SPATIAL AND TEMPORAL VARIABILITY MODIFY DENSITY DEPENDENCE IN POPULATIONS OF LARGE HERBIVORES

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Abstract. A central challenge in ecology is to understand the interplay of internal and external controls on the growth of populations. We examined the effects of temporal variation in weather and spatial variation in vegetation on the strength of density dependence in populations of large herbivores. We fit three subsets of the model $\ln(N_t) = a + (1 + b) \times \ln(N_{t-1}) + c \times \ln(N_{t-2})$ to five time series of estimates (N_t) of abundance of ungulates in the Rocky Mountains, USA. The strength of density dependence was estimated by the magnitude of the coefficient b. We regressed the estimates of b on indices of temporal heterogeneity in weather and spatial heterogeneity in resources. The 95% posterior intervals of the slopes of these regressions showed that temporal heterogeneity strengthened density-dependent feedbacks to population growth, whereas spatial heterogeneity weakened them. This finding offers the first empirical evidence that density dependence responds in different ways to spatial heterogeneity and temporal heterogeneity.

Key words: Bayesian hierarchical model; climate variability; density dependence; large herbivores; Markov Chain Monte Carlo Method; normalized difference vegetation index; population dynamics; Rocky Mountains; spatial variability; temporal variability.

INTRODUCTION

Studies of large herbivores in temperate environments have shown that internal processes regulating population growth are shaped by variability in external conditions. Temporally variable weather conditions can synchronize population dynamics (Grenfell et al. 1998, Post and Forchhammer 2002, Aanes et al. 2003) and can add to the effects of density-dependent feedbacks retarding population growth (Forchhammer et al. 1998, Milner et al. 1999, Coulson et al. 2001, Mysterud et al. 2001*b*, Solberg et al. 2001). Elevated population density amplifies the stochastic effects of weather, even when deterministic density dependence is weak (Aanes et al. 2000). In contrast to the emerging understanding of the effects of temporal variability on population dynamics, the effects of spatial variation remain largely unknown.

There is reason to believe that spatial heterogeneity in resources might weaken the effects of weather and density on the population growth of large herbivores by improving nutrition of individuals. For example, variation in topography causes plants to mature at different times. Large herbivores move to track this to-pographically induced variation in plant phenology, thereby extending the interval of time when plants can be consumed at peak nutritional quality (Albon and Langvatn 1992, Frank and McNaughton 1992, 1993, Wilmshurst et al. 1999, Mysterud et al. 2001*a*). Moreover, spatially heterogeneous landscapes often include habitats where food resources are stable in time. These resources remain accessible to herbivores in the face of weather conditions that create seasonal or episodic resource shortages over most of the landscape (Hunter 1962, Wallmo et al. 1977, Gordon 1989, Illius and O'Connor 1999). It follows from these examples that spatial variation in resources may allow herbivores to exploit temporally variable pulses in forage resources and mitigate resource shortages, thereby attenuating the effects of weather and density on vital rates of their populations.

Here, we show how population trajectories of large, mobile herbivores respond to density-dependent feedbacks and how those feedbacks are shaped by temporal variation in weather and spatial variation in vegetation. We offer evidence that temporal variability in weather conditions and spatial variability in vegetation exert opposing effects on the strength of density-dependent control on population growth.

METHODS

We analyzed time series of data on the abundance of five populations of ungulates in the Rocky Moun-

tains, USA. The briefest of these time series spanned 31 years; the longest, 75 years. Data on annual counts of the five populations appear in the Appendix. Variation in abundance (N_t) was analyzed for each population using subsets of the global model

$$\ln(N_t) = a + (1 + b)\ln(N_{t-1}) + c\,\ln(N_{t-2})$$

where a is the intrinsic rate of increase, b represents the effect of direct density dependence, and c is coefficient describing the effects of delayed density dependence. When $1 + b < 1$, increases in the magnitude of b indicate increasingly strong, direct negative feedback between population density and per capita population growth rate. We examined correlations between the absolute value ($|b|$) of b and indices of temporal variation in weather and spatial variation in vegetation. We also regressed the $|b|$ over mean NDVI (Normalized Difference Vegetation Indices) and mean winter temperatures, respectively. We used the AIC_c values (corrected Akaike Information Criterion) to select the best approximating model pairwisely. We calculated 95% posterior intervals of the slopes of the regressions of $1 + b$ and heterogeneity indices.

