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Featured Article

Factors Influencing Elk Recruitment Across Ecotypes in the Western United States

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ABSTRACT Ungulates are key components in ecosystems and economically important for sport and subsistence harvest. Yet the relative importance of the effects of weather conditions, forage productivity, and carnivores on ungulates are not well understood. We examined changes in elk (*Cervus canadensis*) recruitment (indexed as age ratios) across 7 states and 3 ecotypes in the northwestern United States during 1989–2010, while considering the effects of predator richness, forage productivity, and precipitation. We found a broad-scale, long-term decrease in elk recruitment of 0.48 juveniles/100 adult females/year. Weather conditions (indexed as summer and winter precipitation) showed small, but measurable, influences on recruitment. Forage productivity on summer and winter ranges (indexed by normalized difference vegetation index [NDVI] metrics) had the strongest effect on elk recruitment relative to other factors. Relationships between forage productivity and recruitment varied seasonally and regionally. The productivity of winter habitat was more important in southern parts of the study area, whereas annual variation in productivity of summer habitat had more influence on recruitment in northern areas. Elk recruitment varied by up to 15 juveniles/100 adult females across the range of variation in forage productivity. Areas with more species of large carnivores had relatively low elk recruitment, presumably because of increased predation. Wolves (*Canis lupus*) were associated with a decrease of 5 juveniles/100 adult females, whereas grizzly bears (*Ursus arctos*) were associated with an additional decrease of 7 juveniles/100 adult females. Carnivore species can have a critical influence on ungulate recruitment because their influence rivals large ranges of variation in environmental conditions. A more pressing concern, however, stems from persistent broad-scale decreases in recruitment across the distribution of elk in the northwestern United States, irrespective of carnivore richness. Our results suggest that wildlife managers interested in improving recruitment of elk consider the combined effects of habitat and predators. Efforts to manage summer and winter ranges to increase forage productivity may have a positive effect on recruitment. © 2018 The Wildlife Society.

KEY WORDS carnivores, *Cervus canadensis*, climate, elk, forage productivity, recruitment, northwestern United States.

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Ungulates are key components of ecosystems and are economically important because of their widespread harvest by humans for recreation, food, and population management (Gordon et al. 2004). Concerns about the management of ungulates are increasing worldwide (Vors and Boyce 2009) because of broad-scale changes in habitat conditions (Middleton et al. 2013), climate (Gaillard et al. 2013), communities of large carnivores (Bangs and Fritts 1996, Pyare et al. 2004), and their potential effects on the long-term dynamics of populations. For example, across the northwestern United States, Griffin et al. (2011) and Brodie et al. (2013) reported that recovery of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) decreased survival of neonate and adult female elk (*Cervus canadensis*), but that the strength of predation interacted with climate such that effects of predation were dampened in years of high forage productivity.

Generally, for long-lived species, adult female survival is the vital rate with the highest elasticity, but variation in juvenile survival tends to influence annual variation in population growth rate (Gaillard et al. 2000). As a result, many studies focus on survival of juvenile ungulates to understand the most important influence on population dynamics (Gaillard et al. 1998, Raithel et al. 2007, Harris et al. 2008). Studies of survival typically require expensive methods for data collection such as radio-telemetry. Whereas these data can provide excellent insights, maintaining broad-scale, and long-term telemetry studies may not be logistically feasible. Therefore, the scale of these studies tends to be focused on individual populations, which may give minimal insight to processes occurring over large spatial scales.

Studies have highlighted the importance of summer nutrition in influencing ungulate recruitment through changes in maternal and calf body condition (Bonenfant et al. 2002, Cook et al. 2004, Parker et al. 2009, Middleton et al. 2013). Increased precipitation, especially in late summer, improves forage productivity, which increases nutritional condition and pregnancy rates of females (Cook et al. 2004). Thus, effects of spring and summer habitat conditions on maternal body condition may carry forward for $\geq$1 year and influence calf recruitment the following spring (Middleton et al. 2013). Following birth, the summer conditions a juvenile experiences will influence its growth and hence ability to survive the following winter (Portier et al. 1998).

Several factors influence recruitment including environmental conditions during summer and winter, predation, and potential interactions among them. In ungulates, severe winters reduce maternal body condition and juvenile survival (Albon et al. 1987, Smith and Anderson 1998, Garrott et al. 2008*a*, White et al. 2010). Additionally, recovery of large carnivore populations across the northern hemisphere (Bangs and Fritts 1996, Chapron et al. 2014) is potentially changing ungulate population trends and recruitment (Barber-Meyer et al. 2008, Middleton et al. 2013), and these effects may interact with or mask potential climate effects. The effects of predation by large carnivores on ungulates have been reported to vary directly with snow depth, spring precipitation, and primary productivity (Melis et al. 2009, Griffin et al. 2011). The relative strength of these different factors on recruitment or population dynamics is unknown, and likely vary at different spatial and temporal scales.

Across much of North America and Europe, decisions on ungulate management are often based on annual surveys of age ratios (i.e., juveniles: 100 adult females) as an index of population performance (Bender 2006, Apollonio et al. 2010). Age ratios have a long history of use in wildlife management (Leopold 1933) because they are relatively inexpensive to collect, can be obtained over broad scales, and have been monitored for many populations over long time periods. Wildlife management agencies in the western United States commonly collect age ratios for elk as part of harvest management. Typically, these data are collected at spatial scales appropriate to management of individual populations (i.e., elk management units). The spatio-temporal extent of these data surpass any other data source on ungulates, making age ratio data a unique resource for assessing long-term and broad-scale influences on changes in recruitment, and thus, ungulate population dynamics (Raithel et al. 2007, Harris et al. 2008). Despite their ubiquitous application in ungulate management, the value of age ratios has been questioned. Both the numerator (juvenile counts) and denominator (adult female counts) of the age ratio can change direction for reasons that might affect inferences on population trajectories in counter-intuitive ways (Caughley 1974, Bonenfant et al. 2005). Despite these concerns, demographic analyses for elk show that recruitment measured using age ratios was strongly correlated with juvenile survival ($r^2 = 0.93$) and was the main factor associated with population growth rates of elk (Raithel et al. 2007, Harris et al. 2008). Although direct measurement of juvenile survival through the use of marked animals is the best measure of recruitment, these studies demonstrate the utility of age ratios as a reasonable proxy when other data are unavailable.

We sought to understand the relative roles of factors affecting elk recruitment across broad spatial and temporal scales. Like most other temperate ungulates, elk recruitment is affected by factors influencing maternal body condition and the probability of females becoming pregnant (Bonenfant et al. 2002; Cook et al. 2004, 2013; Proffitt et al. 2014), the birth mass of elk calves (Cook et al. 2004), and additional factors such as forage availability, weather conditions, and predators affecting the probability of calf survival in their first year (Griffin et al. 2011). We hypothesized that animal nutrition, weather conditions, and predation should affect elk recruitment through a variety of mechanisms. Specifically, we evaluated 7 predictions proceeding from 4 hypotheses related to elk recruitment (Table 1). The maternal body condition carry-over hypothesis postulates that nutritional conditions from previous growing season can affect elk body condition, pregnancy, and hence calf survival. Nutrition can affect recruitment through the productivity of the adult female (Cook et al. 2004) and survival of the juvenile (Griffin et al.

