managers is apparent. Many current studies still make use of eigenvalue sensitivities to guide management strategies (e.g., Clark et al., 2008, Enneson and Litzgus, 2008), even though this asymptotic time-scale often does not match shorter management time-scales, severely limiting conclusions based on eigenvalue sensitivity.

Transient sensitivity is also more flexible than asymptotic methods by allowing managers to define specific quantities of interest over multiple time-scales that are pertinent to their system as opposed to just population growth over potentially long time-scales. QOFI's can range from the number of reproductive females to the number of trophy game animals (i.e., large males). This flexibility allows managers to address multiple management questions across multiple time-scales, such as the need to balance population growth while maximizing the number of trophy animals available to hunters, using a single method. This flexibility to consider

multiple time-scales should be particularly useful in the conservation of other long-lived species and can be applied to wide variety of problems already employing matrix population models, such as the impact of long-line fishing mortality in albatross populations (Awkerman et al., 2006, Veran et al., 2007) and the effect of pig predation and harvesting on northern snake-necked turtle populations (Fordham et al., 2008). In each of these situations long-term persistence may not guarantee short-term viability.

With the current interest in applying formal adaptive management decision processes to wildlife management (Williams et al., 2002), the transient methods proposed by Caswell (2007) will be very useful to the short-term decision and reassessment process often embodied in such problems (Bakker and Doak, 2009). Transient sensitivity methods allow short-term predictions to be evaluated using data that is readily available (e.g., annual or semi-annual population counts). In contrast, previous methods of population viability analysis require long-term data sets that are either not available or, in the case of highly variable systems, are quickly outdated with respect to short-term management decisions.

In addition, the ability of transient sensitivity analyses to address the impact of initial population structure on short-term growth is particularly useful for the control of invasive species and the reintroduction of endangered species. In both cases, initial population structure can have a profound effect on population establishment. Traditional asymptotic methods, however, cannot inform studies on the relationship between the structure of an introduced population and the probability of establishment. The transient sensitivity analysis proposed by Caswell (2007) is an ideal tool to address questions of how both short and long-term success of an introduced population varies according to the age, size, or state distribution of the founding population. In our example, we found that introducing populations dominated by breeding age bison created the greatest reproductive output. This type of analysis and result could benefit bison conservation in North America (Larter et al., 2000) and Europe (Kuemmerle et al., 2010) where reintroduction efforts are potentially spread over numerous small sub-populations.

5. Conclusions

We have shown that the BNP bison population is most sensitive in the short-term to culling the most prevalent age classes in the standing population, in our case 0.5 and 1.5 year olds. However, culling these age classes can also lead to drastic declines in population size over longer periods. Thus, short-term strategies, which depend to a large extent on the current population structure, must be balanced against long-term viability of the population (i.e., the effect of future reproduction). We showed that the transient sensitivity methods proposed by Caswell (2007) produce similar management suggestions to their traditional asymptotic counterparts for large time-scales. Because these transient sensitivity analyses can also be used over multiple time-scales, they are a flexible tool that can be used to consider numerous questions over multiple time-scales. Despite their utility, transient methods have been relatively unexplored in management applications. We believe that these methods can be used to address important questions, particularly involving adaptive management schemes, and will become more popular as managers recognize their value to exploring and improving conservation strategies.

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Appendix A. The survival ($S[\vartheta]$), reproduction ($R[\vartheta]$), and harvest ($H[\vartheta]$) matrices

We constructed the survival and transition matrix, $S[\vartheta]$, given in Eq. (A.1),

(A.1)

$$s[\theta] = \begin{bmatrix} 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 \\ 0 & \dots & \text{diag}(\varphi^d \circ [1 - \psi^{dw}]) & \dots & 0 & \dots & \text{diag}(\varphi^d \circ \psi^{wd}) & \dots & 0 & \dots & 0_{19 \times 19} & \dots & 0 & \dots & 0 \\ 0 & \dots & \text{diag}(\varphi^w \circ \psi^{dw}) & \dots & 0 & \dots & \text{diag}(\varphi^w \circ [1 - \psi^{wd}]) & \dots & 0 & \dots & 0_{19 \times 19} & \dots & 0 & \dots & 0 \\ 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 \\ & & 0_{19 \times 19} & & \vdots & & 0_{19 \times 19} & & \vdots & & \text{diag}(\varphi^m) & & \vdots & & 0 \\ & & & & 0 & & & & 0 & & & & 0 & & 0 \end{bmatrix}$$

where \circ is the component-wise Hadamard product and $\text{diag}(\cdot)$ takes an $n \times 1$ vector and places its entries on the diagonal of an $n \times n$ matrix. Next, the reproduction matrix, $R[\vartheta]$, is defined by Eq. (A.2),

(A.2)

$$R[\theta] = I + \begin{bmatrix} 0 & \dots & 0 & \dots & 0 & 0 & \frac{1}{\gamma}0.5 & \dots & \frac{1}{\gamma}0.5 & 0 & \dots & 0 & \dots & 0 \\ & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & 0 \\ 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 & \dots & 0 \\ & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & 0 \\ 0 & \dots & 0 & \dots & 0 & 0 & \frac{1}{\gamma}0.5 & \dots & \frac{1}{\gamma}0.5 & 0 & \dots & 0 & \dots & 0 \\ & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & \mathbf{0}_{19 \times 19} & & \vdots & & 0 \\ & & & & 0 & & & & 0 & & & & 0 & & 0 \end{bmatrix}$$

where I is the 60×60 identity matrix. As bison have harem based mating, we assume a sufficient number of males to mate with available females. Finally, the harvest matrix is given by Eq. (A.3).

