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Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics

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Abstract. Understanding the relative effects of climate, harvest, and density dependence on population dynamics is critical for guiding sound population management, especially for ungulates in arid and semi-arid environments experiencing climate change. To address these issues for bison in southern Utah, we applied a Bayesian state-space model to a 72-year time series of abundance counts. While accounting for known harvest (as well as live removal) from the population, we found that the bison population in southern Utah exhibited strong potential to grow from low density ($\beta_0 = 0.26$; Bayesian credible interval based on 95% of the highest posterior density: BCI = 0.19 to 0.33), and weak but statistically significant density dependence ($\beta_1 = -0.02$, BCI = -0.04 to -0.004). Early spring temperatures also had strong positive effects on population growth ($\beta_{\text{febaprtemp1}} = 0.09$, BCI = 0.04 to 0.14), much more so than precipitation and other temperature-related variables (model weight > 3 times more than that for other climate variables). Although we hypothesized that harvest is the primary driving force of bison population dynamics in southern Utah, our elasticity analysis indicated that changes in early spring temperature could have a greater ‘relative effect’ on equilibrium abundance than either harvest or the strength of density dependence. Our findings highlight the utility of incorporating elasticity analyses into state-space population models, and the need to include climatic processes in wildlife management policies and planning.

Key words: Bayesian statistics, conservation, elasticity analysis, hierarchical model, phenology, wildlife management.

INTRODUCTION

According to Malthus' (1798) first law of population dynamics, all species have the potential to grow exponentially in number given ample resources. He recognized, however, that competition for resources and other crowding mechanisms (e.g., pathogen transmission and predator functional responses) eventually regulate populations from escaping to infinity. These principles of 'density dependence' have since been central to the way of thinking about population dynamics. In fact, harvest management revolves around the very concept of density dependence, whereby population density is manipulated in an attempt to optimize long-term yield or keep abundance at a targeted level below carrying capacity (e.g., Beverton and Holt 1957, Getz and Haight 1989). Density-independent variables (e.g., climate) also affect population dynamics, often quite strongly (Berteaux and Stenseth 2006), which can make it difficult to sustainably manage populations in stochastic systems (Sale 1990).

Identifying the relative impacts of density-dependent and density-independent drivers of population dynamics has thus been of long interest and the topic of vigorous debate (Andrewartha and Birch 1954, Lack 1954). The debates have dissipated, but detection and proper estimation of density dependence remains a challenge. For example, analyses of density dependence in commonly collected time series of population counts have been plagued by a lack of independence between ordinate and abscissa variables. This leads to shared sampling variation between the analyzed axes that, if not accounted for, biases estimation towards greater strength (and presence) of density dependence than actually exists (Bulmer 1975, Shenk et al. 1998, Freckleton et al. 2006). In part because of this problem, Krebs (1995) related the search for density dependence in time series data to that 'for the holy grail'. Modern state-space models have nevertheless allowed ecologists to overcome issues with such data by decoupling sampling

from process variation (DeValpine and Hastings 2002, Clark and Bjørnstad 2004, Dennis et al. 2006); making it possible to use widely available monitoring data to gain insight into the density-dependent and density-independent mechanisms that affect population dynamics (e.g., Stenseth et al. 2003, Wang et al. 2006, Rotella et al. 2009).

Herbivorous mammals can be particularly sensitive to climate-driven changes in primary productivity and the phenological timing of plant greening (Pettorelli et al. 2005a, b, c, 2007). In addition, density-related competition for available forage can compound the effects of density-independent variation in climate, and together strongly affect herbivore fitness components and population dynamics (e.g., Karels and Boonstra 2000, Coulson et al. 2001, Hone and Clutton-Brock 2007, Creel and Creel 2009). Not surprisingly, state-space models are increasingly being used to hone our understanding of how climate, density dependence, and harvest collectively shape herbivore population dynamics in a changing world (e.g., Sæther et al. 2007, Colchero et al. 2009). A logical extension would be to couple perturbation analyses with state-space models in order to provide managers with measures of the relative impact each variable (harvest rate, precipitation, etc.) has on equilibrium abundance (Grant and Benton 2000, 2003).

The American bison (*Bison bison*; hereafter 'bison') was once a numerous keystone herbivore that played an instrumental role in shaping North America's prairies and rangelands (Knapp et al. 1999). Although hunted to near the brink of extinction, significant conservation efforts have helped bison recover in isolated areas but significant challenges remain (Soper 1941, Cahalane 1944, Freese et al. 2007). Through these efforts, the bison remains an icon of the American west that instills a connection to nature and America's history among millions of tourists, nature enthusiasts, and sportsmen each year (American Bison Society 1908, Rudzitis 1999, Rasker and Hansen 2000).

