

Variation in stability of elk and red deer populations with abiotic and biotic factors at the species-distribution scale

FARSHID S. AHRESTANI,^{1,2,7} WILLIAM K. SMITH,^{3,4} MARK HEBBLEWHITE,⁵ STEVEN RUNNING,³ AND ERIC POST^{1,6}

¹The Polar Center and Department of Biology, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

²Frontier Wildlife Conservation, Mumbai 400007 India

³Numerical Terradynamic Simulation Group, Department of Ecosystem and Conservation Science, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA

⁴School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA

⁵Wildlife Biology Program, Department of Ecosystem and Conservation Science, College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA

⁶Department of Wildlife, Fish & Conservation Biology, University of California, Davis, California 95616 USA

Abstract. Stability in population dynamics is an emergent property of the interaction between direct and delayed density dependence, the strengths of which vary with environmental covariates. Analysis of variation across populations in the strength of direct and delayed density dependence can reveal variation in stability properties of populations at the species level. We examined the stability properties of 22 elk/red deer populations in a two-stage analysis. First, we estimated direct and delayed density dependence applying an AR(2) model in a Bayesian hierarchical framework. Second, we plotted the coefficients of direct and delayed density dependence in the Royama parameter plane. We then used a hierarchical approach to test the significance of environmental covariates of direct and delayed density dependence. Three populations exhibited highly stable and convergent dynamics with strong direct, and weak delayed, density dependence. The remaining 19 populations exhibited more complex dynamics characterized by multi-annual fluctuations. Most (15 of 19) of these exhibited a combination of weak to moderate direct and delayed density dependence. Best-fit models included environmental covariates in 17 populations (77% of the total). Of these, interannual variation in growing-season primary productivity and interannual variation in winter temperature were the most common, performing as the best-fit covariate in six and five populations, respectively. Interannual variation in growing-season primary productivity was associated with the weakest combination of direct and delayed density dependence, while interannual variation in winter temperature was associated with the strongest combination of direct and delayed density dependence. These results accord with a classic theoretical prediction that environmental variability should weaken population stability. They furthermore suggest that two forms of environmental variability, one related to forage resources and the other related to abiotic conditions, both reduce stability, but in opposing fashion: one through weakened direct density dependence and the other through strengthened delayed density dependence. Importantly, however, no single abiotic or biotic environmental factor emerged as generally predictive of the strengths of direct or delayed density dependence, nor of the stability properties emerging from their interaction. Our results emphasize the challenges inherent to ascribing primacy to drivers of such parameters at the species level and distribution scale.

Key words: Bayesian hierarchical models; density dependence; growing season; normalized difference vegetation index; Royama parameter plane; second order autoregressive; winter temperature.

INTRODUCTION

Stability is a necessary component of the long-term persistence of populations because increasingly stochastic dynamics render populations more likely to undergo local extirpation (May 1973a, Turchin 1993, Hanski and Ovaskainen 2002). In completely deterministic environments, point stability may result from direct density-dependent feedback on population growth, as long as it is not too strongly overcompensating (May

1973b, Grenfell et al. 1992). In variable environments, however, the stabilizing influence of density dependence on population dynamics may be opposed by the destabilizing influence of variation in resources or abiotic environmental conditions (Saether 1997, Bjornstad and Grenfell 2001). In this case, stability may only be considered in the more dynamic sense of an equilibrium probability distribution, with the probability of stability declining in relation to increasing environmental variability (May 1973b). While studies of population-level responses to environmental variability have a lengthy history, these have focused nearly exclusively on dynamics, rather than stability. Focus on patterns of

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⁷E-mail: farshid.ahrestani@gmail.com

variation in population stability and the potential drivers of such variation are increasingly warranted in the context of ongoing environmental change and its consequences for species-level persistence.

Stability in populations of species with overlapping generations, such as vertebrate herbivores, is a function of the relationship between the strength of direct (non-lagged) and delayed (lagged) density dependence (Stenseth et al. 1996, Bjornstad et al. 1998). The stability implications of variation in the strengths of direct and delayed density dependence, and the relationship between them, can be revealed through statistical analysis of time series data using the parameter plane of the linear second-order density-dependent autoregressive AR(2) model (Royama 1992) (Fig. 2a). In the Royama framework, populations with either point stability or highly dampened oscillations are characterized by weak delayed density dependence and moderate or strong direct density dependence, respectively. Dynamic variability, on the other hand, results from strengthening of delayed density dependence, characterized by increasing amplitude, and a weakening of direct density dependence and increasing periodicity. The details of the Royama parameter plane are made more explicit in *Material and Methods*.

In populations of species displaying second-order dynamics, delayed density dependence tends to arise through vertical exploitation interactions such as consumer–resource and pathogen–host interactions, whereas direct density dependence relates mainly to horizontal intraspecific competition and the resultant potential for self-regulation (Framstad et al. 1997, Post 2013). The periodic crashes of Soay sheep on St. Kilda constitute a well-known example of the consequences of over-compensatory direct density dependence for population stability (Grenfell et al. 1992, CluttonBrock et al. 1997). Examples of the stability implications of variation in the strength of delayed density dependence include decreasing stability in fox dynamics with a strengthening of delayed density dependence under the spread of sarcoptic mange in Denmark (Forchhammer and Asferg 2000), and increasing stability with a weakening of delayed density dependence of moose dynamics on Isle Royale, Michigan, USA, during a decline in the resident wolf population (Post et al. 2002).

