

Density dependence in northern ungulates: interactions with predation and resources

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Abstract Variation in the abundance of animals has traditionally been explained as the outcome of endogenous forcing from density dependence and exogenous forcing arising from variation in weather and predation. Emerging evidence suggests that the effects of density dependence interact with external influences on population dynamics. In particular, spatial heterogeneity in resources and the presence of capable predators may weaken feedbacks from

density dependence to growth of populations. We used the Kalman filter to analyze 23 time series of estimates of abundance of northern ungulate populations arrayed along a latitudinal gradient (latitude range of 40°–70°N) to evaluate the influence of spatial heterogeneity in resources and predation on density dependence. We also used contingency tables to test whether density dependence was independent of the presence of carnivores (our estimate of predation) and multiple regressions to determine the effects of spatial heterogeneity in resources, predation, and latitude on the strength of density dependence. Our results showed that the strength of density dependence of ungulate populations was low in the presence of large carnivores, particularly at northern latitudes with low primary productivity. We found that heterogeneity in elevation, which we assume acted as a surrogate for spatial heterogeneity in plant phenology, also reduced effects of density dependence. Thus, we show that external forces created by heterogeneity in resources and predation interact with internal feedbacks from population density to shape dynamics of populations of northern ungulates.

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Introduction

Ecologists increasingly appreciate that the responses of organisms to variation in environmental conditions may exceed the importance of their responses to the average condition (Ruel and Ayres 1999; Lundberg et al. 2000; Benedetti-Cecchi 2005; Boyce et al. 2006; Brassil 2006). For many years, understanding this variation over time

dominated efforts to understand population dynamics. Temporal heterogeneity in forces external to populations, particularly influences of weather and predation, has been studied alongside internal forces, particularly feedback from population density and age structure (Ranta et al. 2000). These efforts initially gave rise to debates about the importance of density-dependent versus density-independent regulation of population growth. A contemporary view considers temporal variation in external forcing, particularly variation in weather, as an important influence modifying the operation of internal forcing from density dependence.

Predation exerts profound effects on the distribution and dynamics of mammals (Messier 1994; Crete 1999; Oksanen et al. 2001; Festa-Bianchet et al. 2006). However, the way that predation interacts with population density to regulate animal abundance remains unclear (Messier 1994; Oksanen et al. 2001; Festa-Bianchet et al. 2006). Studies of populations of wild ungulates in a wide range of ecosystems have recently revealed that the strength of density dependence can be modified by predation (Messier 1994; Crete 1999; Oksanen et al. 2001). For example, wolf predation in high latitudes of North America maintained a low-density equilibrium of wolf-ungulate systems where density dependence was weak or undetectable, whereas in low latitudes free of wolves a high-density equilibrium of deer populations appeared to exist (Crete 1999). The strength of density dependence can depend on predation because (1) vulnerability of herbivores to predators correlates with resource availability (Owen-Smith and Mills 2006), (2) prey switching can modify demographic sensitivities to density (Owen-Smith et al. 2005; Owen-Smith 2006), and (3) predation can alter effects of temporal autocorrelation in resources (Wilmers et al. 2007). Furthermore, severe winter climate indicative of high North Pacific Oscillation values resulted in a lower elk (*Cervus elaphus*) population growth rate in the presence of wolves compared to the absence of wolves because deep snow enhanced the wolf predation rate (Hebblewhite 2005). Therefore, climate can influence density dependence of herbivores through modifying the herbivore–carnivore interaction (Lima et al. 2002; Stenseth et al. 2004). These observations suggest a complex interaction among climate, density, and predation in shaping population dynamics.

The exploitation ecosystem hypothesis (EEH) predicts that herbivore biomass increases linearly with increasing net primary productivity ($\text{NPP} \leq 700 \text{ g m}^{-2} \text{ year}^{-1}$), but remains relatively constant in the presence of carnivores in productive ecosystems ($\text{NPP} > 700 \text{ g m}^{-2} \text{ year}^{-1}$); thus, the removal of carnivores from these productive systems would substantially increase herbivore biomass and result in a decrease in plant biomass due to heavy herbivory (Oksanen 2001; Oksanen et al. 1981). In the absence of

predators, herbivores are regulated by density dependence (Messier 1994), leading to a positive correlation between herbivore biomass and plant productivity. Crete (1999) found that the distribution of deer biomass density (kg m^{-2}) in North America was consistent with the EEH predictions: deer biomass density was low and relatively constant in the wolf range in the north; south of the wolf range, deer biomass density was positively related to NPP. According to the EEH, we hypothesized that the strength of density dependence would decrease along a low-high latitudinal gradient due to the presence of large carnivores and severe winter climate in the north and high ungulate biomass density in low latitudes free of large carnivores.

