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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.

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

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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:

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

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