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POPULATION ECOLOGY - ORIGINAL RESEARCH

Effects of climate and plant phenology on recruitment of moose at the southern extent of their range

Kevin L. Monteith[1] · Robert W. Klaver[2] · Kent R. Hersey[3] · A. Andrew Holland[4] ·
Timothy P. Thomas[5] · Matthew J. Kauffman[6]

Abstract   Climate plays a fundamental role in limiting the range of a species, is a key factor in the dynamics of large herbivores, and is thought to be involved in declines of moose populations in recent decades. We examined effects of climate and growing-season phenology on recruitment (8–9 months old) of young Shiras moose (*Alces alces shirasi*) over three decades, from 18 herds, across a large geographic area encompassing much of the southern extent of their range. Recruitment declined in 8 of 18 herds during 1980–2009, whereas others did not exhibit a temporal trend (none showed a positive trend). During those three decades, seasonal temperatures increased, spring–summer precipitation decreased, and spring occurred earlier, became shorter in duration, and green-up occurred faster. Recruitment was influenced negatively by warm temperatures during the year before young were born, but only for herds with declining recruitment. Dry spring–summers of the previous year and rapid rates of spring green-up in the year of birth had similar negative influences across declining and stable herds. Those patterns indicate both direct (year$_t$) and delayed (year$_{t-1}$) effects of weather and plant phenology on recruitment of young, which we hypothesize was mediated through effects on maternal nutritional condition. Suppressed nutrition could have been induced by (1) increased thermoregulatory costs associated with warming temperatures and (2) shortened duration of availability of high-quality forage in spring. Progressive reductions in net energetic gain for species that are sensitive to climate may continue to hamper individual fitness and population dynamics.

Keywords   *Alces alces* · Climate change · Heat stress · Irruptive paradigm · Nutrition

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✉   Kevin L. Monteith
    kevin.monteith@uwyo.edu

[1]   Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

[2]   US Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA 50011, USA

[3]   Utah Division of Wildlife Resources, Salt Lake City, UT 84114, USA

[4]   Colorado Parks and Wildlife, Fort Collins, CO 80526, USA

[5]   Wyoming Game and Fish Department, Sheridan, WY 82801, USA

[6]   US Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

Introduction

Exposure of species to altered climatic regimes has resulted in modified behavior, adjusted phenology, loss of geographic range, numeric declines and, in some instances, extinction (Parmesan 2006; Walther et al. 2002). Climate is increasingly viewed as playing a fundamental role in determining range limits for individual species; nonetheless, the diversity in species-specific responses complicates expectations concerning a changing climate (Parmesan 2006). Even within species, effects of climate change are not consistent, with range expansion and population growth

occurring in some regions while range contraction and population decline occur in others (Grøtan et al. 2009; Murray et al. 2012). One consistent generalization is that populations occurring at the periphery of their geographic range often are most sensitive to environmental change (Caughley et al. 1988).

In large herbivores, variation in environmental conditions, interacting with population density, shape life-history variation and thus population dynamics (Sæther 1997). In temperate ungulates, young are the age class most sensitive to factors that affect resource availability (Gaillard et al. 2000), which can have delayed and life-long effects on their survival, growth, and reproduction (Monteith et al. 2009). With warming temperatures associated with climate change (Shuman 2011), energy expended for thermoregulation by large-bodied herbivores adapted to cold climates may influence the performance of populations at the southern extent of their range (Murray et al. 2006). In domestic ruminants, heat stress can reduce foraging time and suppress appetite (De Rensis and Scaramuzzi 2003). Although free-ranging herbivores seek thermal refugia and alter activity patterns to reduce stressful climatic conditions (Bourgoin et al. 2011; Dussault et al. 2004), such behavioral responses may not fully compensate for the expenditure required to thermoregulate or may come at the expense of forage quality (van Beest et al. 2012). Indeed, even slight reductions in net energy gain through time could impair resource acquisition and thus individual performance over the long term (White 1983).

Large herbivores typically give birth in late spring and early summer to coincide with spring green-up, thereby allowing them to consume early-emergent, high-quality forage to support the energetic demands of late gestation and lactation. Nevertheless, climate change is altering patterns of vegetation phenology (Walther et al. 2002), which can affect nutritional resources available for reproduction and accumulation of fat reserves in ungulates (Monteith et al. 2013). In temperate environments, food quantity increases with a long season of photosynthetic activity (Ericsson et al. 2002), but cold and wet springs and summers increase forage quality and nutrient gain by slowing phenological advancement and increasing heterogeneity in the onset of green-up (Lenart et al. 2002); crude protein and digestibility of forage peak early in the growing season, then decline rapidly as vegetation matures (McArt et al. 2009). Consequently, climatological shortening of the period when forage quality is highest can reduce net energetic gain and lower the performance of large herbivores (Albon and Langvatn 1992). For example, years with rapid green-up resulted in poor growth and survival of young in two populations of bighorn sheep (*Ovis canadensis*) in Canada (Pettorelli et al. 2007). Nonetheless, few studies have connected temporal trends in climate with phenological change and long-term population performance.