Table 1. Hypotheses for factors that could influence elk recruitment in the Western United States from 1989–2010. Where stated, sub-hypotheses (A and B) postulate different but complementary mechanisms behind each hypothesis. Predictions represent expected observations if the hypotheses were true. Covariates represent data included in a suite of generalized additive mixed models to test predictions based on Akaike's Information Criterion (AIC) values of models, magnitude, and direction of model coefficients, and model fit. Results indicate outcome of tests.

Hypothesis	Predictions	Covariates	Result
Maternal body condition carry-over hypothesis:			
A. Environmental conditions from previous growing season can affect maternal body condition, pregnancy rates, and hence calf survival.	As precipitationthe previous summerincreases, age ratios will increase.	Precipitation in current year (t), split into early (May–15 Jul) and late (15 Jul–30 Sep)	Unsupported
B. Environmental conditions from previous winter can affect maternal body condition, pregnancy rates, and hence calf survival.	As winter severity the previous year increases, age ratioswill decrease.	Precipitation (*t*-1), measured over the whole winter *t*-1	Weak support for a negative effect of previous winter precipitation
Calf survival hypothesis:			
A. Early winter calf survival declines with increasing winter severity (only early winter survival because data collection occurred before late winter).	As winter severity increases, age ratioswill decrease.	Precipitation (*t*), focused on early winter pre-survey (Nov–Dec)	Unsupported
B.Favorable habitat conditions in the current year can positively affect calf survival.	As precipitation the current summer increases, age ratios will increase.	Precipitation (*t*), for early (May–15 Jul) and late (15 Jul–30 Sep) summer	Weak support for early summer precipitation having a positive effect at low values of summer precipitation
Primary productivity hypothesis:			
A. Increasing amount of forage productivity across management units will increase recruitment.	As average cumulative forage productivity of a unit increases, age ratios will increase.	Average NDVI[a] within a unit over all years for a unit	Supported for winter range
B. Increasing variability of forage productivity within management units will increase recruitment.	As anomalies in cumulative forage productivity increase, age ratios will increase.	Residual NDVI within a unit and year for summer and winter range	Supported for winter range
Predation hypothesis:			
Addition of gray wolves and grizzly bears to predator communities will decrease recruitment.	As the number of predator species increases, age ratios will decrease.	Predators: 3 species (black bear, coyote, mountain lion), 4 (+wolf), and 5 (+grizzly bear)	Supported for reduced recruitment in the presence of wolves and grizzly bears

[a] Normalized difference vegetation index.

2011, Eacker et al. 2016). There is increasing evidence from detailed studies of maternal nutrition that summer forage conditions may be more important than winter conditions in some settings (Cook et al. 2004, Johnson et al. 2013, Middleton et al. 2013). However, whether these influences on maternal nutritional condition translate to recruitment dynamics is unknown. We predicted that favorable nutritional conditions (i.e., relatively high primary productivity and precipitation) during the growing season should have a positive effect on reproductive output of adult females in the following year (Cook et al. 2004, Proffitt et al. 2014). The calf survival hypothesis states that good growing season conditions can positively affect calf survival. We predicted that favorable habitat conditions during early summer would have a positive effect on survival of juvenile elk because of improved nutrition acquired from the lactating mother (Cook et al. 2004, Proffitt et al. 2014). Similarly, we predicted that favorable habitat conditions during late summer would have a positive effect on survival of juvenile elk because they will acquire high fat reserves that would carry them through winter. We predicted that mild winters (i.e., low precipitation) would have a positive effect on both reproductive output of adult females and overwinter survival of juveniles. Whereas high precipitation has been shown to negatively affect elk survival during winter (Brodie et al. 2013), we expected our analyses to show a relatively weak relationship with recruitment because age ratio data are typically collected in January and February before major mortality events occur later in winter. The primary productivity hypothesis states that increasing the amount of primary productivity will increase recruitment. We predicted that high average primary productivity across elk management units would be associated with high average recruitment (Cook et al. 2004, 2013). We also predicted that high variability in primary productivity (i.e., rapid green up of high magnitude) within elk management units would be associated with high recruitment (Mysterud et al. 2001, Pettorelli et al. 2007). We predicted that this relationship would be true for summer and winter ranges, where variability in primary productivity could influence survival and body condition of neonatal calves and their overwinter survival as juveniles, respectively. Finally, the predation hypothesis predicts that as the number of predator species increases recruitment will decrease. The primary predators of juvenile elk in recent history, mountain lions (*Puma concolor*), black bears (*U. americanus*), and coyotes (*C. latrans*), are common throughout the range of elk. In the northern Rocky Mountains of the United States, however, recovering populations of gray wolves and grizzly bears may exert additional pressure on elk recruitment (Griffin et al. 2011, Brodie et al. 2013). We therefore

predicted that the addition of gray wolves and grizzly bears to predator communities would have a negative effect on recruitment.

STUDY AREA

Our study area consisted of 101 elk management units (i.e., units) from 7 states in the Western United States: Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming (Fig. 1). Unit boundaries were defined by state wildlife management agencies based on a combination of biological, logistical, and political boundaries. The study area covered a substantial portion of nearly 20° of longitude and 10° of latitude. Climate, topography, vegetation, and large carnivore communities varied across latitudinal, altitudinal, and precipitation gradients (Table S1, available online in Supporting Information).

We assigned each unit to 1 of 3 ecotypes based on common habitat characteristics that we assumed would influence the role of climate and habitat conditions on elk recruitment (Fig. 1 and Table S1). These ecotypes represented a balance between accounting for regional variation in climate and geology and providing a sufficient number of replicate units to test our hypotheses. We identified the ecotypes as northern mountain, southern mountain, and shrub-steppe, with boundaries based on merged Commission for Environmental Cooperation Level III ecoregions (CEC; http://www.cec.org/, accessed 28 May 2014). The northern mountain ecotype consisted of the Rocky Mountains in the northern United States and parts of Oregon and Washington (CEC ecoregions 6.2.9, 6.2.10, and 6.2.15), and was characterized by coniferous forests at high elevations and occasionally severe winter conditions. The southern mountain ecotype consisted of the southern Rocky, Wasatch, and Uinta mountains (CEC ecoregions 6.2.13 and 6.2.14), and was characterized by relatively high summer precipitation and expansive aspen (*Populus tremuloides*) stands, which are productive summer habitat for elk. The shrub-steppe ecotype included the relatively arid Wyoming and Colorado plateaus (CEC ecoregions 10.1.4 and 10.1.6), and was characterized by cold desert, sagebrush-steppe communities. Within each ecotype, we delineated coarse summer and winter ranges of elk for each unit using radio-telemetry data or expertise of local wildlife agency biologists.