Annual counts were obtained for a population of bison (*Bison bison*) in northern Yellowstone National Park (NYP); 44°43′ N, 110°38′ W), Wyoming; and for populations of elk (*Cervus elaphus*) in Rocky Mountain National Park (RMNP; 40°23′ N, 105°38′ W), Colorado; the National Elk Refuge (NER; 44°02′ N, 110°38′ W), Wyoming; the northern range of Yellowstone National Park (YNP; 44°56′ N, 110°32′ W); and the Gravelly Mountains, Montana (44°38′ N, 111°52′ W). Counts were obtained by aerial survey during late winter (Singer et al. 1997, Lubow et al. 2002, Lubow and Smith 2004). We chose these populations because they experienced reasonably similar climatic conditions and because all populations provided a time series exceeding 30 years.

Density-independent ($b = c = 0$) and autoregressive (AR) models of order (p) 1 and 2 were fitted to the abundance data. Counts of animals have inherent measurement errors that may bias estimates of the strength of density dependence (Stenseth et al. 2003). To account for measurement errors, we used the classic Kalman filter (Harvey 1989), a state–space time series model, to analyze the time series of counts (N_t). In the state space model (SSM), a true state variable X_t is unobservable; however, the observation of the true density Y_t ($= \ln N_t$) is the true state (X_t) plus a random measurement error (u_t), i.e., $Y_t = X_t + u_t$. Therefore, the structural form of the AR(p) Gompertz model (Royama 1992) is

$$X_t = a + (1 + b)X_{t-1} + c_2 X_{t-2} + \cdots + c_p X_{t-p} + e_t \quad (1)$$

$$Y_t = X_t + u_t. \quad (2)$$

Error terms e_t and u_t are assumed to be normal and independent of each other and independent over time,

i.e., $e_t \sim \mathcal{N}(0, \sigma_e^2)$, $u_t \sim \mathcal{N}(0, \sigma_u^2)$, $\mathrm{Corr}(e_t, u_t) = 0$. Given these assumptions, the AR(p) Gompertz model was arranged as

$$\mathbf{X}_t = \mathbf{F}_t \mathbf{X}_{t-1} + \mathbf{w}_t \quad (3)$$

$$\mathbf{Y}_t = \mathbf{H}_t \mathbf{X}_t + \boldsymbol{\varepsilon}_t \quad (4)$$

$$\begin{pmatrix} \mathbf{w}_t \\ \boldsymbol{\varepsilon}_t \end{pmatrix} \sim \mathcal{N}\left[\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \begin{pmatrix} \mathbf{Q}_t & \mathbf{0} \\ \mathbf{0} & \mathbf{R}_t \end{pmatrix} \right] \quad (5)$$

where $\mathbf{Q}_t$ is the variance–covariance matrix of $\mathbf{w}_t$, $\mathbf{w}_t$ is the vector of process errors, and $\mathbf{R}_t$ is the variance–covariance matrix of measurement errors $\boldsymbol{\varepsilon}_t$. At $p = 2$, we have

$$\mathbf{X}_t = \begin{pmatrix} a \\ X_t \\ X_{t-1} \end{pmatrix} \quad (6)$$

$$\mathbf{F}_t = \begin{pmatrix} 1 & 0 & 0 \\ 1 & 1+b & c \\ 0 & 1 & 0 \end{pmatrix} \quad (7)$$

$$\mathbf{H}_t = (0 \quad 1 \quad 0). \quad (8)$$

Model parameters a, b, and c and variance σ_u^2 and σ_e^2 were estimated using maximum-likelihood methods. We maximized the complete data log-likelihood function (Shumway and Stoffer 2000) using the expectation–maximization (EM) algorithm (Dempster et al. 1977):

$$\log L_{X,Y}(\boldsymbol{\theta})$$

$$= -\log|\boldsymbol{\Sigma}_0| - (\mathbf{X}_0 - \boldsymbol{\mu}_0)'\boldsymbol{\Sigma}_0^{-1}(\mathbf{X}_0 - \boldsymbol{\mu}_0)$$

$$- \log|\mathbf{Q}_t| - \sum_{t=1}^{T} (\mathbf{X}_t - \mathbf{F}\mathbf{X}_{t-1})_t' \mathbf{Q}_t^{-1}(\mathbf{X}_t - \mathbf{F}\mathbf{X}_{t-1})$$

$$- \log|\mathbf{R}_t| - \sum_{t=1}^{T} (\mathbf{Y}_t - \mathbf{H}\mathbf{X}_t)_t' \mathbf{R}_t^{-1}(\mathbf{Y}_t - \mathbf{H}\mathbf{X}_t).$$