(A.3)

$$H[\theta] = I - \text{diag}(h_1^d \dots h_{20}^d \quad h_1^w \dots h_{20}^w \quad h_1^m \dots h_{20}^m)$$

References

- Awkerman et al., 2006 J.A. Awkerman, K.P. Huyvaert, J. Mangel, J.A. Shigueto, D.J. Anderson **Incidental and intentional catch threatens Galapagos waved albatross** *Biol. Conserv.*, 133 (2006), pp. 483-489
- Bakker and Doak, 2009 V.J. Bakker, D.F. Doak **Population viability management: ecological standards to guide adaptive management for rare species** *Front. Ecol. Environ.*, 7 (2009), pp. 158-165
- Berger and Cunningham, 1994 J. Berger, C. Cunningham (Eds.), **Bison: Mating and Conservation in Small Populations**, Columbia University Press, New York (1994)
- Bradley and Wilmshurst, 2005 M. Bradley, J. Wilmshurst **the fall and rise of bison populations in Wood Buffalo National Park: 1971 to 2003** *Can. J. Zool.*, 83 (2005), pp. 1195-1205
- Caswell, 2001 H. Caswell. **Matrix Population Models – Construction, Analysis and Interpretation (2nd ed.)**, Sinauer Associates, Inc., Sunderland, Massachusetts (2001)

- Caswell, 2007H. Caswell **Sensitivity analysis of transient population dynamics** *Ecol. Lett.*, 10 (2007), pp. 1-15
- Clark et al., 2008W.R. Clark, T.R. Bogenschutz, D.H. Tessin **Sensitivity analysis of a population projection model of ring-necked pheasants.** *J. Wildlife Manage.*, 72 (2008), pp. 1605-1613
- Crowder et al., 1994L.B. Crowder, D.T. Crouse, S.S. Heppell, T.H. Martin **Predicting the impact of turtle excluder devices on loggerhead sea-turtle populations** *Ecol. Appl.*, 4 (1994), pp. 437-445
- Daleszczyk and Bunevich, 2009K. Daleszczyk, A.N. Bunevich **Population viability analysis of European bison populations in Polish and Belarusian parts of Bialowieza Forest with and without gene exchange.** *Biol. Conserv.*, 142 (2009), pp. 3068-3075
- Enneson and Litzgus, 2008J.J. Enneson, J.D. Litzgus **Using long-term data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*).** *Biol. Conserv.*, 141 (2008), pp. 1560-1568
- Ezard et al., 2010. T.H.G. Ezard, J.M. Bullock, H.J. Dalglish, A. Millon, F. Pelletier, A. Ozgul, D.N. Koons **Matrix models for a changeable world: the importance of transient dynamics in population management** *J. Appl. Ecol.*, 47 (2010), pp. 515-523
- Fordham et al., 2008 D.A. Fordham, A. Georges, B.W. Brook **Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation** *J. Appl. Ecol.*, 45 (2008), pp. 52-62
- Fox and Gurevitch, 2000G.A. Fox, J. Gurevitch **Population numbers count: tools for near-term demographic analysis** *Am. Nat.*, 156 (2000), pp. 242-256
- Freese et al., 2007
C.H. Freese, K.E. Aune, D.P. Boyd, J.N. Derr, S.C. Forrest, C.C. Gates, P.J.P. Gogan, S.M. Grassel, N.D. Halbert, K. Kunkel, K.H. Redford
- Fuller et al., 2007. **Second chance for the plains bison** *Biol. Conserv.*, 136 (2007), pp. 175-184
J.A. Fuller, R.A. Garrott, P.J. White, K.E. Aune, T.J. Roffe, J.C. Rhyan
- Gaillard et al., 1988. **Reproduction and survival of Yellowstone bison.** *J. Wildlife Manage.*, 71 (2007), pp. 2365-2372
J.M. Gaillard, M. Festa-Bianchet, N.G. Yoccoz
- Gaillard et al., 2000. **Population dynamics of large herbivores: variable recruitment with constant adult survival** *Trends Ecol. Evol.*, 13 (1998), pp. 58-63
J.M. Gaillard, M. Festa-Bianchet, N.G. Yoccoz, A. Loison, C. Toigo. **Temporal variation in fitness components and population dynamics of large herbivores.** *Annu. Rev. Ecol. Syst.*, 31 (2000), pp. 367-393
N.G. Yoccoz, A. Loison, C. Toigo.
- Keyfitz **Introduction to the Mathematics of Population** Addison-Wesley, Reading, Massachusetts (1968)
- D.N. Koons, J.B. Grand, B. Zinner, R.F. Rockwell **Transient population dynamics: relations to life history and initial population state** *Ecol. Model.*, 185 (2005), pp. 283-297
- D.N. Koons, R.R. Holmes, J.B. Grand **Population inertia and its sensitivity to changes in vital rates and population structure** *Ecology*, 88 (2007), pp. 2857-2867
- Kummerle et al., 2010.T. Kummerle, K. Perzanowski, O. Chaskovskyy, K. Ostapowicz, L. Halada, A.T. Bashta, I. Kruhlov, P. Hostert, D.M. Waller, V.C. Radeloff **European Bison habitat in the Carpathian Mountains** *Biol. Conserv.*, 143 (2010), pp. 908-916
- N.C. Larter, A.R.E. Sinclair, T. Ellsworth, J. Nishi, C.C. Gates **Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada** *Anim. Conserv.*, 4 (2000), pp. 299-309