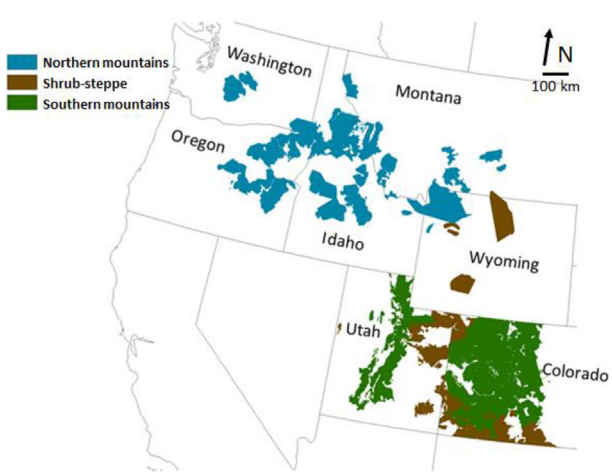

Figure 1. Elk management units included in the analysis of age ratio (calves/100 adult females) data collected across 7 states in the Western United States from 1989–2010. Colors indicate the ecotype assigned to each unit.

METHODS

Age Ratio Data

We examined age ratio data collected in 101 units for all years available between 1989 and 2010, resulting in 1,512 unit-years of age ratios (Table 2). State wildlife agency and National Park Service personnel collected data during helicopter or fixed-wing aerial surveys as a part of routine (typically annual) monitoring conducted primarily on winter ranges. Surveyors conducted flights at low altitude and made efforts to classify animals into age and sex classes by circling or causing the elk to form a line while trying to flee. Timing of the classification counts varied from December to March, although the exact date of the counts was not always recorded. Of the 1,512 counts, 14 were conducted in December, 1,393 in January and February, 27 in March, and 78 in April. Although timing of the count may affect the ratio because of the loss of calves over winter, we deemed it unlikely that this affected our results because survival of elk calves is high relative to the amount of time over which the counts were conducted.

Explanatory Variables

In our analysis, we considered how precipitation, vegetation productivity (indexed by normalized difference vegetation index [NDVI]), and presence wolves and grizzly bears affected elk recruitment. We screened against including collinear variables using a Pearson's correlation coefficient of $< |0.7|$. We accessed the parameter-elevation regressions on independent slopes model (PRISM) data to extract precipitation and temperature values for each unit in each year (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 20 May 2014). Precipitation and temperature data were available by month and year and we spatially averaged them across each unit. For precipitation data, we summed values for early summer (1 May–15 Jul) corresponding to the lactation period and late

Table 2. Summary statistics for elk calf recruitment as age ratios (calves/100 adult females) by states and ecotypes among those states, across the Western United States during winters from 1989–2010.

	Units	Observed ratios	$\bar{x}$	SD
State				
CO	41	633	44.6	9.6
ID	5	29	33.2	8.6
MT	8	274	33.7	12.4
OR	15	320	28.8	10.4
UT	24	110	42.7	10.2
WA	2	26	25.1	5.4
WY	6	120	31.9	9.1
Ecotype				
Northern mountains	34	729	30.8	11.1
Shrub-steppe	26	281	40.3	9.5
Southern mountains	41	502	46.0	9.4

summer (16 Jul–30 Sep) during the period where juveniles are foraging on their own to gain fat reserves for the upcoming winter. We summed winter precipitation from 1 November–31 December to represent its effects on early winter mortality in the current year. We also summed winter precipitation from 1 November–30 April to represent the cumulative winter effect from the previous year on adult body condition and the next year's recruitment of juveniles.

We assumed that NDVI derived from moderate resolution imaging spectroradiometer (MODIS) advanced very high resolution radiometer (AVHRR) data represented forage biomass as an index of forage productivity annually for each unit (Hamel et al. 2009, Pettorelli 2013, http://phenology.cr.usgs.gov/index.php, accessed 4 Aug 2014). We clipped NDVI data to non-forested areas of each unit to reduce the effect of trees on the NDVI value (Hamel et al. 2009). We smoothed raw satellite data temporally using a weighted, least-squares linear regression based on a moving temporal window approach (Eldenshink 2006). We summed NDVI across the growing season (1 May–30 Sep; i.e., summer range). We then calculated the mean summed NDVI across years for each unit to represent the relative effect of NDVI among ranges on elk recruitment; the mean summed NDVI represented an index of relative forage quantity of each unit to differentiate higher and lower overall productivity. We also calculated annual residual NVDI value (observed–mean) for each year in each unit to represent effects of annual variation in NDVI on elk recruitment within a unit. We calculated NDVI for summer ranges and for winter ranges; the growing season values of NDVI from the previous summer reflected forage availability on the winter range the following season.

Information on abundance of carnivores was not available across most elk units we studied. All units contained populations of mountain lions, black bears, and coyotes; therefore, we characterized large carnivore communities by the presence or absence of established populations of wolves ($n = 13$) and grizzly bears ($n = 3$). All units that contained grizzly bears also contained wolves, but wolves existed in units without grizzly bears. Authors on this paper from wildlife management agencies provided information about where their agency knew that wolves or grizzly bears existed with breeding populations in each elk management unit.

Finally, we included the number of antlerless elk harvested reported by state wildlife management agencies for each unit in each year as a covariate in all models to account for the potential effects of adult female harvest on elk recruitment. We treated harvest as a nuisance variable because it did not directly influence our biological questions, but it did affect age ratios.

Separately, we modeled the year elk recruitment data were collected as a linear relationship with elk recruitment by unit to account for potential trends in elk recruitment for which we had no other explanatory variable. These trends may be due to changing elk density, changing habitat, or climate change.

Statistical Modeling

We chose a flexible statistical modeling framework for our analysis because we expected complex relationships between elk recruitment and forage productivity indexed by NDVI, precipitation, and wolf and grizzly bear presence covariates. We fit generalized additive mixed models (GAMMs) with elk recruitment in each unit and year as the response variable. We used a normally distributed error structure and identity link for the analysis. Generalized additive mixed models allow additional flexibility compared to linear models because they model the relationship between explanatory variables and response as a smoothing function rather than as a strictly linear function. We evaluated explanatory variables as fixed effects. We considered state and unit as random effects to account for variation in elk management strategies across state and unit levels. We fit GAMMs using maximum likelihood functions with the mgcv package (Wood 2011) in R version 3.1.0 (R Development Core Team 2014).

We fit models to test hypotheses about the effects of precipitation, vegetation productivity measured using NDVI, and presence of wolves and grizzly bears (Table 1). We included mean integrated NDVI and number of antlerless elk harvested in all models to account for unit-level differences in average recruitment rates. We included interactions between precipitation and ecoregion and NDVI and ecoregion. We represented presence or absence of either wolves or grizzly bears as binary covariates. We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and model diagnostics such as residual plots for model selection. We considered models with ΔAIC $<$ approximately 2 as competitive models but favored simpler models in cases where 2 competitive models differed substantially in numbers of parameters.

RESULTS

Age ratios varied substantially across the 7-state region (Fig. 2). Southern mountain units tended to have the highest average elk ratios $\bar{x} = 46.0 \pm 9.4$ [SD]), shrub-steppe units were intermediate relative to other ecotypes ($\bar{x} = 40.3 \pm 9.5$), and northern mountain units had the lowest average ratio ($\bar{x} = 30.8 \pm 11.1$). Age ratios were highest in Colorado and Utah and lowest in Washington. Throughout the 22-year study, elk age ratios declined by 0.48 ± 0.04 (SE) calves/year. Over the period of our evaluation, 74 elk units had declining age ratios, whereas 23 units had increasing age ratios (Fig. 3).