Density dependence can thus be viewed as a dynamic feature of populations that varies with geographical and temporal gradients in environmental conditions across a species' distributional range (Bjornstad et al. 1995, Stenseth et al. 1999, Post 2005, Post et al. 2009, Imperio et al. 2012). While large-scale gradients in the strength of density dependence have been examined in multiple species of mammals (Bjornstad et al. 1995, Stenseth et al. 1996, 1999, Post 2005), very few studies have examined comparatively large-scale variation in population stability (Stenseth et al. 1996), and none, to our knowledge, has done so at the species-distribution scale.

In mid- to high-latitude systems, the seasonality of primary production and winter conditions, mainly

temperature and precipitation, are key factors in the reproduction and survival of large herbivores (Post and Stenseth 1999, Coulson et al. 2001, Pettorelli et al. 2005, Mysterud and Ostbye 2006, Tyler 2010). Variation in reproductive and survival rates can influence the strength of either or both direct and delayed density dependence, and in turn stability, within populations of large herbivores (Post and Forchhammer 2008, Bonenfant et al. 2009, Griffin et al. 2011). We focused on elk and red deer (*Cervus elaphus*) in our investigation of large-scale variation in density dependence and resultant stability properties of population dynamics because this species complex is distributed widely across the Northern Hemisphere, encountering an array of highly variable biotic and abiotic environmental conditions.

MATERIALS AND METHODS

Population time series

We used time series of estimates of annual abundance of 22 elk and red deer populations located in eight countries (Fig. 1; see also Appendix S1: Table S1 and Fig. S1). These time series comprised either raw counts, or counts that were adjusted to account for sampling issues such as detectability, and were, in each case, obtained from the literature. Because Normalized Difference Vegetation Index (NDVI) data were available only from 1982 onward, we truncated the population time series to exclude counts prior to 1982. After truncating the data, the length of time series for different populations ranged 12–24 yr (mean = 20.8), and four of the time series were missing data for 2–5 yrs.

Environmental covariates

The temporal and spatial distributions of forage abundance and quality during the summer are known to be important drivers of population dynamics and density dependence in large herbivores in the northern hemisphere (Forchhammer et al. 2001, Hebblewhite et al. 2008, Bonenfant et al. 2009). To maintain consistency in the quality of data, and facilitate comparison across elk and red deer populations under a wide range of environmental conditions, we used NDVI data as an index of primary productivity representing forage abundance and its variation through time (Pettorelli et al. 2011). We selected four parameters representative of summer primary productivity with relevance to large herbivore ecology and population dynamics: variability in annual estimates of growing season NDVI (Wang et al. 2006); and the start, length, and end of the growing season (Pettorelli et al. 2007, Hebblewhite et al. 2008, Bischof et al. 2012).

These four biotic covariates were derived from five arc-minute spatial resolution Global Inventory Modeling and Mapping Studies (GIMMS) NDVI (NDVI3g) data available at bimonthly temporal resolution from 1982 to

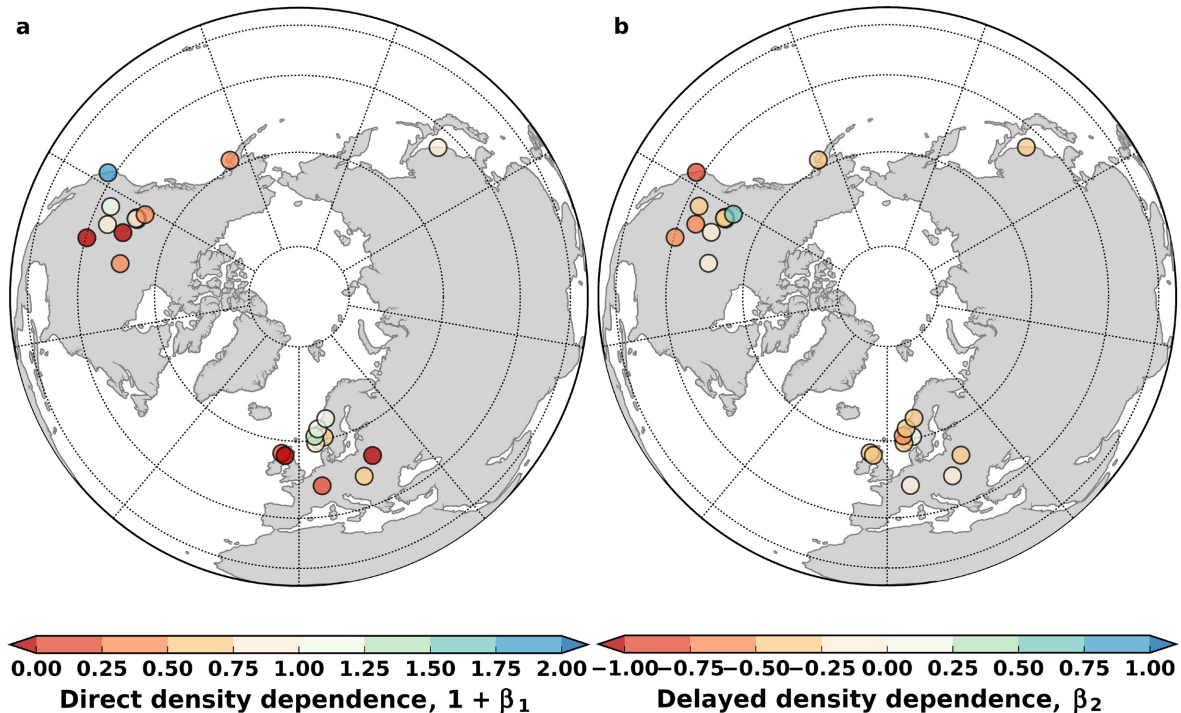


FIG. 1. Location and the estimates of (a) direct and (b) delayed density dependence in 22 elk and red deer populations whose time series were analyzed by a Bayesian state-space hierarchical Gompertz linear, second-order, density-dependent, autoregressive AR(2) model. Negative direct density dependence ($1 + \beta_1$) and delayed density dependence (β_2) in a population are indicated by values of less than one and less than zero, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