Controlled hunting and translocation (collectively, ‘extraction’) are used to manage bison numbers in and between areas within metapopulation management programs. Managers must also be mindful of density-dependent competition for available forage because of feedback effects on bison dispersal and demography, as well as the potential to create conflict with the cattle industry (Fuller et al. 2007a, b, Plumb et al. 2009, Koons et al. 2012). Understanding the influences of perturbations to extraction rates, climate variables, and strength of density dependence on population dynamics will thus be especially critical for managing bison amidst the significant pressures imposed by land-use, water-use, and climate change (Lemly et al. 2000, Pringle 2000, Northrup and Wittemyer 2013). Here, we use long-term datasets to examine the impacts of these processes on the population dynamics of bison in the Henry Mountains of southern Utah using Bayesian state-space models. We additionally apply an elasticity analysis to our models in order to identify the relative influence of extraction, climate, and density dependence on bison population dynamics.

METHODS

Study area and data collection

In 1941, 18 plains bison (*Bison bison bison*; 3 bulls and 15 cows) were moved from Yellowstone National Park to a desert location just north of the Henry Mountains (HM) in south-central Utah. An additional 5 bulls were released in 1942 because of some bull dispersal out of the herd, and the herd eventually moved to the HM where the introduced population has remained ever since (Popov and Low 1950). The HM study area consists of arid, semi-arid, and sub-alpine habitats that bison utilize during their seasonal migrations from low to high altitudes (see Nelson 1965 and van Vuren and Bray 1986 for study area descriptions). The HM bison population is unique in a number of ways. For example, surrounding deserts and cliffs keep the

population closed to natural emigration. Mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) utilize the study area, but focus their foraging efforts on abundant deer rather than risking the injuries that adult bison could impose on such predators (Lott 1991). Bison are thus largely free of natural predation on the study area (van Vuren and Bray 1983). Moreover, the HM population is free-ranging and genetically pure; making it a population of great conservation value (Halbert and Derr 2007).

Without a natural regulator to control population growth, however, the Utah Division of Wildlife Resources (UDWR) began managing the HM bison population through a limited-entry hunt in 1960, as well as by translocating bison to other areas in the state. With few exceptions, the number of bison legally harvested from the HM each year is known (from 2004 onward, all hunters were legally mandated to report their harvest; prior to this period all hunters were surveyed). In addition to these harvest and translocation data, the UDWR has conducted annual surveys to count the number of bison at the end of July or in early August each year since 1949 (with the exception of 1968). Historically these surveys involved 12 or more personnel on foot, horseback, or in a vehicle counting bison in specified zones across the study area, but since 1990 an aerial helicopter survey has been used (R. Hodson personal communication). The helicopter crew usually consisted of 4 individuals: the pilot, an experienced primary observer seated next to the pilot, an experienced secondary observer and recorder seated behind the primary observer, and an additional observer seated behind the pilot. Because the rugged topography of the HM study area prevents the crew from flying systematic transects, the pilot and primary observer dictate a flight path that safely and efficiently follows the terrain, and can be completed in < 2 days. Once a herd is sighted, the pilot typically circles the herd such that counting can take place from the primary observer's side, while the third observer watches for stray individuals on the

pilot's side of the helicopter. In order to reduce counting error, a slow hover is used such that both the primary and secondary observers have enough time to attain counts that agree with one another. Upon completion of herd enumeration, the helicopter returns to the original flight path. A recent assessment of the helicopter survey indicated a nearly 100% coverage of the study area (Terletzky 2013).

The HM bison herd also shares the open range with cattle, which is an instrumental component of the current UDWR bison management plan. Through input from multiple stakeholder groups, the currently agreed upon objective is to use hunting and translocations to maintain 325 adults in the population after the annual hunting season (UDWR 2007). Common to most conservation and management issues, a better understanding of demographic mechanisms is nevertheless needed to consistently meet this objective (see Koons et al. 2012).

To help fill these gaps and test our predictions presented below, we sought climate variables that could affect bison demography via effects on plant forage at crucial times of the year (e.g., leading up to parturition). Specifically, we focused on mean temperature measured annually or in a specific season, as well as total precipitation occurring annually, in a specific season, or in a specific month. We set the bison year as that beginning on August 1 when the HM abundance survey occurs, and defined 4 × 3-month seasons for the climate variables: August–October, November–January, February–April, and May–July. Given that bison have high life expectancy (Peterson et al. 1991) and delayed age at maturity (2+, with primiparity being most frequent at age 3; Wolfe et al. 1999), their population dynamics could be influenced by lagged cohort effects driven by climate variability (Descamps et al. 2008, Hamel et al. 2009). We thus considered immediate as well 1- and 3-yr lagged effects of each climate variable on HM bison population dynamics (see below). A lag-1 climate effect could result from variables in the birth year

affecting juvenile survival and abundance in the following year, whereas a lag-3 effect could result from climate variables in the birth year eventually affecting the net number that recruit to the breeding population and the pulse (or lack thereof) of offspring they contribute in that year. All climate variables were z-standardized before analysis (i.e., (observation-mean)/standard deviation).