Mean NDVI and recruitment relationships varied seasonally and regionally. Mean summer range NDVI was a strong predictor of recruitment in 2 ecotypes and was included in the top-ranked model (Table 3). Mean summer range NDVI was negatively related to elk recruitment in the northern mountain and shrub-steppe units and weakly negatively related with elk recruitment in the southern mountain units (Fig. 4). In the northern mountain units, expected elk recruitment dropped by >15 calves/100 adult females across the range of observed mean summer range NDVI values. Residual variation in summer range NDVI was largely negatively related to recruitment in the northern mountain and shrub-steppe units, whereas it was weakly negatively related in the southern mountain units (Fig. 4). On summer range, years with higher than average NDVI were negatively associated with recruitment.

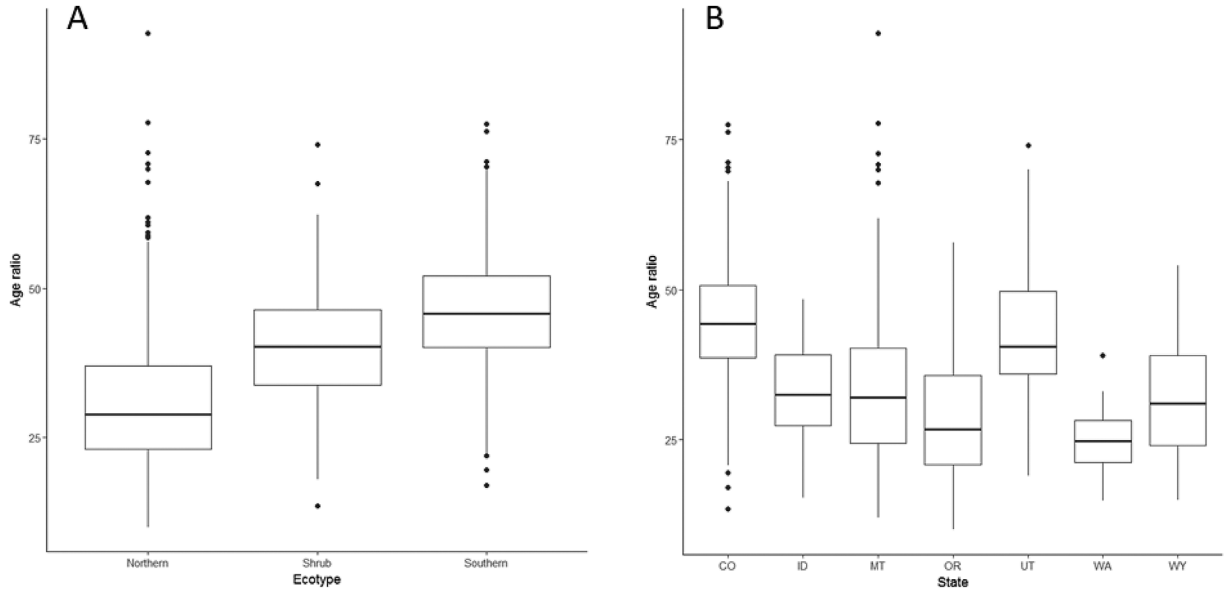

Figure 2. Boxplots of elk age ratios (calves/100 adult females) by ecotype (A) and state (B) from 1989–2010.

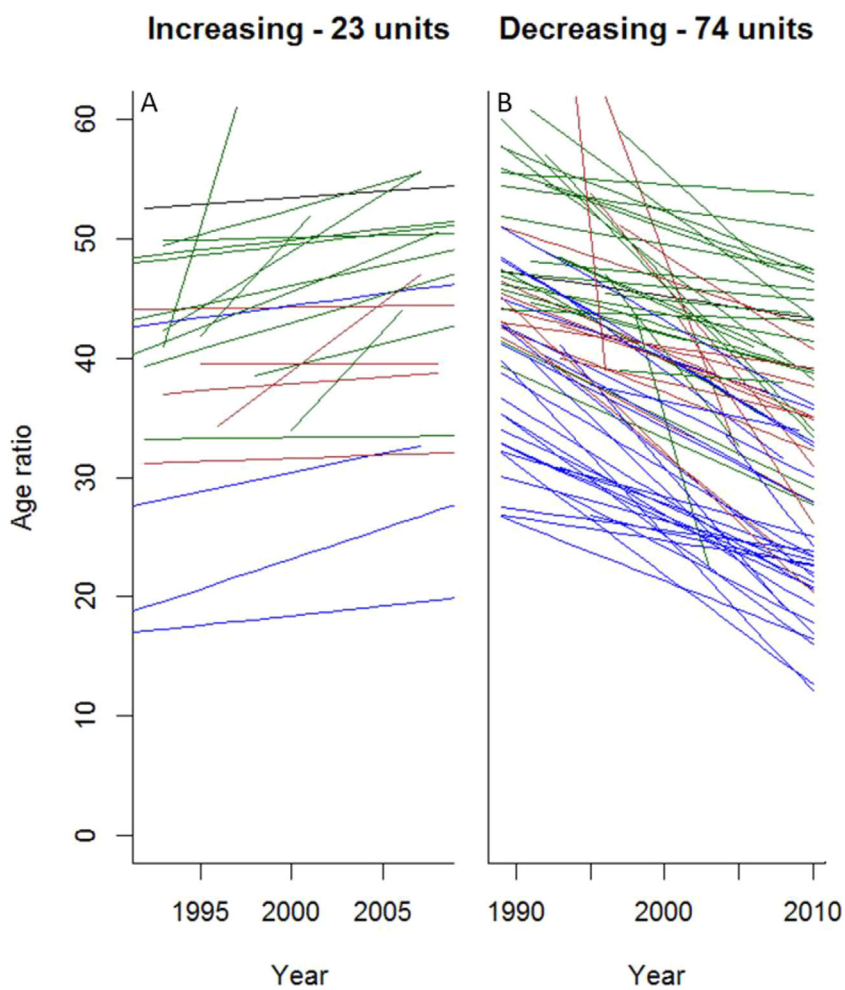

Figure 3. Age ratio trend lines by year for elk management units that were increasing (A) and decreasing (B). Ratios were collected from 1989–2010 in 7 states across the western United States. Northern mountains units are presented in blue, shrub-steppe in brown, and southern mountains in green.

Table 3. Model rankings based on Akaike's Information Criterion (AIC) for generalized additive mixed models (GAM) of elk calf recruitment (early winter age ratio; calves/100 adult females) as a function of seasonal weather (precip), forage productivity ($\bar{x}$ normalized difference vegetation index [NDVI]), variation in forage productivity (residual NDVI), wolf and grizzly bear presence (carnivores), and harvest (number of antlerless elk harvested) across 7 Western states from 1989–2010.