Here T is the sample size, $\mathbf{Q}_t$ and $\mathbf{R}_t$ are defined as in Eq. 5, $\mathbf{X}_t$ is the state vector at time t, $\mathbf{Y}_t$ is the observation at time t, $\mathbf{F}$ is the transition matrix as in Eq. 3, $\mathbf{H}$ is the measurement matrix as in Eq. 4, $\mathbf{X}_0$ and $\boldsymbol{\mu}_0$ are the initials of state vector and its expectation, and $\boldsymbol{\Sigma}_0$ is the covariance matrix of $\mathbf{X}_0$. The EM algorithm is an iterative algorithm. Each iteration j has two steps, expectation (E step) and maximization (M step). In the E step, the conditional expectation of the complete data likelihood with respect to the state vector $\mathbf{X}_t$,

$$Q[\boldsymbol{\theta} \mid \boldsymbol{\theta}^{(j-1)}] = E[\log L_{X,Y}(\boldsymbol{\theta}) \mid \mathbf{Y}, \boldsymbol{\theta}^{(j-1)}]$$

is evaluated using current estimates of $\boldsymbol{\theta}$, i.e., $\boldsymbol{\theta}^{(j-1)}$. In the M step, the estimates of unknown parameters $\boldsymbol{\theta}$ comprising $\boldsymbol{\mu}_0$, $\mathbf{F}$, $\mathbf{Q}_t$, and $\mathbf{R}_t$ are updated to maximize the conditional expectation of the complete data likelihood. In the linear and normal case, the close-form solutions for the updating exist (Shumway and Stoffer 2000). To resolve the invertibility of covariance matrix

$\mathbf{Q}_t$ of our AR(2) model, we adopted the modified forward-filtering and backward-smoothing algorithms of Wu et al. (1996) for the parameter estimations. This allowed element-wise updating of matrices $\mathbf{F}$, $\mathbf{Q}_t$, and $\mathbf{R}_t$ with some elements of the matrices being restricted as the known (Wu et al. 1996). The maximized likelihood was used to compute the corrected Akaike information criterion (AIC_c) and Akaike weights (Burnham and Anderson 2002). Akaike weights were used to obtain model-averaged estimates of parameters. For example, the model-averaged estimate ($\tilde{b}$) of the parameter b was obtained as the weighted average of maximum-likelihood estimates ($\hat{b}_i$) from each of the three models in the candidate set (Burnham and Anderson 2002):

$$\tilde{b} = \sum_{i=1}^{3} w_i \hat{b}_i$$

where w_i is the Akaike weight for model i.

We checked assumptions on model errors following Harvey (1989:259). The residuals of the best-approximating Kalman filter model were not autocorrelated (Box-Ljung statistic Q, $P > 0.05$; Harvey 1989). Inspection of the sample autocorrelation function (ACF) also indicated that the residuals were not serially correlated. The Q–Q plots confirmed the assumption of normally distributed residuals.

To examine effects of spatial and temporal heterogeneity on the strength of density dependence, we regressed estimates of the absolute value of the model-averaged estimate of b on indices of temporal variation in weather and spatial variation in plant biomass, i.e., $|\tilde{b}| = \alpha + \beta x$, where x is the value of the index of heterogeneity. We used the regression model $|\tilde{b}| = \alpha$ as a null model and compared the strength of evidence for the single-parameter null model relative to model parameters representing effects of heterogeneity, i.e., those including α and β.