Density dependence may, in turn, interact with spatial heterogeneity in resources. Emerging evidence (Fryxell et al. 2005; Wang et al. 2006) suggests that landscape heterogeneity also attenuates the effects of density-dependent feedbacks on population growth rates of large herbivores. A plausible mechanism for this effect is that landscape heterogeneity allows animals to be selective for resources that vary over space, compensating for variation that occurs over time (Frank and McNaughton 1992; Mysterud et al. 2001; Fryxell et al. 2004). For example, Mysterud et al. (2001) found a positive correlation between body mass of red deer and spatial heterogeneity in elevation that they attributed to spatial variation in plant phenology and thus variation in nutritional content. Ungulates exploit this variation by moving among areas of the landscape where plants support maximum nutrient gains (Albon and Langvatn 1992). Mysterud et al. (2001) suggested that the enhanced condition of individual red deer resulting from their responses to heterogeneity in plant quality would translate into increased rates of population growth.

Thus, predation and resources may create an external context that modifies the effects of internal feedbacks from population density to population growth. Our goal in this study was to examine the role of predation and resource heterogeneity in shaping density dependence in northern ungulates. We hypothesized that increasing spatial heterogeneity and predation would reduce the strength of density-dependent feedbacks to population growth rate.

Methods

We analyzed 23 time series of estimates of abundance of north temperate ungulate populations (Table 1) to estimate the strength of density-dependent feedbacks to population growth rates. Census methods include aerial surveys and ground counts. The abundance of the moose population in northern Norway was estimated with the population reconstruction method using harvest data (Solberg et al.

Table 1 Sources of data for studies of dynamics of populations of northern ungulates and results of selection among autoregressive Gompertz population models describing temporal variation in abundance of populations of northern ungulates

Species	Study site	Geographic location	Study period	Survey time	Predation	Source of data	AR order ^a	w_i^b	\hat{b}^c
Alpine ibex <i>Capra ibex</i>	Grand Paradiso National Park, Italy	45.53 N, 7.27 E	1956–2000	September	No or negligible	Jacobson et al. (2004)	1	0.56	−0.15
Bighorn sheep <i>Ovis canadensis</i>	Ram Mountain, Canada	52.35 N, 115.78 W	1975–2001	June	Yes	Festa-Bianchet (pers. comm.)	Exp	0.69	0.0
Bighorn sheep <i>Ovis canadensis</i>	Sheep River, Canada	50.61 N, 114.69 W	1982–2001	March	Yes	Festa-Bianchet (pers. comm.)	Exp	0.62	0.0
Bison <i>Bison bison</i>	Yellowstone National Park, Wyoming	44.72 N, 110.64 W	1966–1999	December–January	Yes	Taper and Gogan (2002)	2	0.99	−0.56
Bison <i>Bison bison</i>	Wood Buffalo National Park, Canada	59.00 N, 113.00 W	1971–1998	February or March	Yes	Carbyn et al. (1998)	Exp	0.62	0.0
Caribou <i>Rangifer tarandus</i>	Denali, Alaska	64.00 N, 150.00 W	1981–2002	July	Yes	Layne Adams (pers. comm.)	Exp	0.85	0.0
Elk <i>Cervus elaphus</i>	Rocky Mountain National Park, Colorado	40.39 N, 105.64 W	1965–1999	February–March	No or negligible	Lubow et al. (2002)	1	0.81	−0.11
Elk <i>Cervus elaphus</i>	Jackson, Wyoming	44.04 N, 110.63 W	1912–1986	February	Yes	Lubow and Smith (2004)	1	0.82	−0.38
Elk <i>Cervus elaphus</i>	Gravelly Mountains, Montana	44.64 N, 111.86 W	1967–1997	January–March	Yes	Wang et al. (2006)	Exp	0.66	0.0
Elk <i>Cervus elaphus</i>	Yellowstone National Park, Wyoming	44.93 , 110.54 W	1969–2000	December–January	Yes	Coughenour and Singer (1996)	1	0.91	−0.28
Fallow deer <i>Dama dama</i>	New Forest, UK	50.83 N, 1.58 W	1962–1985	April	No	Putman and Sharma (1987)	1	0.85	−0.46
Moose <i>Alces alces</i>	Southern Nordland, Norway	65.50 N, 13.90 E	1967–1993	N/A	Yes	Solberg et al. (1999)	Exp	0.65	0.0
Mule deer <i>Odocoileus hemionus</i>	Sprague River, Oregon	42.60 N, 120.50 W	1964–1988	March	Yes	Peek et al. (2002)	Exp	0.62	0.0
Muskox <i>Ovibos moschatus</i>	Nunivak Island, Alaska	60.05 N, 166.12 W	1947–1968	July	Not	Spencer and Lensink (1970)	Exp	0.72	0.0
Red deer <i>Cervus elaphus</i>	New Forest, UK	50.83 N, 1.58 W	1962–1985	April	No	Putman and Sharma (1987)	1	0.81	−0.31
Red deer <i>Cervus elaphus</i>	Rum Island, UK	57.00 N, 6.33 W	1957–2000	May	No	Clutton-Brock et al. (2002)	1	0.83	−0.46
Reindeer <i>Rangifer tarandus</i>	Alakyla, Finland	67.40 N, 24.92 E	1968–1990	September–January	Yes	Helle and Kojola (1994)	Exp	0.68	0.0
Reindeer <i>Rangifer tarandus</i>	Muotkatunturi, Finland	68.00 N, 26.00 E	1968–1990	September–January	Yes	Helle and Kojola (1994)	Exp	0.78	0.0