			Covariate terms	
Model	**AIC**	**ΔAIC**	**Linear**	**GAM smooth**
Harvest + summer NDVI + winter NDVI + carnivores	11,128.93	0.00	4	6
Harvest + carnivores + mean NDVI + residual NDVI	11,129.25	0.32	10	8
Harvest + carnivores + mean NDVI + residual NDVI + winter precip	11,130.24	1.31	10	7
Harvest + summer precip + summer NDVI + winter precip + summer NDVI + wolf	11,156.95	28.02	3	12
Harvest + summer NDVI + winter NDVI	11,193.09	64.16	2	6
Harvest + summer NDVI	11,201.23	72.30	2	3
Harvest + summer precip + winter precip + carnivores	11,239.69	110.76	4	6
Harvest + carnivores	11,242.37	113.44	4	0
Harvest + winter NDVI	11,269.98	141.05	2	3
Harvest + summer precip + winter precip	11,327.64	198.71	2	6
Harvest + winter precip	11,328.66	199.73	2	2
Harvest	11,337.50	208.57	2	0
Harvest + summer precip	11,347.63	218.70	2	4

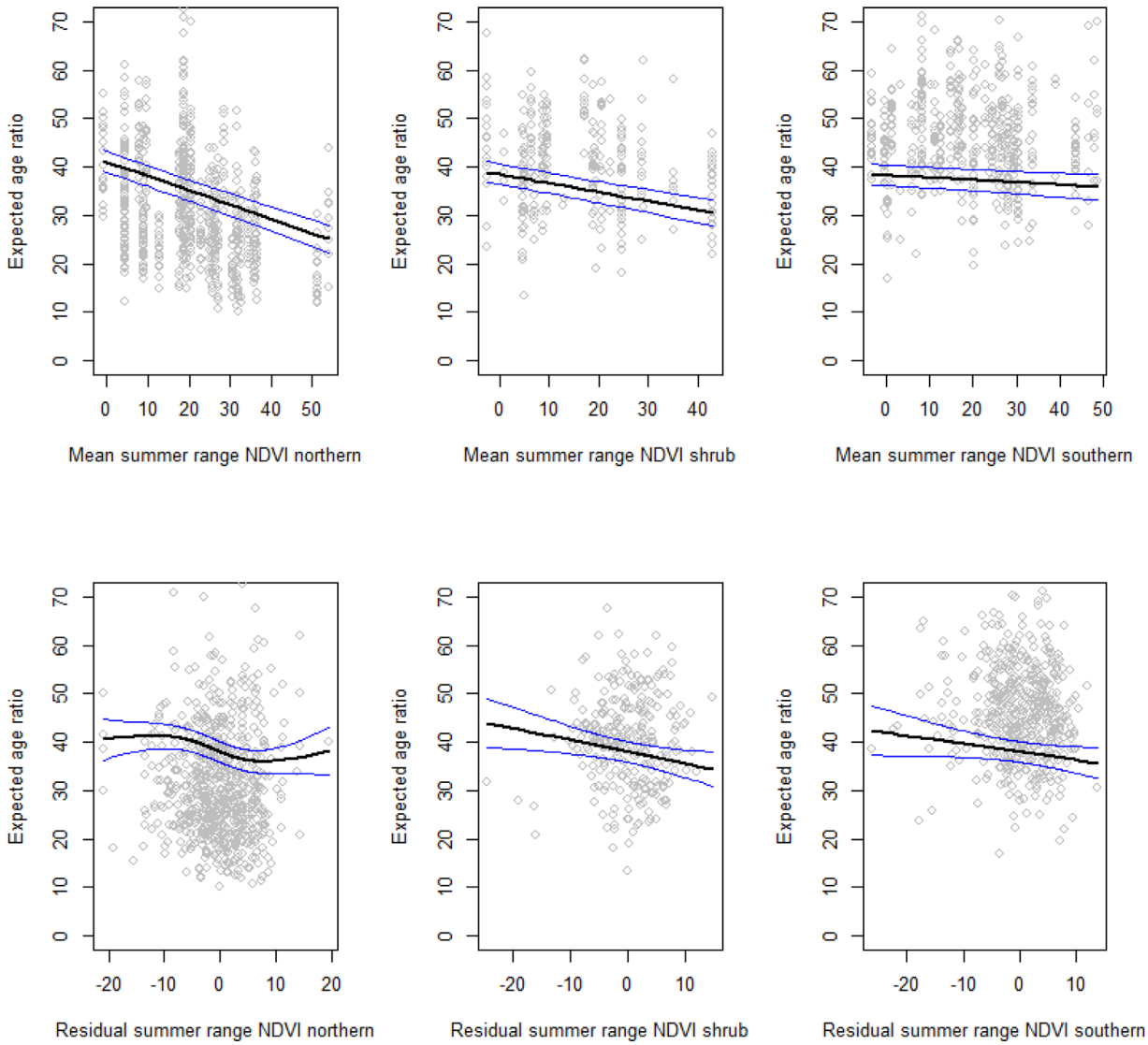

Figure 4. Model-expected response of elk age ratios (calves/100 adult females) as a function of mean integrated summer range normalized difference vegetation index (NDVI) by ecotype and residual integrated summer range NDVI by ecotype from 1989–2010 in 7 western states. Dark line indicates the model prediction and blue lines indicate the standard error of the prediction. Gray circles represent the observed age ratio data.