We used Bayesian hierarchical modeling (Gelman et al. 2004) to estimate the 95% posterior intervals of α and β. The hierarchical modeling was based on the AR(1) Gompertz models (Eqs. 3–5). We specified the prior distributions of state $X_{i,t}$ and the likelihood function as

$$X_{i,t} \sim \mathcal{N}(\mu_{X_{it}}, \tau_{i,1})$$

$$\mu_{X_{it}} = a_i + (1 + b_i)X_{i,t-1}$$

$$Y_{i,t} \sim \mathcal{N}(X_{i,t}, \tau_{i,2})$$

$$X_{i,0} \sim \mathcal{N}(\mu_{X_{i0}}, \tau_{i,1})$$

and the prior distribution of the hyperparameters as $b_i' = (1 + b_i) \sim \mathcal{N}(\mu_{bi}, \tau_3)$, $\mu_{bi} = \alpha + \beta X_{env}$, $\alpha \sim \mathcal{N}(0, \tau_4)$, $\beta \sim \mathcal{N}(0, \tau_4)$, τ_3 and $\tau_4 \sim \text{Gamma}(0.001, 0.001)$, $\tau_{i,1}$ and $\tau_{i,2} \sim \text{Gamma}(0.001, 0.001)$, $i = 1, 2, 3, 4, 5$, where $X_{i,t}$ is the natural logarithm of the true population size of population i at the time t; $X_{i,t-1}$ is the natural logarithm of the true population size of population i at the time $t - 1$; $\mu_{X_{it}}$ is the expectation or mean of $X_{i,t}$; $\tau_{i,1}$ is the precision of $X_{i,t}$, i.e., the reciprocal of the process variance of $X_{i,t}$; $\tau_{i,2}$ is the reciprocal of measurement variance of $Y_{i,t}$; a_i is the intrinsic rate of population growth of population i; b_i is the strength of direct density dependence in population i; X_{env} is the CV in winter temperatures or the CV in the NDVI; and α and β are the regression coefficients. Notations $\sim\mathcal{N}(\cdot)$ and $\sim\text{Gamma}(\cdot)$ stand for being distributed as the normal and the gamma distribution, respectively. In a preliminary run, we specified the intrinsic rate of population growth as a stochastic variable distributed normally. However, the posteriors of a_i and b_i' were highly correlated. We reparameterized the hierarchical model using the MLE (maximum likelihood estimate) values of a_i estimated with the EM algorithm to facilitate the convergence of the chain (Congdon 2001). Our main objective of the hierarchical modeling is to model the relationship between the strength of density dependence and environmental heterogeneity among the five ungulate populations. We used the most recent 31 years of survey data for all five ungulate populations in our hierarchical model. The Monte Carlo Markov chain was run for 10 000 iterations. The first 5000 iterations were the burn-in period and were discarded. The second 5000 iterations were used to construct the posterior distributions. The model was implemented using WINBUG 1.4.1 (Spiegelhalter et al. 2003). The convergence of the chain was checked by monitoring the trace or trajectories of the posteriors of variances and estimated parameters b, α, and β (Raftery and Lewis 1996). Two chains were initialized with two sets of different initial values of unknown parameters. The trajectories of monitored parameters were well mixed.

We used the coefficient of variation (CV) in average annual winter (October–March) temperature as an index of temporal heterogeneity. The mean and coefficient of variation of average annual winter temperatures coincident with the period of ungulate surveys were calculated for each site.

Spatial heterogeneity was indexed using NDVI, which reflect vegetation biomass (Paruelo et al. 1997) and are correlated with ungulate stocking rates (Oesterheld et al. 1998). We acquired 183 NDVI images for each study area from April 1998 to April 2003. For each image, we calculated the CV in NDVI across all 1-km² pixels within a 25-km radius of the centroid of each study area. For each study site, we averaged the CV across all images to represent spatial heterogeneity in vegetation. We verified that the estimate of the CV was largely independent of scale by showing that the estimate of the CV with the 25-km radius did not depend on the resolution of the analysis, i.e., the pixel size.