2011 (Zeng et al. 2013). We used the TIMESAT software package to approximate the start, end, and length of the growing season by fitting the 30-yr bimonthly NDVI time-series data for each population with a double logistic function, and then applying a threshold value of 50% of the seasonal amplitude (Appendix S1: Fig. S2; Jonsson and Eklundh 2004). Variability in NDVI was indexed by calculating the coefficient of variation (CV) over the estimated length of the growing season for each population-specific location. The CV of growing-season NDVI is, hence, intended here as an index of biotic environmental variability, one component of environmental variability that theory predicts should reduce population stability (May 1973b). We also considered a static measure of primary production, annual maximum NDVI, but rejected its use in this analysis because vegetation structure presumably varies considerably among areas inhabited by these populations.

Through direct or indirect influences on mortality, severity of winter abiotic conditions may influence population dynamics, and thereby stability, in large herbivores in northern environments (Forchhammer et al. 1998, Post and Stenseth 1998, Coulson et al. 2001, Martinez-Jauregui et al. 2009, Simard et al. 2010). Therefore, two of the three abiotic predictor variables included annual wintertime (December–February) precipitation and the CV of annual wintertime (December–February) temperature. As a complement to the CV of growing-season NDVI, the CV

of winter temperature was intended here as an index of abiotic environmental variability, presumed, according to theory (May 1973b), to reduce population stability. Annual winter precipitation data were obtained from the Global Precipitation Climatology Centre (GPCC; Rudolf and Schneider 2005; data *available online*),⁸ and winter temperatures from the National Centre for Environmental Prediction Reanalysis II (NCEP II; Kanamitsu et al. 2002; data *available online*).⁹ We also included as a potential abiotic predictor annual values of Northern Hemisphere land surface temperature anomalies (NHLTA). We chose NHLTA data because these generally describe climatic variability over large areas better than absolute temperatures (Mann et al. 1998); these data were obtained from the National Climatic Data Center of the National Oceanic and Atmospheric Administration (data *available online*).¹⁰ To match the spatial scale of the NDVI data, all covariate data were spatially interpolated using the binomial method.

Although there was considerable variation in the spatial extent of the ranges inhabited by the populations (20–15000 km²; Appendix S1: Table S1), a sensitivity analysis revealed that the covariates varied negligibly

⁸ <http://www.esrl.noaa.gov/psd/data/gridded/data.gpcc.html>

⁹ http://www.esrl.noaa.gov/psd/data/gridded/data.ncep_reanalysis2.gaussian.html

¹⁰ <http://www.ncdc.noaa.gov/monitoring-references/faq/anomalies.php>

over a large spatial range (Appendix S1: Fig. S3). Data for the covariates were, therefore, aggregated over a radial 2,000 km² area originating from a centroid for each population, and we checked the degree to which the initial set of seven covariates (four NDVI, two temperature, and one precipitation covariate) were correlated (Appendix S1: Fig. S4). We found that the end of the growing season was correlated with both start ($r = 0.55$) and length of growing season ($r = 0.58$; Appendix S1: Fig. S4), and was therefore not used. Since start and the length of growing season were only marginally related ($r = 0.36$; Appendix S1: Fig. S4), both were included in the final list of covariates. The CV of winter precipitation was highly correlated with NHLTA ($r = 0.69$), and because the influence of temperature patterns in driving precipitation is generally greater than the influence of precipitation patterns in driving temperature, we included NHLTA and not CV of winter precipitation. The initial list of seven predictor variables considered initially, therefore, reduced to a final list of five environmental covariates.

Bayesian state-space population modeling

Bayesian state-space modeling is well suited for this analysis because it hierarchically models the biological (system) process separately from the observation process, dissecting process variation in populations dynamics from observation error in the data, which, in turn, reduces the probability of overestimating density dependence (De Valpine and Hastings 2002, Clark and Bjornstad 2004, Ahrestani et al. 2013). As mentioned earlier, stability characteristics in population dynamics can be statistically assessed from the relationship in the Royama parameter plane between estimates of direct ($t - 1$) and delayed ($t - 2$) density dependence (Royama 1992). A Gompertz linear, second-order, density-dependent, autoregressive AR(2) model was used to statistically approximate both direct and delayed density dependence (Gompertz 1825, Royama 1992)

$$X_{i,t} = \beta_{i,0} + (1 + \beta_{i,1})X_{i,t-1} + \beta_{i,2}X_{i,t-2} + \varepsilon_{i,t} \quad (1)$$

in which $X_{i,t}$ represents the \log_e -transformed abundance $x_{i,t}$ for population i at time t , $\beta_{i,0}$ represents the intrinsic rate of increase, $\beta_{i,1}$ the strength of statistical direct density dependence, and $\beta_{i,2}$ the strength of statistical delayed density dependence (Stenseth et al. 1998b). In this model, values of $(1 + \beta_{i,0}) < 1$ indicate negative direct density dependence and values of $\beta_{i,2} < 0$ indicate negative delayed density dependence (Forchhammer et al. 1998). The process variation, $\varepsilon_{i,t}$ was assumed to be normally distributed with mean zero and standard deviation $\sigma_{i,x}$ [$\varepsilon_{i,t} \sim \mathcal{N}(0, \sigma_{i,x}^2)$].