Table 1 continued

Species	Study site	Geographic location	Study period	Survey time	Predation	Source of data	AR order ^a	w_i^b	\hat{b}^c
Reindeer <i>Rangifer tarandus</i>	Palojarvi, Finland	68.50 N, 22.78 E	1968–1990	September–January	Yes	Helle and Kojola (1994)	Exp	0.64	0.0
Reindeer <i>Rangifer tarandus</i>	Kaldoaivi, Finland	69.75 N, 28.00 E	1968–1990	September–January	Yes	Helle and Kojola (1994)	Exp	0.64	0.0
Roe deer <i>Capreolus capreolus</i>	New Forest, UK	50.83 N, 1.58 W	1962–1985	April	No	Putman and Sharma (1987)	Exp	0.78	0.0
Sika deer <i>Cervus nippon</i>	New Forest, UK	50.83 N, 1.58 W	1962–1985	April	No	Putman and Sharma (1987)	1	0.71	−0.38
Soay sheep <i>Ovis aries</i>	St Kilda, UK	57.82 N, 8.59 W	1955–2000	August	No	Coulson et al. (2001)	1	0.76	−0.45

^a AR order is the largest order of autocorrelated terms identified in the model selection. Exp indicates exponential or density-independent population growth

^b w_i is the Akaike weight (Burnham and Anderson 2002)

^c \hat{b} is the bootstrapped mean of coefficient b over 2,000 repetitions and is a measure of the strength of density dependence. Estimates of $b < 0$ provide estimates of negative feedback from population density to per capita population growth rate

1999). Surveys or censuses were conducted in different times of a year for different populations (Table 1). Sightability was adjusted only for the estimates of elk abundances in RMNP and NER (Lubow et al. 2002; Lubow and Smith 2004). Some of the North American ungulate populations were harvested annually prior to the surveys. We added the number of harvested animals to the post-season counts to estimate pre-hunting population size when harvest data were available (Merrill and Boyce 1991; Coughenour and Singer 1996). Other populations studied were culled during part of the study periods to avoid overabundance; however, we had no access to information on those occasional harvests.

We assumed that the estimates of population size (N_t) have a log-normal distribution and transformed all time series by taking the natural logarithm of animal counts or densities, i.e., $Y_t = \log_e N_t + u_t$, where u_t is measurement error distributed as $u_t \sim N(0, \sigma_u^2)$. Variation in abundance (Y_t) was analyzed for each population using subsets of the global model $Y_t = a + (1 + b)Y_{t-1} + cY_{t-2}$, where a is the intrinsic rate of increase, b represents the effect of direct density dependence, and c is a coefficient describing the effects of delayed density dependence. Thus, the coefficients b and c represent the slopes of the relationship between population density and per capita population growth rate for direct and lagged density dependence. When the sign of b is negative, increases in its magnitude indicate increasingly strong, direct, negative feedback between population density and per capita population growth rate. A similar interpretation follows for c . Density-independent (DI: $b = c = 0$) and autoregressive (AR) models of order (p) 1 (or direct density dependence-DDD) and 2 (or direct and indirect density dependence-DIDD) were fit to the abundance data as described below.