We used the autocorrelation coefficient of the linearized population model at a particular time lag (p) to measure direct density dependence ($p = 1$) and delayed density dependence ($p = 2$), as did Turchin (1990) and
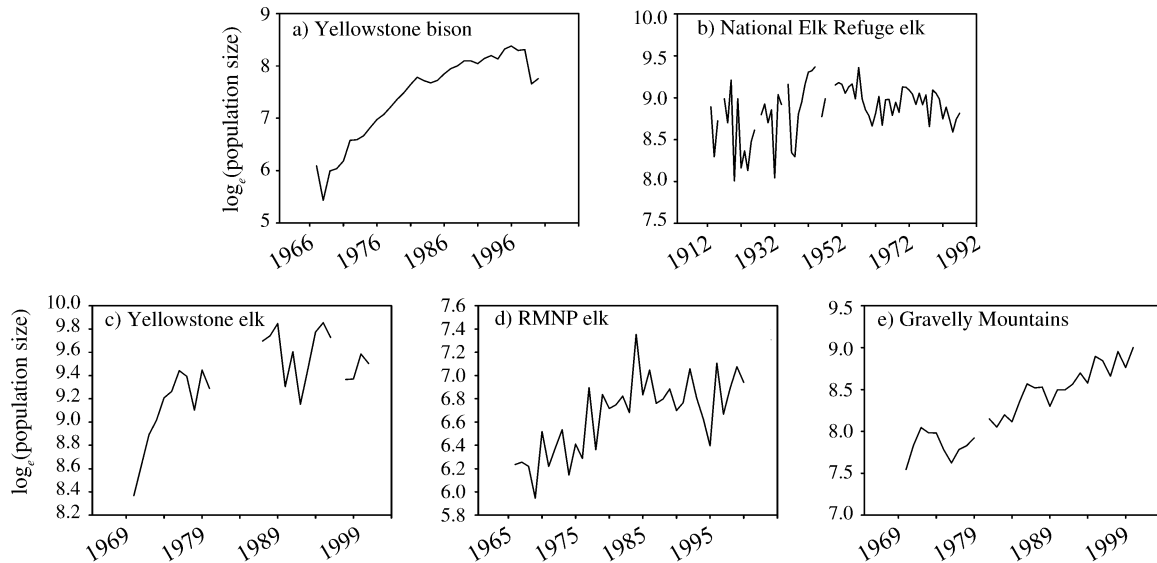
Fig. 1. Time series of the natural logarithm of population sizes of (a) bison (*Bison bison*) in northern Yellowstone Park and elk (*Cervus elaphus*) in (b) the National Elk Refuge, Wyoming, USA, (c) Yellowstone National Park, (d) the Rocky Mountain National Park (RMNP), Colorado, USA, and (e) the Gravelly Mountains, Montana, USA.

Royama (1992). Alternatively, Lande et al. (2002) developed an age-structured life history model to estimate the total density dependence with the autoregression coefficients estimated with the time series of juveniles. In this model, the individual autoregression coefficient does not measure the strength of density dependence. Here, $1 -$ the sum of autoregression coefficients up to certain order measures the total density dependence in fecundity and first-year survival. A similar stage-structured life history model also was developed by Lande et al. (2002) to estimate the total density dependence in the survival of younger stages exerted by adults only, and density dependence in adult fecundity. In ungulates, change in survival of calves and yearlings accounts for most of the fluctuation in populations (Gaillard et al. 1998), whereas the survival of adults remains relatively constant regardless of population abundance (Gaillard et al. 1994). Additionally, recruitment often is regulated by density dependence in ungulates (Sæther 1997, Gaillard et al. 2000). However, the approach of Lande et al. (2002) requires time series of adults and/or young, which are not available in our study. Besides, in the age- or stage-structured life history model of Lande et al. (2002), the total density dependence is evaluated at the stable equilibrium (with stable age structure distribution and unity of finite rate of increase; i.e., $\lambda = 1$) or a small deviation from the equilibrium. We have no data to assess this assumption in our study.

RESULTS

Considerable variation existed in the dynamics of the five ungulate populations (Fig. 1). The coefficients of variation of population abundance over survey pe-riods were 0.32, 0.27, 0.32, 0.41, and 0.59 for elk populations of RMNP, NER, Gravelly Mountains, and YNP, and for the bison population of NYP, respectively. Variances of measurement errors on the logarithm scale were 0.031, 0.03, 0.006, 0.015, and 0.016 for elk populations of RMNP, NER, Gravelly Mountains and YNP, and for the bison population of NYP, respectively.