Across much of the southern distribution of their range, which includes the northern conterminous United States and southern Canada, moose (*Alces alces*) have experienced population declines in recent decades. Such region-wide and somewhat synchronous declines in abundance suggest a broad-scale explanatory factor. Research in northern Minnesota has consistently associated the changing climate with nutritional stress, reduced survival and productivity, and high parasite loads in moose (DelGiudice et al. 2011; Lenarz et al. 2010; Murray et al. 2006). Meanwhile, other populations within their southern distribution appear resilient to similar changes in climate and have exhibited range expansion and population growth (Brimeyer and Thomas 2004; Murray et al. 2012), which challenges the uniformity of a northward recession of viable habitat for moose (Murray et al. 2006) and supports the notion that vulnerability to climate change differs among populations.

The effects of climate on the demography and population performance of large herbivores are difficult to disentangle from other confounding factors, especially when data are collected over short temporal windows when climate variation may be minimal. Therefore, long-term data that comprise a range of demographic rates and climate variability are useful to understand relationships that are likely complex and may involve lagged or cumulative effects (Monteith et al. 2009). We used a long-term dataset on the recruitment of young (8- to 9-month-old) Shiras moose (*Alces alces shirasi*) across the southernmost distribution of their range to evaluate the relative support for hypotheses proposed to explain broad-scale declines in moose populations, including climate warming and its effects on heat stress and nutrition as well as altered plant phenology. Incorporating long-term data from multiple populations should enhance our ability to detect broad-scale processes that may be responsible for disparate trends in moose populations in the Rocky Mountains.

Moose are uniquely adapted to a northern climate and are consequently more susceptible to thermoregulatory constraints associated with warm weather than other northern ungulates (Schwartz and Renecker 2007). Rising ambient temperatures may negatively affect female moose via increased heat loads and may foster increased parasite loads (Murray et al. 2006), and warm temperatures with dry springs can negatively affect the nutritional quality of forage in temperate regions (Pettorelli et al. 2007), all of which could result in lowered nutrition and reduced reproductive performance (Testa and Adams 1998). We therefore predicted the recruitment of young would be associated negatively with ambient temperature and positively with spring and summer precipitation (H_1, hypothesis 1). In addition, patterns of plant phenology affect the productivity

of herbivore populations by modifying the timing and duration of access to quality forage (Grøtan et al. 2009; Herfindal et al. 2006b; Pettorelli et al. 2007). Thus, we predicted that early onset of vegetation growth, slow spring green-up, and a longer spring would be related positively to recruitment of young (H_2; hypothesis 2). Finally, because moose rely partially on somatic reserves to support reproduction (Testa and Adams 1998), we expected conditions from preceding years to potentially carry over to influence recruitment in subsequent years through effects on fecundity and nutritional condition (H_3, hypothesis 3).

Materials and methods

Study area and moose data

The absence of fossil evidence indicates that the presence of moose in the central and southern Rocky Mountains is partially a result of an historical southward expansion of the Shiras subspecies by natural dispersal. Moose are believed to have entered northwest Wyoming from Idaho and Montana within the past 150 years, and have expanded southward into viable moose habitat, resulting in established moose populations from northwest Wyoming through northeastern Utah. More recently, moose were transplanted into the Bighorn Mountains, Wyoming in the 1950s (Brimeyer and Thomas 2004), to North Park, Colorado in the late 1970s (Kufeld and Bowden 1996), and into multiple herd units in Utah beginning in 1973 (Wolfe et al. 2010).

Although some populations contained nonmigratory individuals, moose in our study area were mostly migratory, and occupied high-elevation ranges during summer and low-elevation riparian areas during winter (Kufeld and Bowden 1996). Terrain within herd units was mountainous; mean elevation ranged from 2000 to 3050 m. In most regions, moose were associated closely with riparian communities, especially those dominated by *Salix*, including Drummond's (*S. drummondiana*), Booth's (*S. boothii*), planeleaf (*S. planifolis*), and Geyer's willow (*S. geyeriana*). Winter ranges were generally characterized by large riparian complexes; however, mixed-mountain shrub communities, including sagebrush (*Artemesia tridentata*) and bitterbrush (*Purshia tridentata*), also were used by moose (Brimeyer and Thomas 2004; Wolfe et al. 2010). At higher-elevation summer ranges, riparian areas dominated by *Salix* commonly were scattered within extensive stands of lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), cottonwood (*Populus augustifolia*), Englemann spruce (*Picea enelmannii*), Douglas fir (*Psuedotsuga menziesii*), and subalpine fir (*Abies lasciocarpa*). Most moose experienced some predation from black bears (*Ursus americana*)

and mountain lions (*Puma concolor*), but only 2 of 18 herds (Targhee and Jackson herds in northwest Wyoming) were exposed to growing populations of gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) since the mid-1990s (Brimeyer and Thomas 2004; Wolfe et al. 2010).