Complementing Eq. 1, the observation model component analyzed the state of the system process $X_{i,t}$ as observed indirectly through abundance counts $Y_{i,t}$

$$Y_{i,t} \sim \mathcal{N}(x_{i,t}, \sigma_{i,y}^2). \quad (2)$$

The \log_e observed abundance $Y_{i,t}$ is assumed to be randomly drawn from a normal distribution with the true abundance $x_{i,t}$ as the mean and an observation error standard deviation $\sigma_{i,y}$.

To investigate whether the dynamics of any of the populations were associated with the aforementioned environmental covariates, we subsequently fit five modified Gompertz models, each of which included an individual environmental covariate, for each population. For example, the modified AR(2) model that included start of the growing season (SGS) as a covariate was

$$X_{i,t} = \beta_{i,0} + (1 + \beta_{i,1})X_{i,t-1} + \beta_{i,2}X_{i,t-2} + \beta_{i,3}\text{SGS}_{i,t-1} + \varepsilon_{i,t}. \quad (3)$$

To avoid confusion with the covariate models, the original Gompertz model with no covariate is henceforth referred to as the skeleton AR(2) model.

Stationarity of the time series is a requirement for evaluating stability using the Royama parameter plane in classical time series models (Royama 1992, Bjornstad et al. 1995, Stenseth et al. 2003). To achieve stationarity, we detrended the log-transformed time series. To ensure that the estimates of $\beta_{i,1}$ and $\beta_{i,2}$ were comparable across the six models (skeleton and five covariate models), we also detrended all covariate time series.

The Bayesian Markov Chain Monte Carlo approach requires that prior probabilities are assigned to parent parameters of the model, which, in the case of our model, were $\beta_{i,0}$, $\beta_{i,1}$, $\beta_{i,2}$, $\beta_{i,3}$, $\sigma_{i,x}$, and $\sigma_{i,y}$. Assigning informed priors for the intrinsic growth rate, $\beta_{i,0}$, improves the precision and reduces bias in estimating density dependence (Lebreton and Gimenez 2013). We therefore assigned $\beta_{i,0}$ with an informed prior of both the mean (0.03) and maximum (0.56) intrinsic growth rate using values reported for the species (Benton et al. 1995, Eberhardt et al. 1996, Eberhardt 2002, Hebblewhite et al. 2002, Taper and Gogan 2002, Clutton-Brock et al. 2004, Creel and Creel 2009). However, we found that when the time series were detrended, model estimates of density dependence were no different than when $\beta_{i,0}$ was assigned a vague prior derived from a normal distribution with mean of 0 and precision of 10^{-6} , i.e., $\beta_{i,0} \sim \mathcal{N}(0, 10^{-6})$. We also discovered that, when time-series were not detrended, model estimates of density $\beta_{i,0}$ were different when using different priors (Appendix S1: Fig. S5). It was apparent, therefore, that detrending the time series made estimates of density dependence insensitive to informed priors, and hence we followed the general practice of assigning vague probabilities for all parent parameters $\beta_{i,0} \sim \mathcal{N}(0, 10^{-6})$, $\beta_{i,1} \sim \mathcal{N}(0, 10^{-6})$, $\beta_{i,2} \sim \mathcal{N}(0, 10^{-6})$, $\beta_{i,3} \sim \mathcal{N}(0, 10^{-6})$, $\sigma_{i,x} \sim \mathcal{U}(0, 1)$, $\sigma_{i,y} \sim \mathcal{U}(0, 1)$. Furthermore, because of detrending the data, the value of $\beta_{i,0}$ for all populations was approximately zero (Appendix S1: Table S2) (Bjornstad et al. 1995), and was therefore not discussed.

State-space models were analyzed using the Gibbs Sampler in JAGS 3.3.0, which was implemented with the jagsUI library (Kellner 2016) in the R statistical computing environment (R Core Team 2015). Posterior distributions of density dependence estimates for each

population were derived by successive application of the Bayes theorem using 200,000 simulations, a burn-in of 100,000 simulations, a thinning rate of 5, and by running three Markov chains of the Gibbs sampler (Gelman and Hill 2007). The Markov chains were determined to have successfully converged if \hat{R} values were <1.1 for posterior estimates of all parameters (Gelman and Hill 2007).