- Link and Doherty, 2002 W.A. Link, P.F. Doherty **Scaling in sensitivity analysis** *Ecology*, 83 (2002), pp. 3299-3305
- S.M. McMahon, C.J.E. Metcalf. **Transient sensitivities of non-indigenous shrub species.** *Biol. Invasions*, 10 (2008), pp. 833-846
- Meagher, 1986 M. Meagher. **Bison bison.** *Mamm. Species*, 266 (1986), pp. 1-8
- S.K. Mertens, J.M. Yearsley, F. van den Bosch, C.A. Gilligan. **Transient population dynamics in periodic matrix models: methodology and effects of cyclic permutations.** *Ecology*, 87 (2006), pp. 2338-2348
- L.S. Mills, M.S. Lindberg. **Sensitivity analysis to evaluate the consequences of conservation actions.** S.R. Beissinger, D.R. McCullough (Eds.), *Population Viability Analysis*, University of Chicago Press, Chicago (2002), pp. 338-366.
- J.J. Millspaugh, R.A. Gitzen, D.S. Licht, S. Amelon, T.W. Bonnot, D.S. Jachowski, D.T. Jones-Farrand, B.J. Keller, C.P. McGowan, M.S. Pruett, C.D. Rittenhouse, K.M.S. Wells. **Effects of culling on bison demographics in Wind Cave National Park, South Dakota.** *Nat. Areas J.*, 28 (2008), pp. 240-250
- J.D. Nichols, J.E. Hines, J.D. Lebreton, R. Pradel **Estimation of contributions to population growth: a reverse-time capture-recapture approach** *Ecology*, 81 (2000), pp. 3362-3376
- Ozgul et al., 2009 A. Ozgul, M.K. Oli, K.B. Armitage, D.T. Blumstein, D.H. Van Vuren **Influence of local demography on asymptotic and transient dynamics of a yellow-bellied marmot metapopulation** *Am. Nat.*, 173 (2009), pp. 517-530
- Pfister, 1988. C.A. Pfister. **Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications** *Proc. Natl. Acad. Sci. USA*, 95 (1998), pp. 213-218
- M.I. Pyne, K.M. Byrne, K.A. Holfelder, L.N. McManus, M. Buhnerkempe, N. Burch, E. Childers, S. Hamilton, G. Schroeder, P.F. Doherty Jr. **A multi-state approach to examining the effects of age, sex, breeding status, and climatic variables on survival and breeding transitions for a reintroduced population of bison.** *J. Wildlife Manage.*, 74 (2010), pp. 1463-1471
- Radeke, R.E., Cole, R.S., 1969. Soils and vegetation of the Badlands National Monument. In: Larson, J.W. (Ed.), *Natural Resources Basic Data for Badlands National Monument*. Soil Conservation Service, Rapid City, South Dakota.
- M. Schaub, R. Zink, H. Beissmann, F. Sarrazin, R. Arlettaz **When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps** *J. Appl. Ecol.*, 46 (2009), pp. 92-100
- J.H. Shaw, T.S. Carter **Calving patterns among American bison** *J. Wildlife Manage.*, 53 (1989), pp. 896-898
- Tenhumberg et al., 2009. B. Tenhumberg, A.J. Tyre, R. Rebarber. **Model complexity affects transient population dynamics following a dispersal event: a case study with pea aphids** *Ecology*, 90 (2009), pp. 1878-1890
- S. Veran, O. Gimenez, E. Flint, W.L. Kendall, P.F. Doherty, J.D. Lebreton **Quantifying the impact of longline fisheries on adult survival in the black-footed albatross.** *J. Appl. Ecol.*, 44 (2007), pp. 942-952
- B.K. Williams, J.D. Nichols, M.J. Conroy. **Analysis and Management of Vertebrate Populations.** Academic Press, San Diego (2002)

J.M. Yearsley **Transient population dynamics and short-term sensitivity analysis of matrix population models***Ecol. Model.*, 177 (2004), pp. 245-258