Because the nearest meteorological station (Hanksville, Utah) was at a lower elevation and more arid location than our study area, we used the Parameter-elevation Regressions on Independent Slopes Model (PRISM; <http://www.prism.oregonstate.edu/>; Daly et al. 2000) to attain climate data at a mid-elevation location near the west-central part of the study area that bison frequently use (38° 2' N, 110° 54' W; mean temperature of 9.75 ° C, and 24.85 cm of precipitation annually).

Hypothesis development and predictions

Although adult survival in bison and other large ungulates is often high and robust to density-dependence as well as environmental variability (Gaillard and Yoccoz 2003, Eberhardt 2002, Fuller et al. 2007b, Bonenfant et al. 2009), offspring recruitment is often highly responsive to these processes (Gaillard et al. 1998, Bonenfant et al. 2009, Koons et al. 2012). Moreover, the effects of climate on primary productivity and the phenological timing of plant greening leading up to parturition and lactation may play a particularly important role in shaping the early-life demography of ungulates (Pettorelli et al. 2005a, b, c, 2007). Given that climate at particular times of the year can have strong effects on plant growth and productivity in arid and semi-arid environments (Noy-Meier 1973; Rosenzweig 1968), and in turn affect offspring development in bison (Craine et al. 2009), we hypothesized that climate in the season preceding parturition would have a greater influence on bison population dynamics in the Henry Mountains than in

other seasons. However, we predicted that extractions have been the primary driver of population dynamics, offering managers the ability to adapt rates of extraction in response to other environmental perturbations.

Bayesian state-space models for population dynamics

We base our analysis of HM bison population dynamics on the discrete-time Gompertz model

$$N_t = N_{t-1} \exp(r + b * \log(N_{t-1})), \quad (1)$$

where r is the intrinsic rate of growth from low abundance ($N = 1$) and b is the strength of density dependence (Turchin 2003, Dennis et al. 2006). Given its tendency to better describe compensatory density dependence (Sibly et al. 2005), we chose the Gompertz model for bison that exhibit delayed age at maturity and maximum of one calf per year among mature females (Meagher 1986) rather than, e.g., the Ricker model that might be preferred for a more fecund species that could experience over-compensatory dynamics (Turchin 2003). On the logarithmic scale, the Gompertz model becomes linear and easier to work with:

$$\log(N_t) = x_t = x_{t-1} + r + bx_{t-1}. \quad (2)$$

Hunting of the HM bison population occurs in the autumn following the survey, and when translocations occur, they are typically done shortly after the hunting season. We thus implemented known extractions (E : usually known harvest, but sometimes the combination of known harvest and translocations) into eqn. 2 using a post-harvest parameterization

$$x_t = x_{t-1} + e_{t-1} + r + b(x_{t-1} + e_{t-1}), \quad (3)$$

where $e_{t-1} = \log|1 - E_{t-1}/N_{t-1}|$ is the logarithmic integration of extractions occurring in the season following the survey at $t-1$, which is zero in the absence of extractions and negative otherwise (see Colchero et al. 2009 for a pre-harvest parameterization). Given the timing of the

survey, this parameterization is appropriate for the HM bison population because density after extractions is that which is most likely to influence bison demography (see Iijima et al. 2013 for a similar model). For example, density following the autumn hunt could influence the level of competition for forage during the stressful winter and spring seasons, which could in turn affect offspring development or rates of abortion during mid and late parturition. Moreover, competition for forage during late spring and early summer could influence lactation and calf survival up to the August surveys; whereas pre-harvest densities would only influence the processes of conception and early gestation.

To estimate the parameters of a Gompertz model with extractions, we fit a Bayesian state-space model to the HM survey data, which consisted of the following pair of equations:

$$x_t = f(x_{t-1}) + \varepsilon_t \quad (4a)$$

$$y_t = g(x_t) + \eta_t. \quad (4b)$$

Equation 4a represents the ‘process model’ for population dynamics, and $f(x_{t-1})$ is a model like that on the right-hand side of eqn. 3, with $\varepsilon_t \sim N(0, \sigma_p^2)$ representing a Gaussian error term that measures the process variance of population dynamics not explained by $f(x_{t-1})$. The ‘observation model’ in eqn. 4b links the underlying latent process model of population dynamics to the observed count data y_t while controlling for η_t , the observation or ‘sampling’ error (Clark and Bjørnstad 2004). Most often, y_t represents the log of observed counts and a $N(0, \sigma_o^2)$ distribution is used to model η_t (i.e., a log-normal observation model). For reasons discussed in appendix 1, however, we chose to use a Poisson distribution for the observation errors. Regardless of the chosen distribution, η_t nicely accounts for random under- and over-counting each year (Kéry and

Schaub 2012), both of which can occur in surveys of bison abundance and other animals (Marques et al. 2009, Terletzky 2013).