Population stability characteristics

We plotted the coefficients of direct and delayed density dependence derived from the AR(2) skeleton model for each population within the Royama parameter plane to estimate their stability properties. The relative locations within the Royama parameter plane of the estimates of the coefficients of statistical direct and delayed density dependence derived from the skeleton AR(2) model (Fig. 2a) indicate the stability properties of a population (Royama 1992, Bjornstad et al. 1995, Forchhammer et al. 1998, Stenseth et al. 2003, Wang et al. 2013) as follows: Region I, point stability characterized by moderate direct and weak delayed density dependence, and assumed to be steadily converging to carrying capacity; Region II, variable point stability characterized by strong direct and weak delayed density dependence, and assumed to fluctuate with a small amplitude over short intervals (~ 1 – 2 yr) while converging toward carrying capacity eventually; Region III, short-term fluctuations characterized by moderate to strong direct and strong delayed density dependence; and Region IV, longer-term fluctuations characterized by moderate to weak direct and strong delayed density dependence. Hence, populations occurring within the triangle but above the parabola are stable, while those within the triangle but below the parabola are variable, with the degree of variability increasing downward and to the right within the parabola (Royama 1992, Bjornstad et al. 1995). Areas outside the bounded triangular space indicate statistical instability that will eventually result in local extinction (Royama 1992, Bjornstad et al. 1995). This gradient away from stability and toward variability can thus be interpreted a consequence of increasing delayed density dependence and weakening direct density dependence (Bjornstad et al. 1995).

We assumed that a covariate model that fit a population time-series better than the skeleton model would identify the environmental covariate associated with the stability properties of a given population. Hence, we examined locations of the density dependence coefficients of populations obtained with the AR(2) skeleton model within the Royama parameter plane according to their best-fit environmental covariates. The model with the lowest Deviance Information Criteria (DIC) was determined to be the best fit model for each population time-series; DIC employs a penalized deviance approach and is the most commonly used criterion to select models that are analyzed using MCMC methods (Spiegelhalter et al. 2002).

Cross-population meta-analysis

To determine whether the strengths of direct and delayed density dependence varied among environmental covariates, we employed a meta-analysis of the skeleton model AR(2) coefficients. This meta-analysis was performed as a Generalized Additive Model (Hastie and Tibshirani 1999) that included a categorical nominal predictor, the best-fit environmental covariate, and a continuous numerical predictor, latitude. We included latitude in this analysis because, in north temperate mammals, density dependence is expected to be stronger at a species' southern range limit than at its northern range limit, where environmental limitation should be stronger (Hansson and Henttonen 1985, Albon and Clutton-Brock 1988), and several previous studies have documented this empirically (Bjornstad et al. 1995, Saitoh et al. 1998, Stenseth et al. 1998a, Post 2005). We also included time series length as a continuous numerical predictor in the GAM to account for variation attributable to any statistical artifact effect. Finally, although there is no a priori reason to expect any statistical association between the coefficients of direct- and delayed density dependence (Royama 1992), we included each as a potential covariate in separate GAMs of the other in order to account for any relationship between the two.

RESULTS

The signs and magnitudes of coefficients of direct and delayed density dependence derived from the AR(2) skeleton model varied considerably across the distribution of populations (Fig. 1). The plot of these coefficients in the Royama parameter plane revealed that only three of the 22 focal populations, or 13.6%, can be categorized as stable, and all three of these occur within Region I of the plane (Fig. 2b). The remaining 19 populations all occur below the parabola in the Royama parameter plane, and are thus categorized as variable. Among these 19, the majority (15, or 78.9%) occur in the region of greatest variability and hence lowest stability, Region IV (Fig. 2b).

After accounting for density dependence, best-fit models (Appendix S1: Table S3) included environmental covariates in the dynamics of 17 of the 22 focal populations (77.3%; Table 1). Variability in growing-season primary productivity (CV NDVI) appeared in the best-fit model for the dynamics of the greatest number populations (6 of 22, or 27.3%), followed by variation in winter temperature (CV WT; 5 of 22, or 22.7%), and Northern Hemisphere warming (NHLTA; 4 of 22, or 18.2%) (Table 1). The annual length of the vegetative growing season (GSL) and the annual start of the vegetative growing season (GSS) each appeared in the best-fit model describing the dynamics of a single population (Table 1). Hence, variation in primary productivity and in winter temperature appeared to be the most common predictors of dynamics and stability of the focal populations, with each accounting