Rates of population growth declined as population density increased in four of the five populations, providing evidence consistent with density-dependent feedback to survival and/or reproduction. Best-approximating models of population growth showed no effect of density in one population, direct feedback from density to population growth rate in three populations, and direct and delayed density dependence in one population. The means and 97.5% posterior percentiles of $(1 + b)$ were <1.0 for all but one of the populations studied.

The coefficient of variation in average annual winter temperatures was positively related to the strength of the model-averaged estimate of density dependence (Fig. 2b), indicating that increasing variability in winter severity also strengthened the effect of density (Akaike weight $= 0.79$, $r^2 = 0.70$). In contrast, the strength of density dependence was inversely related to spatial heterogeneity in vegetation (Fig. 2a; Akaike weight $= 0.92$, $r^2 = 0.51$), suggesting that access to heterogeneous vegetation attenuated feedbacks between population density and per capita growth rate (Table 1). Akaike weight (w_i) indicates that the model with mean winter temperatures ($w_i = 0.41$) was a competing model with the null model of interception term only ($w_i = 0.58$). There is a substantial weight of evidence to support the model of winter temperatures (Fig. 2c). The
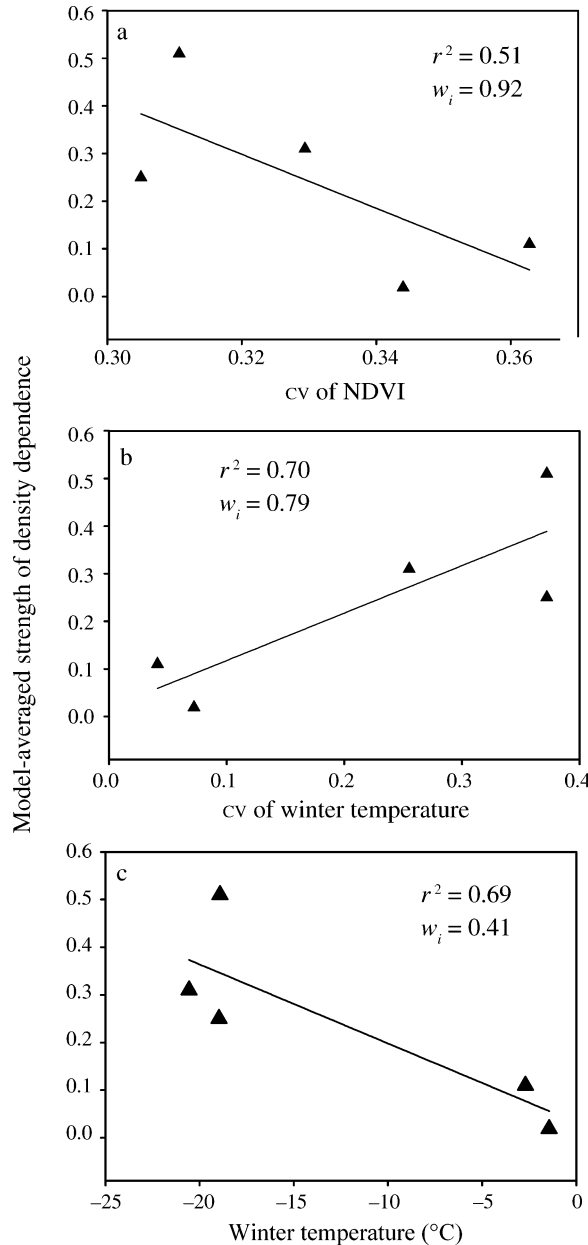
FIG. 2. Effects of spatial heterogeneity in (a) vegetation (Normalized Difference Vegetation Index, NDVI), (b) temporal variability in winter temperatures, and (c) mean winter temperatures on the model-averaged strength of density dependence in the bison (*Bison bison*) of northern Yellowstone National Park and elk (*Cervus elaphus*) of the Gravelly Mountains, Montana, Rocky Mountain National Park, Colorado, Yellowstone National Park, and National Elk Refuge, Wyoming, USA. The Akaike weights (w_i) show the strength of evidence for the model including an intercept and a slope relative to the null model containing a single term for the intercept.