Counts of animals have inherent measurement errors that may bias estimates of the strength of density dependence (Stenseth et al. 2003; Freckleton et al. 2006). To account for these errors, we used the classic Kalman filter (Kalman 1960), a state-space time series model, to analyze the time series of counts (Y_t). In the state-space model (SSM), a true state variable X_t is unobservable, but the observation ($Y_t = \ln N_t$) of the true density 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(2) Gompertz model (Gompertz 1825; Royama 1992) is:

$$X_t = a + (1 + b)X_{t-1} + cX_{t-2} + e_t, \quad (1)$$

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

Error terms e_t and u_t are assumed normal and independent of each other and independent over time, i.e., $e_t \sim N(0, \sigma_e^2)$, $u_t \sim N(0, \sigma_u^2)$, $\text{Corr}(e_t, u_t) = 0$. The matrix representation of Eqs. 1 and 2 can be found in Wang et al.

(2006). Equations 1 and 2 were cast into the Kalman filter (KF). Model parameters a , b , and c and variances σ_u^2 and σ_e^2 were estimated using maximum likelihood methods and the expectation-maximization (EM) algorithm (Dempster et al. 1977; Shumway and Stoffer 2000). The DI (Eq. 3), DDD (Eq. 4), and DIDD (Eq. 5) models were fitted to each ungulate time series:

$$X_t = a + X_{t-1} + e_t \quad (3)$$

$$X_t = a + (1 + b)X_{t-1} + e_t \quad (4)$$

$$X_t = a + (1 + b)X_{t-1} + cX_{t-2} + e_t. \quad (5)$$

The maximized likelihood was used to compute corrected Akaike Information Criteria (AIC_c) and Akaike weights for each of the three models (Burnham and Anderson 2002). Akaike weight measures the strength of evidence for the DI, DDD, and DIDD models given observed data. The best approximating model was the one of the lowest AIC_c value or highest Akaike weights.

Stoffer and Wall (1991) showed the superiority of the bootstrapped Kalman filter for small data sets and hypothesis testing of parameters. We used Stoffer and Wall's method to bootstrap the Kalman filter 2,000 times for the selected DDD and DIDD models with the highest Akaike weight to measure the precision of the parameter b . The mean and 95% confidence intervals of the coefficient b were estimated with 2,000 repetitions in the bootstrapping. The coefficient b of the exponential growth model was treated as known, and its value was set to zero. We checked assumptions on model errors following Harvey (1989, p. 259). The normality of the residuals of the best approximating Kalman filter model was checked and confirmed by the Q–Q plots. The residuals were not autocorrelated in the inspection of the sample autocorrelation function (ACF) plots, with the exception of those for the Norwegian moose.

Large mammalian carnivores were present in 14 study sites, but were essentially absent in 9 other sites (Table 1). These nine populations included alpine ibex (*Capra ibex*) in Gran Paradiso National Park, Italy (Jacobson et al. 2004), fallow deer (*Dama dama*), red deer, roe deer (*Capreolus capreolus*), and sika deer (*Cervus nippon*) in New Forest, UK (Putman and Sharma 1987), Soay sheep (*Ovis aries*) on St. Kilda, UK (Coulson et al. 2001), red deer on Rum Island, UK (Clutton-Brock et al. 2002), and elk in Rocky Mountain National Park, CO, USA (Lubow et al. 2002), and muskox (*Ovibos moschatus*) on Nunivak Island, Alaska, USA (Spencer and Lensink 1970). Lacking data on the intensity of predation, we analyzed predation as a qualitative factor, using a 2×2 contingency table to test whether the frequency distribution of the occurrence of density dependence of ungulates was independent of the presence of large carnivores (Zar 1999). We also used a t test to detect the difference in the bootstrapped means of

coefficient b between the sites with and without large carnivores. The values of coefficient b were set to zero for the ungulate population whose dynamics were best approximated by density-independent growth models.