We obtained data on recruitment of young from observational data collected as part of the routine monitoring of moose populations by State management agencies for 18 herds (Fig. 1) in Wyoming ($n = 9$), Utah ($n = 8$), and Colorado ($n = 1$). Herd units were delineated by agencies based on hydrologic divides, major rivers, and other natural and man-made barriers to movement (Brimeyer and Thomas 2004). Since 1980, postseason classifications of moose were conducted on an annual basis for most herds; however, data were sparse for some (e.g., in Utah, surveys were often conducted every 3rd year; Wolfe et al. 2010). Helicopter surveys to classify herds by sex and age class were conducted by agency personnel between December and February when moose were congregated on winter ranges. Surveys were performed when good snow cover was present, and encompassed areas of riparian, deciduous, and conifer habitat that were frequented by moose during winter (Brimeyer and Thomas 2004). Occasionally, surveys were conducted from the ground to augment data collected during helicopter surveys or cover areas not surveyed from helicopter. Each moose encountered during surveys was classified as an adult male (≥ 2 years old), yearling male, adult female (including yearlings), young, or unclassified adult. Young were distinguished from yearlings and adults based on body size and features of the head, including relatively small ears and short, pointed noses. The sex of each adult moose was determined with criteria that included antler or pedicel scars, vulva patch, behavior, bell conformation and size, group composition, and body conformation.

Our study included data on recruitment of young representing 304 herd-years from 18 herd units during 1980–2009. Data were available for 21 herd units; however, we included only those herd units ($n = 18$) where surveys had occurred for a minimum of 10 years with an average number of observations ≥ 50 individuals. Although reliable estimates of population size were not available, moose populations in this region were variable in size, ranging from herds comprising as few as 60 animals up to an estimated 4500 animals. The average number of individuals classified to estimate an annual recruitment rate, across all herds and years, was 346.3 (SE = 20.7). We used the number of young per 100 adult females (young to adult female ratio) as our estimate of recruitment rate at the population (i.e., herd unit) level. The relative number of young per female provides a robust representation of annual patterns of reproductive success, because adult survival is generally high and invariable (Gaillard et al. 2000), the
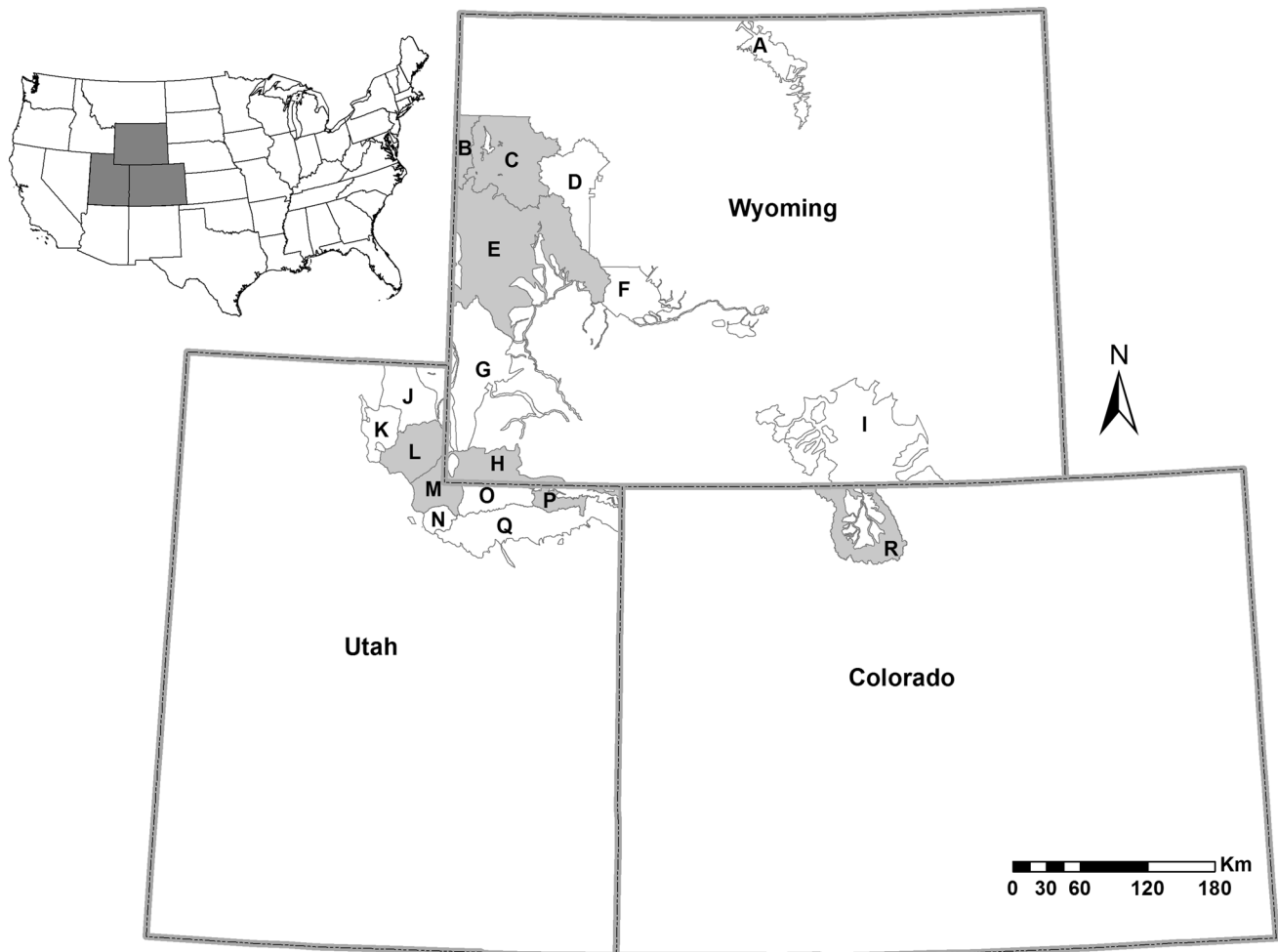
Fig. 1 Locations of 18 herd units of Shiras moose populations in the Rocky Mountains of Wyoming, Utah, and Colorado, USA, in which effects of climate and plant phenology on annual recruitment rates (midwinter number of young per 100 adult females) were evaluated. *Shaded* herd units indicate populations with declining recruitment rates ($P \leq 0.10$), 1980–2009. Herd units included Bighorn (*A*), Targhee (*B*), Jackson (*C*), Dubois (*D*), Sublette (*E*), Lander (*F*), Lincoln (*G*), Uinta (*H*), Snowy Range (*I*), Cache (*J*), Ogden (*K*), Morgan Rich (*L*), Chalk Creek (*M*), Kamas (*N*), North Slope Summit (*O*), North Slope Daggett (*P*), South Slope (*Q*), and North Park (*R*)