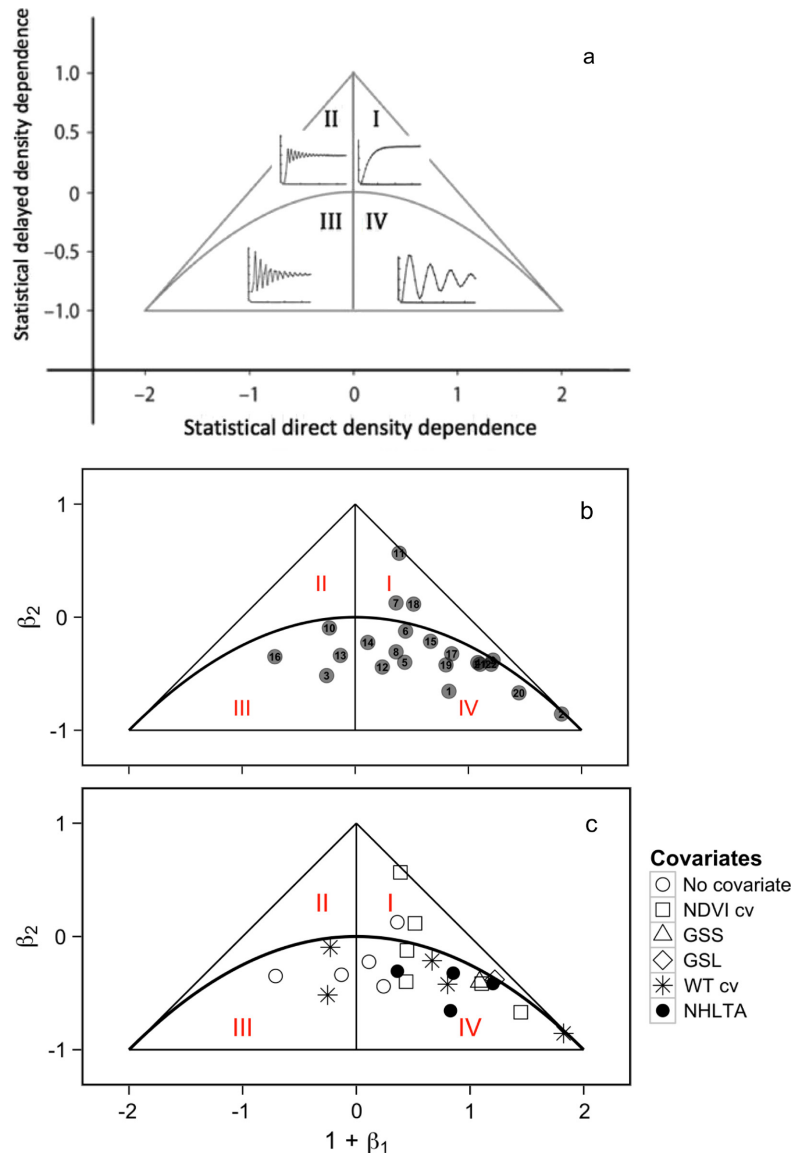


FIG. 2. (a) The expected dynamics related to the strengths of statistical direct ($1 + \beta_1$) and delayed (β_2) density dependence estimated by a linear, second-order, pure, density-dependent, autoregressive AR(2) model illustrated in the parameter ($1 + \beta_1$, β_2) plane. Modified from Royama (1992) and reproduced from Post (2013). Panels b and c plot the direct ($1 + \beta_1$) and delayed (β_2) density dependence parameter pairs estimated in 22 globally distributed elk and red deer (*Cervus* sp.) populations modelled by a linear, second-order, density-dependent, autoregressive AR(2) (skeleton) model using a Bayesian state-space hierarchical approach. The values of the points on the parameter planes in b and c are the same because statistical stability characteristics based on direct and delayed density dependence in populations can be assessed only using a skeleton AR(2) model with no covariate. The symbols in panel c refer to either the no covariate (skeleton) model, or to the covariate that was in the modified AR(2) model that best fit the time-series of each of the 22 elk populations. The best-fit model had the lowest Deviance Information Criteria (DIC) value among the seven models that were fit to each time-series. The five covariates used to modify the skeletal model were (1) NDVI CV, coefficient of variation of Naturalized Difference Vegetation Index (NDVI); (2) GSS, start of the growing season (number of the day from the beginning of a calendar year); (3) GSL, length of the growing season (number of days); (4) WT CV, coefficient of variation of Winter temperature ($^{\circ}\text{C}$, Dec–Feb); (5) NHLTA, Northern Hemisphere Land Temperature Anomaly. [Color figure can be viewed at wileyonlinelibrary.com]

for approximately one-quarter of the populations. Nonetheless, there was no apparent consistency in the directionality of the effects of environmental predictor variables on dynamics (Table 1). Similarly, when mapped onto the Royama parameter plane, the best-fit environmental covariates for each population do not segregate clearly

among the stability regions, except in populations for which Northern Hemisphere warming was a factor in dynamics; all of these occur within the region of lowest stability, Region IV (Fig. 2c).

The low number of time series within each category of best-fit environmental covariate precluded post-hoc

TABLE 1. The linear, second-order, density-dependent, autoregressive (AR2) models, either with (modified) or without (skeleton) a covariate, that best fit the time series of 22 globally distributed elk/red deer populations.

Population	Best-fit model	Association with covariate
Northern Range, Yellowstone, Wyoming, USA	NHLTA	–
Point Reyes, California, USA	CV WT	+
Estes Valley, Colorado, USA	CV WT	+
Jackson Hole, Wyoming, USA	GSS	–
Raspberry Island, Alaska, USA	CV NDVI	+
Riding Mountain National Park, Manitoba, Canada	CV NDVI	+
Ya Ha Tinda, Banff National Park, Alberta, Canada	No covariate	NA
West Bow Valley, Banff National Park, Alberta, Canada	NHLTA	+
Central Bow Valley, Banff National Park, Alberta, Canada	GSL	+
Cypress Hills, Alberta–Saskatchewan, Canada	CV WT	–
Jasper National Park, Alberta, Canada	CV NDVI	–
Isle of Rhum, Scotland	No covariate	NA
Scottish Highlands, Scotland	No covariate	NA
Petite Pierre National Reserve, France	No covariate	NA
Tatra, Slovakia	CV WT	–
Bialowieza Primeval Forest, Poland	No covariate	NA
Sikhote-Alin Zapovednik, Russia	NHLTA	–
Population 1, Norway	CV NDVI	+
Population 2, Norway	CV WT	–
Population 3, Norway	CV NDVI	+
Population 4, Norway	CV NDVI	+
Population 5, Norway	NHLTA	–