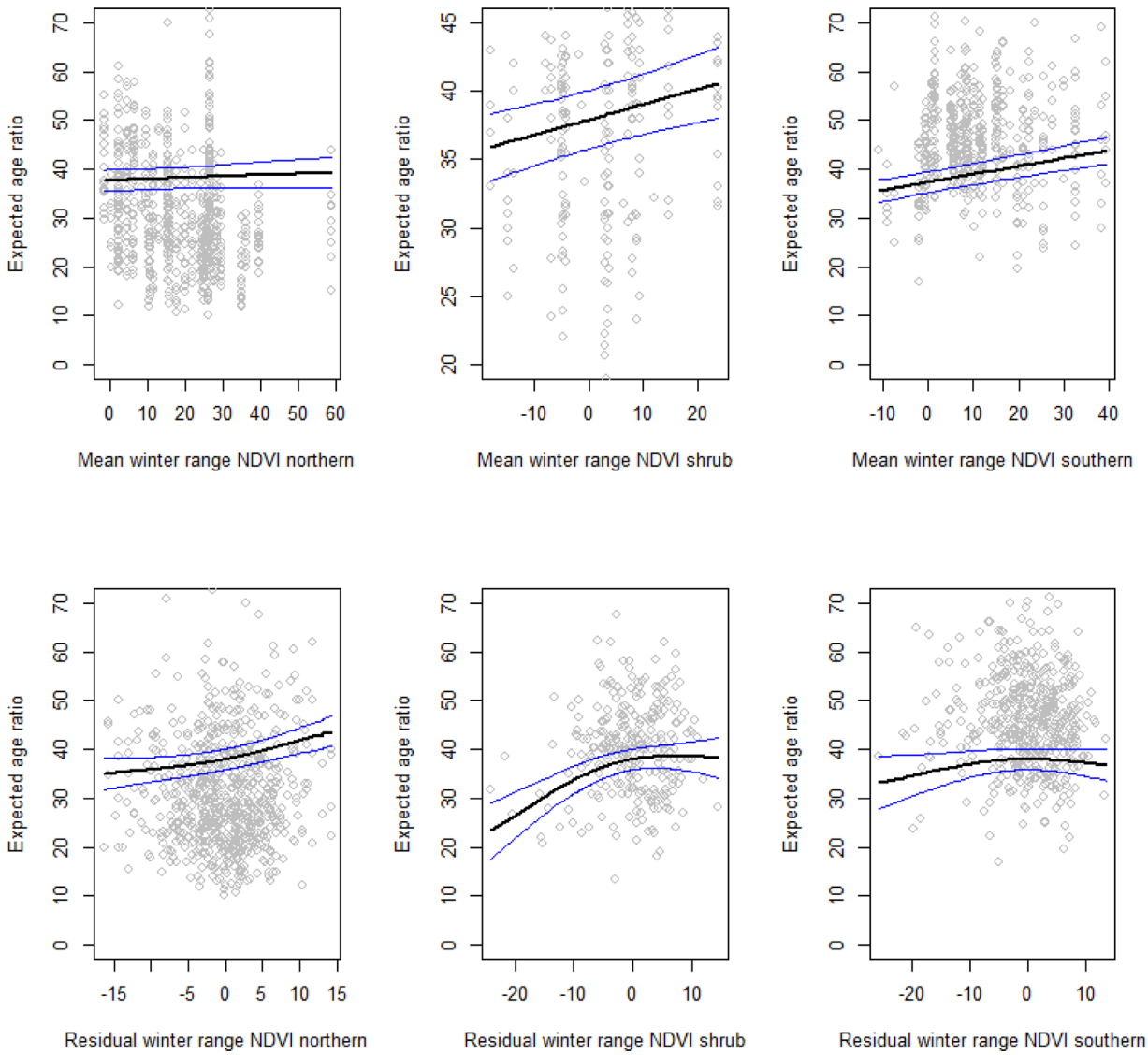

Figure 5. Model-expected response of elk age ratios (calves/100 adult females) as a function of mean integrated winter range normalized difference vegetation index (NDVI) by ecotype and residual integrated winter range NDVI by ecotype from 1989–2010 in 7 western states. Dark line indicates the model prediction and blue lines indicate the standard error of the prediction. Gray circles represent the observed age ratio data.

Winter range NDVI was positively correlated with elk recruitment in the shrub-steppe and southern mountain units but was unrelated to elk recruitment in the northern mountain units (Fig. 5). Expected elk recruitment increased by 10 calves/100 adult females across the range of observed winter range NDVI in the southern mountain units. Residual variation in summer NDVI in the northern mountain units demonstrated a complex relationship with elk recruitment at extreme values, but those relationships may be largely influenced by small sample sizes at the extremes. Residual variation in winter range NDVI was positively related to elk recruitment in the northern mountain and shrub-steppe units and largely unrelated to elk recruitment in the southern mountain units (Fig. 5).

Effects of precipitation on elk recruitment varied within and across seasons. Precipitation effects tended to be weak and were not included in the top-ranked model (Table 3). Total winter precipitation in the previous winter had a negative correlation with elk recruitment. The effect of winter precipitation was stronger than the effect of early summer precipitation, and the expected change in elk recruitment was 7 calves/100 adult females across the entire range of observed previous winter precipitation (Fig. 6B). Early winter precipitation in the current year was unrelated to elk recruitment. Early summer precipitation in the current year was positively related to elk recruitment at low values and negatively related at high values (Fig. 6A), yet the effect of early summer precipitation was small (± 2 calves/100 adult females) compared to the overall variation in elk recruitment (Fig. 2). All other summer precipitation values were unrelated to elk recruitment.

Presence of wolf and grizzly populations was negatively correlated with elk recruitment (Table 4). Wolf presence was associated with a decrease of 5.1 ± 1.1 (SE) calves/100 adult

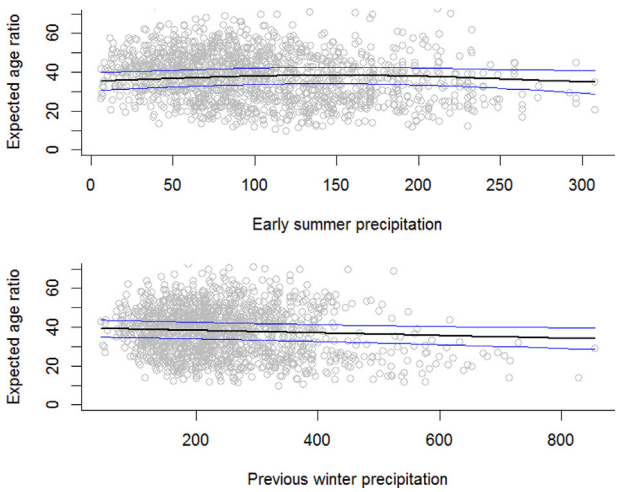

Figure 6. Model-expected response of elk age ratios (calves/100 adult females) as a function of early summer precipitation (mm) and total winter precipitation (mm) in the previous winter. Dark line indicates the model prediction and blue lines indicate the standard error of the prediction. Gray circles represent the observed age ratio data.

females and grizzly bear presence by an additional decrease of 7.4 ± 2.1 calves/100 adult females.

As expected, harvest of antlerless elk showed a positive relationship with elk recruitment (Table 4). A positive relationship between harvest and recruitment is expected because as more adult females are removed in the fall, the recruitment ratio increases accordingly. This result, therefore, does not imply that harvest increases recruitment.

DISCUSSION

Our results demonstrate a decline in recruitment of juvenile elk across a large area of western North America from 1989–2010. This pattern has been noted on finer scales across the study region (Barber-Meyer et al. 2008, White et al. 2010, Johnson et al. 2013, Middleton et al. 2013). Our work is the first synthesis demonstrating that the pattern exists over a broad area with 74 of 101 elk management units showing declines. Average decline across all units amounted to nearly 1 calf/100 females every 2 years over a 22-year study period. Our results suggest that these declines may be related to long-term changes in precipitation patterns, forage conditions, the recovery of wolves and grizzly bears, and interactions among these factors, or factors such as density dependence that we did not evaluate.

Our results suggest that precipitation had a weak influence on recruitment. Early summer precipitation in the current year was positively associated with recruitment at low values and negatively associated at high values, but the total range of variation in expected age ratio was only about 5 young/100 adult females. This relationship is consistent with our hypothesized mechanism that precipitation increases forage productivity (Sala et al. 1988), and thus supported the maternal body condition carry-over and calf survival hypotheses (Table 1; Griffin et al. 2011). However, in years of particularly high early summer precipitation (>200 mm, some of which could occur as spring snow in the mountains) risk of mortality for neonatal elk was elevated. These results support the calf survival hypothesis (Table 1). Nonetheless, summer precipitation appeared to have a small effect on recruitment compared to other sources of variation. Total winter precipitation in the previous year had a strong negative relationship with recruitment. This is likely a reflection of adult female body condition coming out of the winter, whereby more severe winter conditions result in less robust calves in the following spring. These results support the maternal body condition carry-over hypothesis (Table 1) and suggest that the effects of winter conditions on elk survival and reproductive performance should not be overlooked.

Table 4. Parameter estimates, standard errors, *t*-values (linear terms), *F*-values (smoothing terms), *P*-values, and effective degrees of freedom (edf) for the best (identified using Akaike's Information Criterion) generalized additive mixed model of elk age ratios (harvest + summer NDVI + winter NDVI + carnivores) as a function of biotic and abiotic environmental covariates. Data were collected across 7 western states from 1989 to 2010 ($n = 1{,}512$). We calculated normalized difference vegetation index (NDVI) values for 3 ecotypes among the states: northern mountain, shrub-steppe, and southern mountain.