We used the standard deviation in elevation within population ranges as an index of heterogeneity in resources, reasoning that heterogeneity in elevation creates spatial variation in plant phenology during the growing season. Landscapes with heterogeneous aspects and elevations create spatial heterogeneity in the timing of snowmelt and plant growth (Albon and Langvatn 1992), and spatial variation in forage nitrogen content and fibrousness is well explained by date of snow retreat (Mårell et al. 2006). We calculated the standard deviation of elevation of areas within 25 km of the center of herbivore ranges. Elevation data were obtained from the Shuttle Radar Topography Mission (SRTM) in 2000 (resolution = 70–90 m) (Werner 2001). We used the centroids of known ranges or published sampling locations to represent the location of herbivore populations. In past analyses we have used vegetation greenness estimated from satellite images (Normalized Difference Vegetation Indices, or NDVI) to represent vegetation heterogeneity, but those data would not provide reliable comparisons across our sites, which span from low to very high latitudes. High-latitude areas are not sampled well throughout the year using NDVI because of darkness in polar winter, and short growing seasons and dominance by evergreen species make characterizing greenness in those areas challenging (Beck et al. 2006).

To examine effects of spatial heterogeneity in resources and the presence of large predators on the strength of density dependence, we regressed the bootstrapped mean (\hat{b}) on the standard deviation of elevation, an indicator variable of predators (“1” for the presence of large carnivores and “0” otherwise), and latitude for 22 populations. We did not include the muskox population on Nunivak Island, Alaska, because no data on the standard deviation of elevation were available. Latitude was included as an independent variable in our models for two reasons. First, it serves as a proxy for climate and NPP, which have clear effects on the strength of density dependence. Second, the presence or absence of large carnivores varied with latitude. We examine all possible candidate models of different combinations of three independent variables and their interactions (=13 candidate models). We used Akaike weights to compare the strength of evidence for the alternative models.

Results

Ten populations showed evidence of density dependence, i.e., $b < 0$, and larger Akaike weights for the DDD or DIDD models (Table 1). The bootstrapped 95% confidence

intervals of b did not include zero for the ten populations. Evidence for direct density dependence was found in nine populations (DDD models, Table 2). Bison population dynamics in Yellowstone National Park were best approximated by the DIDD model, providing evidence for direct as well as delayed density dependence. We were unable to detect an effect of population density on per capita population growth rate for the other 13 populations of ungulates we studied (Table 1). The Akaike weights of the density-independent model for these 13 populations exceeded 0.6, indicating that although density dependence cannot be ruled out, evidence for these feedbacks was weak.

A 2×2 contingency table indicated that the occurrences of density dependence in the ungulate populations was associated with the absence of large carnivores (Table 2, $\chi^2 = 4.97$, $df = 1$, $P = 0.03$). The mean of the bootstrapped coefficient b of the ungulate populations coexisting with large carnivores was significantly less than that of the ungulate populations where predation was absent, indicating that predation weakens density dependence (two-tailed test: $t = 2.14$, $df = 21$, $P = 0.02$). Model selection revealed support for two models for the strength of density dependence. The best model contained coefficients for latitude, predation, and latitude \times predation interaction (Akaike weight = 0.54). The second supported model included latitude, standard deviation of elevation, predation, and latitude \times predation interaction (Akaike weight = 0.25). The remaining models had considerably less support in the data (Akaike weight < 0.04). We recalculated Akaike weights of the two competing models relative to the null model with an intercept only (Table 3). Our best supported models indicate that latitude interacted with the presence of predators. With increasing

latitude, the strength of density dependence of ungulate populations declined in populations experiencing predation (Table 3). Spatial heterogeneity in elevation reduced the strength of density dependence (Table 3; Fig. 1). For populations that showed density dependence ($n = 10$), the strength of feedbacks on per capita population growth (measured with \hat{b}) was inversely related to the standard deviation of elevation (Fig. 1). The slope was positive and significant ($\beta = 0.0005$, $w_i = 0.96$, $R^2 = 0.56$, $P = 0.01$) in the regression of the bootstrapped mean of b with the standard deviation of elevation.