Notes: The covariates added to the skeleton model were CV NDVI, coefficient of variation of Naturalized Difference Vegetation Index (NDVI); GSS, start of the growing season (number of the day from the beginning of a calendar year); GSL, length of the growing season (number of days); CV WT, coefficient of variation of winter temperature ($^{\circ}\text{C}$, Dec–Feb); NHLTA, Northern Hemisphere Land Temperature Anomaly. The $-/+$ signs in the table indicate the sign of the coefficient of the covariate term in the model that best fit a population time series. NA, not applicable, because “the skeleton model with no covariate best fit the population time series.”

pairwise comparisons of the strengths of density dependence. However, populations for which interannual variation in primary productivity was the best-fit covariate exhibited the weakest combined mean direct (0.73 ± 0.22 [mean \pm SE]) and delayed (-0.16 ± 0.13) density dependence. In contrast, populations for which interannual variation in winter temperature was the best-fit covariate exhibited the strongest combined direct (-0.56 ± 0.14) and delayed (-0.43 ± 0.13) density dependence. Recall that in the log-linear expression of the AR(2) model, the coefficient for direct density dependence includes 1, so difference from 1 indicates the strength of the coefficient.

Previous analyses have documented linear associations between direct density dependence and latitude among populations north of 60° in small mammals (Bjornstad et al. 1995) and north of 51.7° in large mammals (Post 2005). The GAM of direct density dependence we applied here indicated direct density dependence was not linearly related to latitude ($F = 0.22$, $P = 0.65$), but that it varied significantly with time series length ($b = 0.61 \pm 0.14$; $F = 13.17$, $P = 0.003$), delayed density dependence ($b = -0.69 \pm 0.18$; $F = 12.37$, $P = 0.004$), and among best-fit covariates ($F = 6.26$, $P = 0.004$; GAM $R^2 = 0.85$, $F = 11.45$, $P < 0.001$). A subsequent model-fitting analysis revealed that the association between direct density

dependence and latitude was best fit by a cubic spline function ($R^2 = 0.31$, $P = 0.03$), with a nonsignificant association for latitudes south of 51.66° N ($R^2 = 0.11$, $P = 0.3$) and a significant, positive association for latitudes north of 51.66° N ($R^2 = 0.57$, $P = 0.007$; Fig. 3a). The GAM of delayed density dependence produced similar results, indicating a lack of linear association with latitude ($F = 0.06$, $P = 0.81$), but significant associations with time series length ($b = 0.74 \pm 0.21$; $F = 12.36$, $P = 0.003$), direct density dependence ($b = -1.03 \pm 0.25$; $F = 17.19$, $P = 0.001$), and best-fit covariate ($F = 4.98$, $P = 0.008$; GAM $R^2 = 0.78$, $P = 0.001$). The same model-fitting analysis that was applied to the association between direct density dependence and latitude also revealed that the association between delayed density dependence and latitude was best fit by a cubic spline function ($R^2 = 0.33$, $P = 0.02$), but with a significant linear association for latitudes south of 51.66° N ($R^2 = 0.65$, $P = 0.003$), and a nonsignificant association for latitudes north of 51.66° N ($R^2 = 0.29$, $P = 0.09$; Fig. 3b).

DISCUSSION

In species typified by second-order, density-dependent, population dynamics, such as large herbivores, environmental variation may erode population stability in three

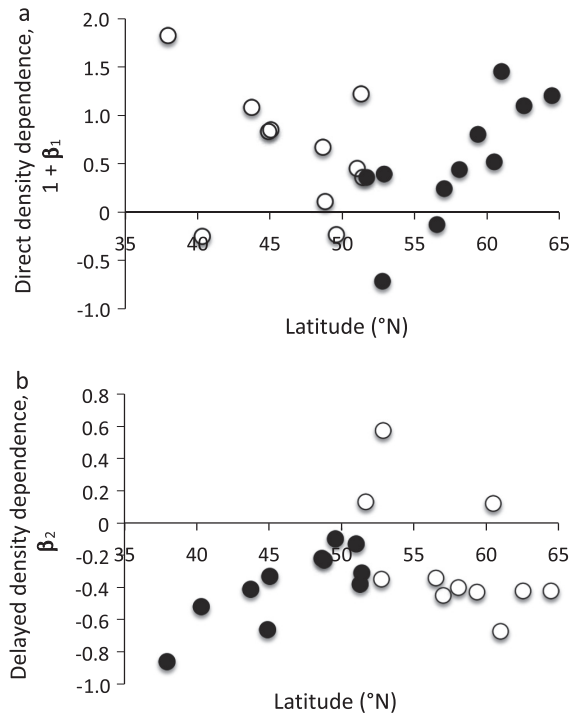


FIG. 3. Associations between the strength of (a) direct and (b) delayed density dependence and latitude. In each panel, significant associations are indicated by solid scatter plots, while open scatter plots are non-significant. See *Results* for the full exposition of statistical tests in each case.

ways: through a weakening of direct density dependence, through a strengthening of delayed density dependence, or both in concert (Royama 1992). Our results indicate that variability in both biotic and abiotic elements of the environment was associated with population variability characteristic of the least stable dynamics represented in the Royama parameter plane, but in opposing ways. Forage resource variability was associated with relatively weak mean direct density dependence, while wintertime temperature variability was associated with relatively strong mean delayed density dependence.