To examine the effects of the aforementioned climate variables on bison population dynamics, we extended eqn. 4a to include covariates:

$$x_t = x_{t-1} + e_{t-1} + \beta_0 + \beta_1(x_{t-1} + e_{t-1}) + \mathbf{X}_t \boldsymbol{\beta}_{\text{clim}} + \varepsilon_t \quad (5)$$

where β_0 and β_1 are the coefficients for r and b in eqn. 3, respectively, and $\boldsymbol{\beta}_{\text{clim}}$ is the vector of coefficients to be estimated for \mathbf{X}_t , the design matrix of time-varying climate covariates.

Although rarely mentioned, β_0 and β_1 are only partially identifiable, but separate estimation of these parameters can be improved in a Bayesian analysis by using external information to inform the prior distributions (Delean et al. 2013, Lebreton and Gimenez 2013).

Prior distributions and model implementation

Given the extensive literature on maximal rates of population growth in mammals, and maximal demographic vital rates in bison (Henneman 1984, Peterson et al. 1991, Duncan et al. 2007, Fuller et al. 2007, Hone et al. 2010, Koons et al. 2012), we were able to estimate an informative Gaussian prior for β_0 with mean = 0.28 and $\sigma = 0.04$. For $-2 < \beta_1 < 0$, a population will experience standard density dependence and approach a stochastic equilibrium, but at 0, density independence occurs. Below -2 the coefficient of density dependence becomes so strong that it leads to unstable chaotic dynamics, and above 0, density has a positive effect on population growth (Dennis et al. 2006). Equation 5 can thus capture a wide range of dynamics, but because bison do not have the kind of life history that can produce unstable dynamics (May 1974), and may sometimes experience positive feedbacks through the benefits grazing can have on plant growth (e.g., through grazing optimization; Van der Graaf et al. 2005), we used a moderately informative Gaussian prior for β_1 with mean = 0 and $\sigma = 2$ truncated at -2 and 2 to

252 exclude impossibilities. When estimating the β_{clim} coefficients, we used vague $N(0,100)$ prior
 253 distributions. We modeled the prior for process variance as $\sigma_p^2 \sim IG(s_1, s_2)$ with $s_1 = s_2 = 0.001$,
 254 and we used $y_t \sim \text{Pois}(\exp(x_t))$ to model observation error in the counts, which required no
 255 prior specification (see App. 1). Therefore, the likelihood for the process and data models is

$$\begin{aligned} Pr(\mathbf{x} | \mathbf{y}, \mathbf{E}, \boldsymbol{\beta}, \sigma_p^2) &= \prod_{t=1}^{T-1} N[x_{t+1} | f(x_t; \boldsymbol{\beta}), \sigma_p^2] \\ &\times \prod_{t=2}^T N[x_t | f(x_{t-1}; \boldsymbol{\beta}), \sigma_p^2] \\ &\times \prod_{t=2}^T \text{Pois}[y_t | x_t]. \end{aligned} \quad (6)$$

257 As such, the general joint posterior of the state-space models we considered can be written as:

$$\begin{aligned} Pr(\boldsymbol{\beta}, \sigma_p^2, \mathbf{x} | \mathbf{y}, \mathbf{E}) &\propto \overbrace{Pr(\mathbf{x} | \mathbf{y}, \mathbf{E}, \boldsymbol{\beta}, \sigma_p^2)}^{\text{Process and data models}} \\ &\times \overbrace{N(\boldsymbol{\beta} | \bar{\boldsymbol{\beta}}, \text{var}[\boldsymbol{\beta}])}^{\text{Priors for parameters}} \\ &\times \overbrace{IG(\sigma_p^2 | s_1, s_2)}^{\text{Prior for error}} \end{aligned} \quad (7)$$

259 where T is the number of years covered by the time series, and $\boldsymbol{\beta}$ is the vector of coefficients in
 260 eqn. 5 (Clark and Bjørnstad 2004). Because a known number of bison were introduced into the
 261 HM in 1941, initial abundance was treated as a constant rather than an unknown random
 262 variable.

263 We obtained posterior distributions for the estimated parameters using a Markov chain
 264 Monte Carlo algorithm (MCMC, Gelfand & Smith 1990) in JAGS 3.3.0 (Plummer 2012), run
 265 from the R2Jags package in R (Su and Yajima 2012; annotated R2jags code provided in the
 266 Supplement). For each model we ran three MCMC chains for 100,000 iterations and discarded
 267 the first 50,000 as burn-in. We then thinned the samples by keeping every 50th sample. The

multiple MCMC chains allowed us to use Gelman's (1996) \hat{R} statistic, along with traceplots, to monitor chain convergence.