Discussion

The effects of density on population growth rate varied among the 23 ungulate populations studied. The estimated value of parameter b , measuring the strength of density dependence, ranged from -0.43 to 0.0 (Table 1). We used the Kalman filter to estimate direct density dependence in northern ungulate populations to account for measurement error in the estimates of ungulate abundance. Our results of negative density dependence of elk in RMNP, YNP, and NER, bison in YNP, red deer on Rum Island, and Soay sheep on St. Kilda were consistent with the results of previous studies using different statistical models (Coulson et al. 2001; Lubow et al. 2002; Taper and Gogan 2002; Wang et al. 2002; Lubow and Smith 2004; Hone and Clutton-Brock 2007). Likewise, density dependence was not found in the Sheep River bighorn sheep by Portier et al. (1998) and this study (Table 1). However, our result of density independence of bighorn sheep in Ram Mountain was inconsistent with Portier et al. (1998). They found negative density dependence on lamb survival, but not on ewe survival. The difference in density dependence between these two studies might be due to the different statistical models. Furthermore, we regressed population growth rate ($r_t = \ln N_{t+1} - \ln N_t$) on logged population size at time t ($\ln N_t$) of the Ram Mountain bighorn sheep and found that the regression was insignificant ($P = 0.99$, $R^2 \approx 0.0$, $n = 25$), suggesting that population growth rates of the Ram Mountain bighorn sheep were not a function of population size. Thus, we concluded that no

Table 2 Frequency distribution of the occurrence of density dependence of ungulate populations between the sites with and without the presence of large carnivores

	Predator	No predator
Density dependence	3	7
Density independence	11	2

Table 3 Results of selection among multiple regression models of the strength of density dependence b on latitude of habitat, presence of predators, and standard deviation of elevation of ungulate habitat

	Intercept	Standard deviation of elevation	Latitude (north)	Predator	Latitude \times predator	Akaike weight
Model 1	0.79	NA	-0.02	-1.39	0.031	0.683
Model 2	0.56	0.00016	-0.017	-1.24	0.028	0.312
Null model	-0.16	NA	NA	NA	NA	0.005

Symbol “NA” indicates that a variable was not included in the regression. The value in each cell was the estimate of regression coefficient

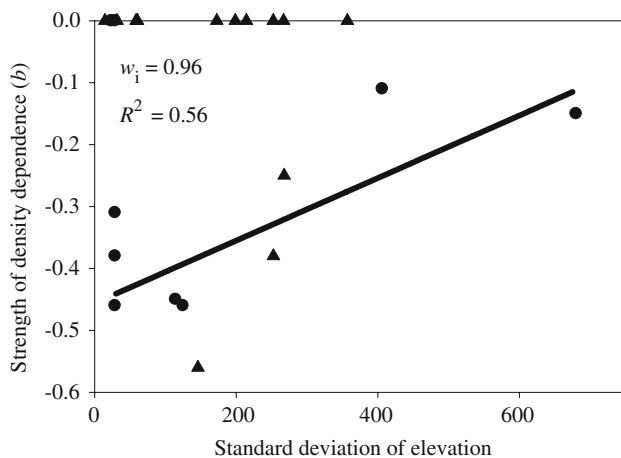


Fig. 1 Relationships between the strength of density dependence of 22 northern ungulate populations and spatial heterogeneity of habitat. The regression was based on data of ten ungulate populations of $b < 0.0$. Circular dots are for the presence of predation, and triangles are for the absence of predation. Symbol w_i is the Akaike weight showing 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

evidence was found for density dependence of the Ram Mountain bighorn sheep at the population level.

Climate and food availability are known to modify the effect of density dependence in ungulate populations (Jacobson et al. 2004; Wang et al. 2006; Hone and Clutton-Brock 2007). In the far north (latitudes $> 59^\circ$), we were unable to detect effects of population density on per capita population growth rate in any population examined. There are two explanations for why we failed to observe density dependence in the most northern populations. First, severe and variable weather in these environments may obscure feedbacks from population density. This interpretation is consistent with findings of Aanes et al. (2000) and Post (2005) who observed density-independent forcing of the dynamics of populations of caribou and reindeer at high latitudes attributable to climate. Second, feedbacks from population density may be attenuated by effects of predators or predator effects interacting with harsh winter climate. Large carnivores were present at all study sites with latitudes greater than 59°N (Table 1), and density dependence was weaker or not detectable in the presence than in the absence of large carnivores. Nevertheless, the effects of climate and predation cannot be disentangled in our work. Ungulate populations at the northern end of the latitudinal gradient we studied lived in habitats containing large carnivores, while carnivores were absent in more southern localities. Additionally, snow is usually deeper in high latitudes than low latitudes. Deep snow might increase a large carnivore's predation rate (Hebblewhite 2005); therefore, density dependence of northern ungulates

decreased from south to north probably because increased predation interacting with harsh winter climate prevented ungulate abundance from reaching a point where resources became limited.