Despite having documented associations between biotic and abiotic environmental variability and variable (i.e., non-stable) population dynamics, the lack of consistency in the directionality of environmental covariates of dynamics among the focal populations may at first pass appear disconcerting. However, our objective here was not to derive generality in the population dynamics of elk and red deer, which could from the outset be labeled a fruitless pursuit, but rather to investigate contributions of environmental variability to population variability, the inverse of stability. Environmental variability drives populations away from point stability by interfering with the stabilizing feedback between density-dependent interactions in successive time steps (May et al. 1974, May 1975). Theory predicts that it is the magnitude of environmental variability, or the so-called

dispersion factor in population dynamics, that reduces population stability, regardless of the directionality of the influence of any environmental factor on changes in abundance (May 1973b). In this context, our results appear to accord with ecological theory.

While we cannot identify mechanisms through which abiotic and biotic environmental variability might reduce population stability here, a wealth of evidence suggests that primary production, winter conditions, and the interaction between climatic conditions and density dependence influences survival rates, reproductive rates, and population dynamics in elk and red deer (Sauer and Boyce 1983, Forchhammer et al. 1998, Coulson et al. 2001, Garrott et al. 2003, Wang et al. 2006, Christianson and Creel 2007, Hone and Clutton-Brock 2007, Pettorelli et al. 2007, Creel and Creel 2009). For instance, in a study of five large herbivore populations, four of which were elk populations, Wang et al. (2006) demonstrated that variation in NDVI was negatively related to the strength of density dependence, attributing this to the ability of ungulates to selectively exploit heterogeneity in plant resources. Wang et al. (2006) also found that interannual variation in winter temperature was positively associated with the strength of density dependence, attributing this to varying temperatures contributing to cycles of icing the thawing that increase snow hardness, in turn reducing the availability of forage.

Drivers of dynamics varied considerably in this analysis across a range of biotic and abiotic environmental conditions, yet variation in vegetation productivity and winter temperature appeared to be the most common (Table 1). Heuristic, process-oriented ecological models that have been used to derive statistical autoregressive models such as the one applied here (Eqn 1) predict that delayed density dependence typically arises through interactions across trophic levels or through cohort effects (Stenseth 1995, Stenseth et al. 1997; Forchhammer et al. 1998, Forchhammer and Asferg 2000, Forchhammer et al. 2001). Hence, the fact that the dynamics of most of the populations occurring in region IV of the Royama plane (Fig. 2c) were associated with interannual variation in winter temperature and primary productivity suggests that these factors contribute to productivity or trophic interactions in elk and red deer. Nonetheless, the inconsistency evident in the direction of such effects on dynamics (Table 1) renders generalizations about their importance or management implications nearly impossible.

Our results complement two other studies that have analyzed the population dynamics of large herbivores using the Royama framework (Forchhammer et al. 1998, Wang et al. 2013). Both of these studies also failed to detect populations characterized by short periodicity, i.e., a complete absence of populations in region II of the Royama parameter plane. Though not strictly cyclical, the mean length of the multi-annual fluctuations among populations analyzed here was 4.7 yr (Appendix S1: Table S1). Highly stable dynamics, which in a completely deterministic environment would result in point stability,

were uncommon among populations included in this analysis. In contrast, Wang et al. (2013) detected dynamics approximating point stability in all 23 of the populations of large herbivores they analyzed. A direct comparison to our results is complicated, however, by the fact that our analysis focused on a single species complex, while that of Wang et al. (2013) incorporated 14 species.

That we detected no significant linear association between direct density dependence and latitude over the full range of latitudes encompassed by our data contrasts with results of a similar analysis of caribou and reindeer population dynamics by Post (2005). However, over approximately the same range of latitudes (i.e., $\geq 51.7^\circ$ N), our results accord with those in Post (2005), and suggest weaker direct density dependence with increasing latitude toward the northern extent of the distribution of *Cervus* sp. Although not investigated in Post (2005), we also detected a strengthening of delayed density dependence at lower latitudes, but only in the southernmost populations. Because direct density dependence arises through intraspecific competition while delayed density dependence can relate to trophic interactions (Stenseth 1995), these two patterns are broadly consistent with the notion that abundance is limited primarily by abiotic conditions at the northern limit of a species' distribution and by biotic interactions at its southern limit (Case and Taper 2000, Case et al. 2005).

Our results indicate that the factors influencing the strength of density dependence, and hence population stability, can vary considerably across the distribution of a species. This likely reflects comparable variation across such geographic scales in biotic and abiotic environmental conditions, both of which are likely as well to vary through time in relation to land use changes and climate change (Sala et al. 2010; Foley et al. 2005). Management and conservation policies and practitioners must account for spatial and temporal variation in drivers of population dynamics and stability of species of considerable cultural and economic importance such as elk and red deer. In theory, long-term studies of individual populations have a greater likelihood of isolating the mechanisms and environmental drivers of population dynamics and stability. However, such studies (e.g., Gaillard et al. 2013, Plard et al. 2014) are rare and difficult to fund, typically do not span species' distributional ranges, and pose challenges for generalizing to other populations. In contrast, time-series analyses, while occasionally criticized for lacking mechanistic insights (Krebs 2013), are less expensive, span longer time periods and greater spatial distributions, and are amenable to distribution-wide analyses. Furthermore, the capacity of Bayesian state-space modeling to specifically account for uncertainty adds value to analyses of time-series data (Ahrestani et al. 2013). Thus, continuing to monitor large herbivore populations at global scales using time-series analysis will be an important step toward detecting changes in dynamic complexity in economically and ecologically important species. Studies that have the luxury of large and

long-term data sets should strive to include multiple analytical approaches to comprehensively evaluate the potentially tremendous variation in sets of variables associated with dynamics and stability across species' ranges.

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