Variable selection

Given the large number of precipitation (51) and temperature (15) variables under consideration, we decided to adopt a tiered approach to selecting climate variables that best explain variation in HM bison population dynamics. First, we allowed precipitation variables to enter eqn. 5 one at a time, and used the random effects implementation of Kuo and Mallick (1998) indicator variables to estimate posterior variable inclusion probabilities for each temperature covariate (O'Hara and Sillanpaa 2009). We then performed the same comparisons for the precipitation covariates. For each climate variable j , we modeled the indicator variable as $\gamma_j \sim \text{Bern}(0.5)$, and the climate variable coefficients as $\beta_{\text{clim},j} \sim N(0, \sigma^2)$ with the hyperparameter $\sigma \sim \text{Unif}(0, 20)$. All other parameters and MCMC settings were modeled as above.

Next, we proceeded to include in eqn. 5 all possible univariate and multivariate combinations of the top-ranking temperature and precipitation covariates from the preceding analyses, including interactions. Using a combination of indicator variables for the covariates and model indicators, we estimated posterior model probabilities using Ntzoufras' (2002) algorithm for

simple model sets: $1 + \sum_{j=1}^p \gamma_j 2^{j-1}$, where p is the number of variables considered inclusive of

interaction terms (see the Supplement for code to implement this algorithm). We assigned a 2^{-p} prior probability to each model under consideration. In the univariate analyses we found that the estimated coefficients for the top-ranking standardized climate variables, and their associated standard deviations, were small ($\ll 1$). Thus, we used more informative priors on β_{clim} with $\sigma \sim \text{Unif}(0, 2)$ to improve mixing among the competing models during MCMC iterations and to

avoid the Lindley-Bartlett paradox (unjust favoring of the simplest model considered; Lykou and Ntzoufras 2013). For the multivariate model comparisons, we increased the number of iterations to 1 million with burn-in of 100,000 and thinning to retain every 90th sample.

Relative effects of demographic mechanisms

For the more commonly implemented Gompertz process model with covariates, but not extractions ($x_t = x_{t-1} + \beta_0 + \beta_1 x_{t-1} + \mathbf{X}_t \boldsymbol{\beta}_{\text{cov}} + \varepsilon_t$), x_t will approach a density-regulated stochastic carrying capacity with a mean of $-(\beta_0 + \mathbf{X}_t \boldsymbol{\beta}_{\text{cov}})/\beta_1$ (or simply $-\beta_0/\beta_1$ if evaluating at the mean of climate anomalies) and a variance of $-\sigma_p^2/(\beta_1(\beta_1 + 2))$ as long as $-2 < \beta_1 < 0$ (Dennis et al. 2006, Allington et al. 2013). Anthropogenic extractions can nevertheless keep populations at sustainable equilibria below the environmental carrying capacity (Lebreton 2005, Hauser et al. 2006). Using our process model (eqn. 5) and parameter estimates from the most supported model, we projected the equilibrium abundance of HM bison at mean climate conditions ($\bar{\mathbf{X}}_t$), the mean rate of extraction since inception of the hunt (\bar{e}_t), and estimated process variance (σ_p^2). To measure the relative effects of extraction (primarily harvest), density dependence, and climate variables on mean equilibrium abundance, we changed each parameter one at a time (by 1%, 5%, or 10%), re-ran the projections, and calculated elasticities numerically according to:

$$e_{\omega} = \frac{\partial \log \theta}{\partial \log \omega} \doteq \frac{\theta_{\text{perturbed}} - \theta_{\text{original}}}{\theta_{\text{original}}} \frac{1}{\delta}, \quad (8)$$

where θ is the response parameter of interest (mean of stochastic equilibrium), ω is the parameter for which the elasticity is being calculated, and δ represents the proportional change in ω (e.g., Koons et al. 2007).

RESULTS

Variable selection

In the first step of selecting temperature variables to include in the process model (eqn. 5), we found that the lag-1 effect of mean temperature during February – April (mean = 4.25 °C, sd = 1.26, range = 1.12–6.64, see Fig. 1) on HM bison population dynamics was by far the most supported temperature variable (model weight $w_j = 0.56$). Temperature between May and July of the immediate year received much less support ($w_j = 0.15$), and other variables even less (Appendix 2). Among the precipitation covariates, a lag-3 effect of precipitation in December (mean = 1.70 cm, sd = 1.18, range = 0–4.81, see Fig. 1) was most supported by the data ($w_j = 0.09$) followed by June precipitation in the immediate bison year ($w_j = 0.07$). Weight-based separation among the precipitation models was weak (Appendix 2).