A positive interaction between latitude and predation on density dependence in northern ungulates (Table 3) is consistent with the EEH prediction: ungulate populations increase substantially with increasing NPP in the absence of large carnivores and consequently are subjected to density dependence at a high-density equilibrium (Oksanen et al. 1981, 2001). The EEH predicts latitudinal patterns of herbivore dynamics based on the NPP gradient and plant-herbivore-carnivore interactions. It is expected that NPP increases from high to low latitudes, whereas winter severity increases from low to high latitudes. Moreover, climate exerts indirect effects on the food web and herbivore dynamics through changing either NPP or predation rate (Messier 1994; Oksanen et al. 2001; Lima et al. 2002).

We observed an inverse relationship between the strength of a density feedback to population growth rate and heterogeneity in elevation: increasing heterogeneity in elevation was associated with shallower slopes in the relationship between per capita population growth rate and population density. We suggest that this effect is mediated by the ability of herbivores to exploit spatial heterogeneity in forage quality. Differences in plant phenology resulting from variation in elevation in mountainous regions create gradients of forage quality (Albon and Langvatn 1992; Mårell et al. 2006); ungulates in mountainous areas respond by moving along these gradients and in so doing, are able to extend the period when they can obtain forage of peak quality (Albon and Langvatn 1992; Frank and McNaughton 1992; Myrsterud et al. 2001), thereby enhancing their body condition (Albon and Langvatn 1992; Myrsterud et al. 2001). Ungulate populations that did not migrate and were free of large carnivore predation in New Forest, St. Kilda, and Rum Island showed strong density dependence of population growth (Table 1). Moreover, heterogeneous topography may create variation in snow conditions that allow for greater access to forage during severe winters (Hobbs 1989). An alternative explanation for the effects of elevation heterogeneity is that high elevation in mountainous terrain retards plant growth and, in so doing, enhances forage quality (reviewed by Hjøljord and Histol 1999). In this case average elevation rather than heterogeneity in elevation would be expected to explain population level effects. However, we found no relationship between average elevation and density dependence, which suggests that variability in elevation rather than elevation per se shapes density dependence.

Our results on the effect of spatial heterogeneity have added another dimension to the connection between NPP

and density dependence of large herbivores. Wang et al. (2006) found that spatial heterogeneity in the NDVI reduced the strength of density dependence in elk and bison populations in the Rocky Mountains of North America. These results together with those we report here are important because they imply a relationship between habitat heterogeneity and ecosystem carrying capacity for populations of large herbivores at a given level of NPP. When density dependence is linear, reduction in the steepness of the slope between per capita population growth rate and population density causes increases in the x -intercept, which is an estimate of carrying capacity. Because we found that habitat heterogeneity is correlated with shallower slopes in this relationship, it follows that heterogeneity in habitat resources available to ungulates may modify the effect of the average amount of resources on animal abundance. Our findings suggest that limiting access to heterogeneity in resources by fragmenting habitats may reduce population carrying capacities entirely apart from effects of fragmentation on habitat area (also see Illius and O'Connor 2000; Boone et al. 2005; Fryxell et al. 2005). Thus, human actions that reduce connectivity among habitats in spatially heterogeneous environments may reasonably be expected to reduce the population performance of mobile, selective consumers. Our results suggest that population viability of consumers may be dependent on access to resources that vary asynchronously over space under influences of climate and predation (Oksanen et al. 2001; Fryxell et al. 2005).

Our analysis reveals complex interactions between internal, regulating forces of density dependence and the external context created by food webs, weather, and resources. Large scale gradients in latitude in the Northern Hemisphere paralleled gradients in severity of climate and presence or absence of predators. These gradients were associated with marked shifts in the operation of density dependence. At finer scales, heterogeneity in altitude, and its assumed affect on plant phenology, weakened density dependent feedbacks to population growth.

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