	Estimate	SE	edf	*t* (linear terms) or *F* (smoothing terms)	*P*
Linear terms					
Intercept	39.255	2.171		18.083	<0.001
Number antlerless elk harvested	0.003	0.000		7.559	0.000
Presence of wolves	−5.086	1.077		−4.724	0.000
Presence of grizzly bears	−7.424	2.092		−3.549	0.000
Mean summer range NDVI (northern mountain)	−0.296	0.045		−6.521	0.000
Mean summer range NDVI (shrub-steppe)	−0.186	0.040		−4.659	0.000
Mean summer range NDVI (southern mountain)	−0.049	0.037		−1.311	0.190
Mean winter range NDVI (northern mountain)	0.028	0.050		0.563	0.573
Mean winter range NDVI (shrub-steppe)	0.111	0.062		1.800	0.072
Mean winter range NDVI (southern mountain)	0.163	0.051		3.216	0.001
Smoothing terms					
Early summer precipitation			2.193	4.288	0.012
Total winter precipitation t-1			1.000	5.569	0.018
Residual summer range NDVI (northern mountain)			2.479	3.138	0.034
Residual summer range NDVI (shrub-steppe)			1.000	1.675	0.196
Residual summer range NDVI (southern mountain)			1.000	0.902	0.343
Residual winter range NDVI (northern mountain)			1.509	5.272	0.012
Residual winter range NDVI (shrub-steppe)			1.973	4.559	0.011
Residual winter range NDVI (southern mountain)			1.662	1.329	0.251

We expected forage resources to vary on summer and winter ranges within a unit over time and across units on broad spatial scales. We used NDVI as an index for forage availability based on the assumption that productivity of plant biomass represents nutrition available to elk (Pettorelli et al. 2005). The relationship between forage productivity and actual nutritional value, however, is complicated (Fryxell 1991, Hebblewhite et al. 2008). As forage biomass increases, dry matter digestibility decreases (Hebblewhite et al. 2008), a pattern that is consistent with ungulates selectively foraging where forage biomass has not yet peaked (Sawyer and Kauffman 2011) and digestibility is still high (Albon and Langvatn 1992, Hebblewhite et al. 2008). This relationship is likely reflected in our results for productivity of summer ranges. In the northern mountain and shrub-steppe units, recruitment declined as mean NDVI for summer ranges increased. This suggests that units with high productivity on the summer range may nonetheless have had less digestible forage over the entire summer than less productive units. This idea is supported by a *post hoc* analysis we conducted comparing percent forest cover in a unit with the mean NDVI value for summer ranges in non-forested habitat of that unit. Summer range NDVI was non-linearly, positively correlated with percent forest cover in the northern mountain. Moreover, the high end of the range of NDVI values on summer range in the northern mountain exceeded that of other ecoregions. These high NDVI values in forested areas may not be due to the presence of highly digestible grasses and forbs but rather to less-digestible or woody vegetation (Hebblewhite et al. 2008). In addition, annual variation in the summer range NDVI residuals suggest that years with high forage productivity were associated with less digestible forage. Our results do not support the primary productivity hypothesis on summer range (Table 1), but the relationship between forage productivity and elk nutrition is likely more complex than we could address with these data. Alternatively, NDVI may be a poor metric of forage production in portions of our study area.

In winter, most of the highly digestible forbs and grasses that provide high levels of nutrition in summer are no longer available in our study area because of senescence. Therefore, the nutritional quality of forbs and grasses tends to equalize at an overall low level. Given that in winter low-quality forage is common across nearly all units, increased biomass of forage should be beneficial to elk (Hobbs et al. 1983, Cook et al. 2013). Our results support the primary productivity hypothesis both in terms of average NDVI in winter ranges and annual variation in NDVI (Table 1). We found winter ranges with high forage productivity (NDVI) were associated with high recruitment, especially in the southern mountain units where plant communities often included high-quality forage species such as bitterbrush (*Pursia tridentada*) and aspen. In the northern mountain and shrub-steppe units, the relationship between forage productivity of winter ranges and recruitment was weak, whereas the relationship with the annual variability in productivity was strong, suggesting that recruitment was more associated with temporal variation in forage productivity than with its spatial variation. These results highlight the importance of both growing season conditions and forage productivity of winter range on the growth and survival of juvenile elk, particularly in the southern mountain units.

We found that recruitment of juvenile elk declined with carnivore richness, supporting the predation hypothesis (Table 1). In addition to the populations of black bears, mountain lions, and coyotes ubiquitous across our study area, the presence of an established wolf population was associated with an average reduction of 5 calves/100 adult females in the northern mountains ecotype. Adding grizzly bears produced an additional reduction of 7 calves/100 females. These are average effects estimated at a broad spatial scale and over a long time period; thus, the rates of decline we estimated should be viewed as a general result. Individual herds may be affected by predation in different ways depending on local conditions and densities of large carnivores. For example, much greater reductions in elk calf survival and recruitment than we observed have been reported for some northern mountain systems with abundant and diverse predator associations (Barber-Meyer et al. 2008, Garrott et al. 2008*b*). Nonetheless, the effects we observed are consistent with the relatively high effect of grizzly bear predation on neonatal elk calf survival reported in another broad-scale synthesis (Griffin et al. 2011), and with research on other ungulate species reporting strong effects of predation on juvenile survival with implications for population dynamics (Nilsen et al. 2009).

Comparing the effects of environmental factors and large carnivore communities provides potential insight to the relative importance of habitat, climate, and large carnivore communities. Abundant and diverse predator populations had a larger effect on elk recruitment than summer or winter precipitation (Table 4 and Fig. 6). The effect of wolves alone that we observed was relatively small (reduction in age ratio of 5) compared to effects of forage productivity (change of age ratio of 15), but if wolves and grizzlies were both present the decline in recruitment was equal to the change across the entire range of observed variation in forage productivity indexed by NDVI. Our inferences on effects of carnivore community structure on recruitment are limited, however, because populations of large carnivores were not evenly distributed across our study areas. Wolves and grizzly bears occurred only in the northern mountain ecotype, precluding us from examining interactions between large carnivore communities and ecotype on recruitment. Potential changes in elk recruitment with expansion of wolf and grizzly bear populations into the southern mountain and shrub-steppe ecotypes where forage productivity is high and winters less severe require further study. Similar to the findings of Melis et al. (2009), we hypothesize that the effects of wolves and grizzly bears on recruitment will be relatively weak in these southern systems, with population dynamics of elk responding primarily to weather and forage productivity because of the high productivity of these systems.