We were prohibited from considering multivariate sequences of like climate covariates (e.g., immediate + lag-1 effects of mean temperature) because of the high degree of multicollinearity among the time series (Pearson $r > 0.75$). Thus, we next focused on comparing the baseline Gompertz process model without climate covariates (eqn. 3) to those including the lag-1 effect of mean temperature during February – April and the lag-3 effect of December precipitation, as well as their additive and interactive effects.

Given this reduced set of models, addition of lag-1 mean temperature during February – April to the Gompertz process model was by far the most supported climate model ($w = 0.51$, Table 1). Simultaneous inclusion of lag-3 December precipitation in an additive or interactive fashion led to sharp declines in model weight (Table 1). On its own ($w = 0.03$), lag-3 December precipitation did not even beat the baseline Gompertz model with extractions ($w = 0.06$). Our posterior distributions from the top model indicated strong potential for the HM bison population to grow from low density ($\beta_0 = 0.26$, median = 0.26, sd = 0.04, Bayesian credible interval based

on 95% of the highest posterior density: $BCI = 0.19$ to 0.33), weak but statistically significant density dependence ($\beta_1 = -0.02$, median = -0.02 , $sd = 0.01$, $BCI = -0.04$ to -0.004), and a positive effect of the lagged February – April temperature on bison population growth ($\beta_{\text{febaprtemp1}} = 0.09$, median = 0.09 , $sd = 0.03$, $BCI = 0.04$ to 0.14). There was additionally a fair amount of unexplained process variability ($\sigma_p = 0.17$, median = 0.17 , $sd = 0.02$, $BCI = 0.13$ to 0.22). Posterior estimates of β_1 , $\beta_{\text{febaprtemp1}}$, and σ_p^2 were insensitive to the specified prior distributions and were highly informed by the data. As expected, however, the data had an effect on the estimated posterior density of β_0 , but so did the informative prior distribution; indicating that previous studies provide valid information about the ability of bison populations to grow from low density (see App. 3). Our top model additionally produced predicted estimates of HM bison abundance that closely tracked surveyed counts in most years (Fig. 2)

Relative effects of demographic mechanisms

We used the top-ranked model described above to examine the relative effects of demographic mechanisms on HM bison population dynamics because of its overwhelming support relative to other models. Using this model and study-wide means of lag-1 temperature during February through April (4.25°C), as well as the mean extraction rate since inception of the hunt (0.13 ; the mean number of extractions, including years without a hunt, was 30 , $sd = 38$, range = 0 – 164 , see Fig. 2), the associated prediction for equilibrium abundance was 437 individuals (inclusive of calves; 6.08 on the log scale). The elasticity analysis indicated that this equilibrium is most responsive to changes in lag-1 temperature between February and April each year, followed by the extraction rate and strength of density dependence (Table 2). Increasing the extraction rate or density dependence logically reduces the equilibrium whereas increasing the February through April temperature increases the equilibrium given its estimated positive effect

on HM bison population dynamics. Moreover, the elasticities were robust to the magnitude of proportional change used, indicating linear or nearly linear relationships between the focal parameters and equilibrium abundance (Table 2).

DISCUSSION

By integrating elasticity analyses into the state-space modeling framework, we were able to not only estimate the effects of density dependence, climate, and extractions on bison population dynamics, but also evaluate their relative impacts. Contrary to our predictions, proportionate changes in early spring temperature could have a greater ‘relative effect’ on the HM bison population than changing the rate of extraction or environmental changes in the strength of density dependence; further highlighting the need to incorporate climatic processes into extraction-based management plans (Colchero et al. 2009). For the time being, it seems that warm early springs are better for HM bison; echoing climate change impacts on other herbivorous mammals in the intermountain west (Ozgul et al. 2010). Although elasticity analyses are most often applied to matrix population models (Caswell 2001), they can readily be applied to any type of model. Our approach could thus be widely useful for guiding conservation and management in an efficient manner by identifying the drivers of population dynamics that have the greatest impact using population models developed from readily available survey data.

However, the ability to estimate density dependence from such data has long been fraught with difficulty and statistical bias (Freckleton et al. 2006). By modeling both the observed count data and the latent population processes of interest, modern state-space models offer a way forward for overcoming these challenges (e.g. Clark and Bjørnstad 2004). One must nevertheless remain aware of potential issues with weak parameter identifiability in these models (Lebreton and Gimenez 2013). Utilizing the wealth of research on mammalian life histories, we were able

to develop logical science-based prior distributions for the maximal rate of population growth from low density and the range of possible density-dependent interactions, which helped us estimate these unique parameters for the HM bison population. We suggest that similar approaches be used to reevaluate existing datasets in an effort to finally gain less biased insight into density dependence across taxa (Delean et al. 2013).