coefficient was −0.018. The *P* value of the coefficient of mean winter temperatures was 0.004. However, in the pairwise comparison between the null model ($w_i = 0.99$) and model of mean NDVI, we found little evi-

dence to support the model of mean NDVI ($w_i = 0.01$). The 95% posterior interval of β (the regression coefficient for $1 + b$) estimated with the Bayesian hierarchical model spanned 4.13 and 5.50 for the effect of spatial heterogeneity (Table 2). Thus, the value of $1 + b$ increased and the absolute value of *b* decreased with increasing CV in NDVI, indicating that density dependence was weakened by spatial heterogeneity in vegetation. The 2.5% and 97.5% posterior percentiles of β for the CV in winter temperature were −0.99 and −0.34, indicating that the value of $1 + b$ decreased and the absolute value of *b* increased with rising CV in winter temperatures; this suggests that temporal heterogeneity in weather increased the strength of density dependence (Table 2).

DISCUSSION

Our results offer the first empirical evidence that spatial and temporal heterogeneity exert opposing effects on density dependence in populations of large herbivores. These results are based on small samples because estimating parameters that reflect density dependence requires relatively long time series of observations of population size, which are rare. Thus, although our final results are based on $n = 5$ populations, this sample is composed of 205 individual census observations. We avoided combining data across regions because of inherent differences in the expression of spatial heterogeneity among them. The independent variables represent similarly synthetic quantities, drawing on many observations to produce a single index of heterogeneity. Our Bayesian hierarchical modeling borrows strength from each of the five time series. Thus, although our sample size is statistically small, the observation set that was distilled to create the statistical analysis was large.

We show that the magnitude of the effect of density on population growth rate depends on variation in winter weather over time. The Pearson correlation coefficient between mean winter temperatures and CV of winter temperatures was −0.92 ($P = 0.02$), suggesting that colder winters were correlated with greater variability in winter temperatures. Variability in temperatures can influence availability of forage by increasing the hardness of snow due to cycles of icing and thawing. These conditions can meaningfully reduce forage availability and increase energy expenditure of ungulates (Parker et al. 1984, Hobbs 1989).

The dependence of the effect of density on variability in weather is plausible because extremes of weather are likely to reduce the carrying capacity of habitats by increasing the food requirements of animals and by reducing food supplies available to meet those requirements (Wallmo et al. 1977, Hobbs 1989). A well-established theoretical result suggests that increasing temporal variability in resources that determine carrying capacity also amplifies density-dependent feedbacks to population growth, causing reduced popula-

TABLE 1. Model selection for the effects of spatial heterogeneity of Normalized Difference Vegetation Indices (NDVI) and temporal variability of winter temperatures on the model-averaged strength of density dependence in five ungulate populations.

Models	AIC$_c$	w_i
$|\tilde{\bar{b}}| = a$	3.9	...
$|\tilde{\bar{b}}| = a + c(\text{NDVI}_{CV})$	−1.2	0.92
$|\tilde{\bar{b}}| = a + c(\text{Temp}_{CV})$	1.1	0.79
$|\tilde{\bar{b}}| = c(\text{Temp})$	3.7	0.41
$|\tilde{\bar{b}}| = a + c(\text{NDVI})$	12.8	0.01

Notes: $|\tilde{\bar{b}}|$ is the model-averaged estimate of $|b|$, a measure of the strength of density dependence; model $|\tilde{\bar{b}}| = a$ serves as a null model; Temp$_{CV}$ is the coefficient of variation in winter temperatures; NDVI$_{CV}$ is the coefficient of variation in NDVI; NDVI is the mean of NDVI; Temp is the mean winter temperatures; a is the intercept; and c is the regression slope. Akaike weights (w_i) show the strength of evidence for each model including an intercept and a slope relative to the null model containing a single term for the intercept.

tion density and equilibrium densities relative to the deterministic case (May 1974). It is plausible, in turn, that these reductions in carrying capacity amplify the intensity of feedback from population density to individual survival and or reproduction. This amplification is manifest in changes in the slope of the relationship between per capita growth rate and population density. In a simulation of effects of climatic variability on the dynamics of the soay sheep (*Ovis aries*) population, Coulson et al. (2001) showed that the strength of density dependence can increase in response to increasing variance of the Northern Atlantic Oscillation (NAO) index.