We could not account in our analyses for all factors potentially influencing recruitment in elk, leading to unexplained variation in our results. First, density

dependence can influence recruitment rates in ungulates (Bonenfant et al. 2009), but we were unable to evaluate this influence because neither elk density nor variation in carrying capacity over time were known across our study area. Not all populations we evaluated, however, were increasing (e.g., Ahrestani et al. 2013); therefore, the large variation in elk recruitment explained by climate effects, forage conditions, and carnivore richness suggests density dependence may not have been an important or consistent factor in the populations we studied. Nonetheless, the increase in average densities of elk across many (but not all) areas of the Western United States combined with the overall decline in recruitment that we observed is consistent with density-dependent populations. Factors influencing density dependence across such a broad scale could include changes in habitat and climate over time that we did not have the data to evaluate. Future studies should consider evaluating possible effects of such changes and using integrated population models (IPMs) to explicitly test for the influence of density dependence on recruitment. Second, we were unable to include densities of large carnivores in our analysis. It is reasonable to expect that combined numerical and functional responses of large carnivores could produce different predation rates across a gradient of elk densities. At low elk densities, large carnivores may switch to alternate prey if it is available (i.e., functional response), whereas increasing large carnivore populations may result in more elk consumed (i.e., numerical response). Differences in predation rate also likely vary across vegetative and ungulate communities (Vucetich et al. 2011). Third, we considered only the relationships between elk recruitment and vegetative productivity without also considering other herbivores in the system. Densities and species composition of wild and domestic herbivores likely complicate the relationship between vegetative productivity and elk recruitment. In some units we evaluated, a significant portion of the vegetation may be consumed by other herbivores before elk have an opportunity to consume it.

Available data, though abundant, limited inferences based on our analyses. Age ratios are not an ideal measure of recruitment because they reflect effects of harvest and 3 different biological processes: pregnancy, juvenile survival, and adult female survival. The confounding of processes in age ratios allows multiple biological hypotheses to produce the same prediction about age ratios (Table 1). Therefore, understanding the implications of correlations between age ratios and explanatory variables becomes muddled. Moreover, age classes are subject to misclassification during surveys (Smith and McDonald 2002), potentially adding additional noise or systematically biasing estimated relationships, depending on the origin of the misclassification. Finally, we did not have data for all combinations of ecotype and carnivore community, therefore limiting our inference on interactions.

There is evidence for a long-term, broad decline in elk recruitment that is of strong concern to elk managers in the northwestern United States. This decline exists in areas with and without wolves and grizzly bears and across a wide range of weather and forage conditions. By combining long-term data across multiple states, we were able to separate effects of predators, weather, and forage on elk recruitment, providing important context for management decisions intended to address the decline.

MANAGEMENT IMPLICATIONS

Our results suggest that wildlife managers interested in improving elk recruitment consider the combined effects of habitat and predators on processes influencing population dynamics. In the northern mountain ecotype, managers may be able to proactively manage harvest or vegetative productivity to compensate for the reduction in elk recruitment caused by recolonizing large carnivores. In the high-productivity southern mountain ecotype, it remains uncertain whether recolonizing wolves or grizzly bears would produce additional calf mortality or if it would be ameliorated by the more productive habitat. Although summer forage conditions may have strong influence on maternal body condition, fecundity, and calf provisioning, our results suggest forage resources on winter ranges may also have important effects calf survival, particularly in the southern mountain and shrub-steppe regions. Weather is beyond the control of wildlife managers, but maintaining habitat in a condition that will respond to changes in weather conditions could be effective. An examination of changes in forest condition potentially resulting in a decrease of understory forage may be useful for better understanding declines in elk recruitment. Efforts to manage summer and winter ranges to increase ungulate forage resources may have a positive effect on recruitment.

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LITERATURE CITED

Ahrestani, F., M. Hebblewhite, and E. Post. 2013. The importance of observation versus process error in analyses of global ungulate populations. Scientific Reports 3:3125. DOI: 10.1038/srep03125.

Albon, S. D., T. H. Clutton-Brock, and F. E. Guiness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69–81.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.

Apollonio, M., R. Andersen, and R. Putman. 2010. European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, United Kingdom.

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin 24:402–413.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Bender, L. C. 2006. Use of herd composition and age ratios in ungulate management. Wildlife Society Bulletin 34:1225–1230.

Bonenfant, C., J.-M. Gaillard, F. Klein, and J.-L. Hamann. 2005. Can we use the young: female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology 42:361–370.

Bonenfant, C., J.-M. Gaillard, F. Klein and A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. Ecography 25:446–458.

Bonenfant, C., J.-M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit and P. Duncan. 2009. Empirical evidence of density-dependence in populations of large herbivores. Advances in Ecological Research 41:313–357.

Brodie, J., H. Johnson, M. S. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, C. Bishop, J. A. Gude, J. Herbert, K. Hersey, M. Hurley, P. M. Lukacs, S. McCorquodale, E. McIntire, J. Nowak, H. Sawyer, D. Smith, and P. J. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, Second edition. Springer-Verlag, New York, New York, USA.

Caughley, G. 1974. Interpretation of age ratios. Journal of Wildlife Management 38:557–562.

Chapron, G., P. Kaczensky, J. D. Linnell, M. Von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, and L. Balčiauskas. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system. Journal of Wildlife Management 80:1345–1359.

Eldenshink, J. 2006. A 16-year time series of 1 km AVHRR satellite data of the conterminous United States and Alaska. Photogrammetry Engineering and Remote Sensing 72:1027–1035.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138:478–498.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367–393.

Gaillard, J. M., A. J. Hewison, F. Klein, F. Plard, M. Douhard, R. Davison, and C. Bonenfant. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. Ecology Letters 16 Supplement 1: 48–57.

Garrott, R. A., P. J. White, and J. J. Rotella. 2008*a*. The Madison headwaters elk herd: stability in an inherently variable environment. Terrestrial Ecology 3:191–216.

Garrott, R. A., P. J. White, and J. J. Rotella. 2008*b*. The Madison headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. Terrestrial Ecology 3:489–517.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. Review: the management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41: 1021–1031.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80:1246–1257.

Hamel, S., M. Garel, M. Festa-Bianchet, J.-M. Gaillard, and S. D. Côté. 2009. Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Harris, N. C., M. J. Kauffman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management 72:1143–1151.

Hebblewhite, M., E. H. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. Journal of Wildlife Management 47:1–16.

Johnson, B. K., P. K. Coe, and R. L. Green. 2013. Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. Journal of Wildlife Management 77: 102–116.

Leopold, A. 1933. Game management. C. Scribner's Sons, New York, New York, USA.

Melis, C., B. Jędrzejewska, M. Apollonio, K. A. Bartoń, W. Jędrzejewski, J. D. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18:724–734.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. D. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915–923.

Nilsen, E. B., J.-M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. Van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology 78:585–594.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23: 57–69.

Pettorelli, N. 2013. The normalized difference vegetation index. Oxford University Press, Oxford, United Kingdom.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth *vs.* rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20:503–510.

Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271–278.

Proffitt, K. M., J. A. Cunningham, K. L. Hamlin, and R. A. Garrott. 2014. Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk. Journal of Wildlife Management 78: 1383–1393.

Pyare, S., S. Cain, D. Moody, C. Schwartz, and J. Berger. 2004. Carnivore re-colonisation: reality, possibility and a non-equilibrium century for

grizzly bears in the southern Yellowstone ecosystem. Animal Conservation 7:71–77.
R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.
Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.
Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.
Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. Journal of Wildlife Management 62: 1036–1045.
Smith, B. L., and T. L. McDonald. 2002. Criteria to improve age classification of antlerless elk. Wildlife Society Bulletin 30:200–207.
Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.
White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74:355–369.
Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.
Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology 80:1236–1245.

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