With respect to HM bison, the population exhibited strong potential to grow from low density after introduction and reductions in density following later perturbations imposed by environmental conditions and extractions ($\beta_0 = 0.26$). This implies that the local ecosystem can support a healthy bison population that could serve as a (genetically pure and disease-free) source for replenishing bison elsewhere as part of large-scale conservation efforts (Halbert and Derr 2007, Hedrick 2009). An over-abundance of bison, however, can force them to seek forage in non-optimal areas that can in turn lead to conflict with other land stakeholders (Fuller et al. 2007a, Geremia et al. 2014). Our model explicitly accounts for the mechanisms of intrinsic density dependence and anthropogenic extractions that can both regulate population dynamics; thereby allowing managers to refine actions based on the difference between actual and objective levels of abundance using demographic models within an adaptive management framework (e.g. Walters 1986, Williams et al. 2007).

Because of its potentially strong impact on population dynamics (Table 2; Wang et al. 2006), climate is now being considered within adaptive management frameworks (Conroy et al. 2011, Nichols et al. 2011). Previous research on a shorter time series of composition counts indicated that annual precipitation could be an important driver of HM bison reproductive success (Koons et al. 2012). However, we found here that precipitation had a lesser effect on long-term bison population dynamics compared to early spring temperatures (Table 1). Warm temperatures

during early spring had a strong, positive effect on population dynamics, perhaps because such conditions are amenable to plant growth and greening (Cleland et al. 2007), whereas cold conditions may delay plant phenology relative to bison parturition and ensuing lactation demands. Logically, this might affect rates of successful birth from late April through June (Nelson 1965) and early calf survival through the summer (Craine et al. 2009); in turn having an immediate impact on bison abundance during August surveys. However, the strong lag-1 effect of spring temperature implies that perhaps the greater demographic impact takes place throughout juvenile development and net survival to the following survey when a cohort is ~ 1.3 years old. In addition to affecting forage phenology, warm temperatures could also help relax the need for young bison to burn valuable fat stores for thermoregulation as they transition out of winter and into the spring season; a time period that is often critical for the survival of young ungulates (Garrott et al. 2003). Through nutritional and thermoregulatory mechanisms, a warming climate (see Fig. 1) could thus enhance bison demographic performance until thresholds are eventually reached where either bison cannot keep up with plant phenology (the mismatch hypothesis; Visser and Both 2005) or experience heat exhaustion (the thermal tolerance hypothesis; Pörtner and Farrell 2008). In addition, if future temperatures become increasingly variable as predicted (Räisänen 2002), enhanced stochasticity of vital rates could eventually reduce the long-term population growth rate of HM bison (Lewontin and Cohen 1969).

Before such thresholds are reached, however, density dependent feedbacks might play a greater role in regulating population dynamics. The estimated strength of density dependence in HM bison population dynamics was nevertheless weak compared to other free-ranging populations in western North America (e.g., Larter et al. 2000, Fuller et al. 2007a, Geremia et al.

2009). The high rates of extraction (up to 32%) that keep the HM population below its carrying capacity undoubtedly diminish intrinsic feedbacks, but the relative lack of disease and severe winter snowpack might also be contributing factors (Geremia et al. 2009, Plumb et al. 2009). Although it was once thought that large animals like bison should experience strong density dependence because of K-selection (Pianka 1970), these ideas have since been replaced (see Reznick et al. 2002), and recent evidence suggests that long-lived species actually tend to experience weaker density dependence than short-lived species (Herrando-Perez et al. 2012). These findings are not altogether that surprising because large gregarious bison are highly mobile, even nomadic, and can range long distances in search of food (Lott 1991); thereby diminishing the forces of density dependence relative to those that might be experienced by a non-hunted or enclosed population that is not able to move freely in an ideal fashion (Fretwell and Lucas 1970, Fretwell 1972). It is nevertheless possible that density-dependent processes were obscured by underlying variation in the population's age structure driven by harvest. For example, when HM bison abundance is low, harvest rates tend to be higher than average, which can create an age structure of young individuals that are less likely to recruit calves successfully, and vice versa (KH pers. obs.). As described below, an age-structured model would be needed to decouple these mechanisms.

It is also important to note that a large amount of process variability in HM bison population dynamics could not be explained by early spring temperatures, extractions, and intrinsic density dependence. Ranchers and cattle have shared the HM with bison since their introduction, and given their high dietary overlap and ecological similarity (van Vuren and Bray 1983, Allred et al. 2011, Kohl et al. 2013), there is strong potential for cattle to compete with bison for forage and impact their population dynamics on shared rangelands, but we could not account for such

effects given the lack of data on the number of cattle that have actually used the HM each year. Using a unique combination of experimental exclosure and space-use studies, however, our colleagues are finding that competition between bison and cattle for forage on the HM is minimal under recent environmental conditions (Ranglack et al. *In Review*, Ranglack and du Toit *In Review*); perhaps because cattle must remain near limited sources of water while bison can range more freely (van Vuren 2001). Complex interactions between climate, phenology and primary productivity, as well as transient fluctuations in age and sex structure induced by extractions (Buhnerkempe et al. 2011) might help explain greater amounts of variability in bison population dynamics on the HM.