In contrast to the effect of temporal heterogeneity, spatial heterogeneity appeared to weaken the effect of density dependence. We propose that this effect is mediated by the ability of herbivores to exploit spatial heterogeneity by selective feeding (Senft et al. 1987, Hobbs 1989, 1996, Illius and Gordon 1999). Selective feeding allows herbivores to cope with food resources containing concentrations of nutrients that vary over time. However, some type of spatial variation is a necessary condition for selectivity (Senft et al. 1987, Bailey et al. 1996); in an environment where resources are homogeneous across all spatial scales, selectivity is impossible. Reductions in spatial heterogeneity in resources can compress the options available to herbivores, and this compression may harm the ability of herbivores to respond to temporal heterogeneity by selective use of space. Our results are purely observational, and hence, there may be alternative explanations for them. It may be that heterogeneity is correlated with average resource amount. However, mean NDVI was not correlated with the CV in NDVI or with strength of density dependence, largely because there was little variation in the mean NDVI across sites. We cannot

rule out confounding relationships between the CV in NDVI and average resource quality or in the availability of other potentially limiting resources, for example, access to hiding or thermal cover.

The implications of spatial heterogeneity for density-dependent feedbacks have been explored via simulation, yielding results similar to ours: increasing spatial variation in resources reduced the impacts of increasing population density on population growth (Illius and O'Connor 2000). Other simulations (Underwood 2004) have shown that spatial heterogeneity can amplify or dampen the effect of density on the population growth rate. The direction and magnitude of this effect depends on the strength of the relationship between the intrinsic rate of population growth and carrying capacity, and the absolute magnitude of carrying capacity.

According to the life history model of Lande et al. (2002), differences in age structure could shape the effect of total density on population growth by age-specific density dependence or generation time. However, it is also legitimate to say that differences in density dependence resulting from environmental fluctuations could cause differences in the age structure of ungulate populations. Discerning cause and effect is difficult without manipulative experiments, which are difficult to impose in large, migratory ungulates. In the absence of experiments, future observations of age- or stage-specific time series are needed to distinguish between these two possibilities.

Extensive theory and observation suggest that heterogeneity at multiple scales is important to the nutri-

TABLE 2. Parameter estimates of hierarchical models for the effects of temporal climate variability and spatial heterogeneity of the Normalized Difference Vegetation Index (NDVI) on the direct density-dependent feedback on ungulate population growth rates.

Parameters	Mean	SD	Posterior percentile	
			2.5%	97.5%
α (NDVI)	−0.76	0.11	−0.99	−0.50
β (NDVI)	4.94	0.31	4.13	5.50
α (temperature)	1.00	0.05	0.89	1.11
β (temperature)	−0.77	0.15	−0.99	−0.37
$1 + b_1$	1.00	0.003	0.99	1.01
$1 + b_2$	0.75	0.007	0.74	0.76
$1 + b_3$	0.85	0.01	0.83	0.87
$1 + b_4$	0.69	0.008	0.68	0.71
$1 + b_5$	0.90	0.01	0.88	0.93

Notes: For parameters, α (NDVI) is the intercept of the regression of b_i' on the CV in the Normalized Difference Vegetation Index (NDVI), β (NDVI) is the slope of the regression on the CV in NDVI, α (temperature) is the intercept of the regression of b_i' on the CV in winter temperature, β (temperature) is the slope of the regression on the winter temperature, b_i' is the density dependence term for the elk population of Montana, b_2 for the bison population of northern Yellowstone Park, b_3 for the elk population of Yellowstone National Park, b_4 for the elk population of National Elk Refuge, and b_5 for the elk population of Rocky Mountain National Park. The posterior distribution and estimates of parameters were obtained using the Markov Chain Monte Carlo method.

tional status of large, mobile herbivores (see reviews of Senft et al. 1987, Coughenour 1991, Laca and Demment 1991, Laca and Ortega 1995, Bailey et al. 1996). Although the benefits of heterogeneity are clear for the individual forager, the translation of these benefits to population performance has not been demonstrated empirically. We show that access to heterogeneity can enhance growth rates of populations of large mobile herbivores.

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APPENDIX

Tables showing annual counts of five ungulate populations in the Rocky Mountain region, USA (*Ecological Archives* E087-003-A1).