In conclusion, climate likely has its strongest effect on bison populations during early life-cycle stages (Koons et al. 2012), as juveniles tend to be more responsive and susceptible to environmental variation than adults in large mammals (Gaillard et al. 1998). However, the impacts of climate and density dependence across the age- and sex-structured life cycle will need to be estimated in order to better understand how these mechanisms affect HM bison population dynamics (e.g., Geremia et al. 2009). Moreover, our unstructured state-space model may have attributed too much of the variation in population dynamics to demographic processes rather than observation error, sometimes resulting in predicted rates of growth that may be unrealistically high (e.g. $\geq 40\%$ growth in 1977, 1978, 1990, 1993, 2006, 2007; Fig. 2). Unlike well-studied federal populations (e.g., Buhnerkempe et al. 2011), long-term age- and sex-structured survival data do not exist for the HM population. We are currently conducting a radio telemetry study of adult bison survival, and plan to eventually couple these data with the long-term count, extraction, and herd composition data to gain insight into age- and sex-structured dynamics of the HM population using an Integrated Population Model (IPM). IPMs simultaneously integrate

the information contained in multiple datasets (Besbeas et al. 2002, Brooks et al. 2004, Conn et al. 2008), which makes it possible to estimate vital rates that are not directly monitored (e.g. juvenile survival), and link changes in management or environmental variables to estimated vital rates throughout the life cycle (e.g. Johnson et al. 2010, Schaub and Abadi 2011). By using monitoring data to provide detailed insight into the dynamics of managed populations, IPMs offer a rigorous estimation tool for bridging management decisions with monitoring programs in an adaptive management framework (Tempel et al. 2014). The insight provided by our state-space model presented here is a critical step in eventually reaching these objectives for bison in Utah and other wildlife populations across the globe.

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SUPPLEMENTAL MATERIAL

Appendix A

Comparison of observation models used in the Gompertz state-space model with extractions.

Appendix B

Posterior Bayesian model weights for temperature and precipitation covariates.

Appendix C

Comparison of posterior and prior probability densities for parameters in the top process model.

Supplement

Annotated R2jags code for implementing Gompertz state-space models of population dynamics with known extractions.

791 Table 1. Posterior Bayesian model weights (w) for univariate and multivariate additions of
 792 February – April mean temperature (temp) and December precipitation (ppt) to the Gompertz
 793 process model with extractions for HM bison population dynamics. Weights were calculated by
 794 normalizing the posterior model probabilities. Subscripted numbers denote the time-lag of the
 795 covariate.

Model	w
Feb-Apr _{temp,1}	0.51
Feb-Apr _{temp,1} + Dec _{ppt,3}	0.27
Feb-Apr _{temp,1} + Dec _{ppt,3} + Feb-Apr _{temp,1} × Dec _{ppt,3}	0.14
Baseline Gompertz model with extractions	0.06
Dec _{ppt,3}	0.03

796 Table 2. Elasticities of mean equilibrium abundance for the HM bison population to proportional
 797 changes (δ) in the extraction rate, coefficient for density dependence (β_1), and (lag-1) average
 798 temperature between February and April relative to study-wide mean environmental and
 799 extraction conditions.

Parameter	Elasticities		
	$\delta = 0.01$	$\delta = 0.05$	$\delta = 0.10$
Extraction rate	-1.211	-1.215	-1.219
β_1	-0.966	-0.929	-0.887
Feb-Apr _{temp,1}	2.405	2.405	2.405

800 Figure 1. A plot of lag-1 mean temperatures (in °C) during February through April ('Feb-Apr
801 temp') each year at the center of the Henry Mountains study area (solid line, left axis), and total
802 lag-3 precipitation (in cm) in December ('Dec ppt', dashed line, right axis).

803
804 Figure 2. Predicted estimates of annual Henry Mountains bison abundance in southern Utah
805 (black line, with 95% credible interval denoted by the grey polygon on the left axis) relative to
806 observed counts (open circles) based on the top-ranking state-space model in Table 1. For years
807 when data were available, the correlation between observed and predicted abundances was 0.99.
808 The annual number of extractions from the population (solid circles) is shown on the right axis.

Feb-Apr temp

7
6
5
4
3
2
1
0

1940

AR-Yellowstone Bison

1950

1960

1970

1980

1990

2000

2010

Year

0533

Dec ppt

7
6
5
4
3
2
1
0