number of young per female reflects pregnancy, twinning rate, and survival of calves to weaning age (Grøtan et al. 2009; Raithel et al. 2007), and young moose are easily distinguished from adult moose. In addition, large temporal variation in recruitment of young is a hallmark of northern ungulate populations, and high variability in this key vital rate is a strong determinant of annual population dynamics (Gaillard et al. 2000; Raithel et al. 2007).

Weather and plant phenology data

We obtained spatially explicit data on monthly precipitation and monthly averages of daily minimum and maximum temperature for seasonal ranges occupied by each herd using modeled values from the parameter-elevation on independent slopes model (PRISM) at a resolution of

4 km (Daly et al. 1994). We extracted mean monthly data on weather for pixels that occurred within summer and winter ranges identified by management agencies. We used a climograph to delineate seasons based on months that grouped within similar ranges of temperature and precipitation (Fig. S1 in the Electronic supplementary material, ESM). Subsequently, we calculated cumulative precipitation and average daily minimum and maximum temperatures within those seasons. We used principal components analysis (PCA) of seasonal weather data to reduce data dimensionality and derive independent composite variables that described seasonal weather patterns.

The normalized difference vegetation index (NDVI) is derived from satellite imagery that measures the greenness of vegetation based on the ratio of ground reflectance of red and near-infrared radiation. NDVI is sensitive to

environmental change (Pettorelli et al. 2005), is associated with net primary production (Reed et al. 1994) and fluctuations in diet quality (Garel et al. 2011; Hamel et al. 2009), and thus, is related to the demography of large herbivores (Garel et al. 2011; Herfindal et al. 2006a; Pettorelli et al. 2007). We obtained a time series of 7-day composite NDVI with a spatial resolution of 1 km^2 recorded by the Advanced Very High Resolution Radiometer aboard the polar-orbiting weather satellites of the National Oceanic and Atmospheric Administration. Data were further processed to remove the effects of atmospheric contamination using the method of Swets et al. (1999). We extracted NDVI values for each 1-week interval from 1989 to 2009 (with the exception of 1990 and 1994, when data were unavailable) for pixels that occurred within the summer ranges of moose.

We expected the timing of spring and summer phenology to vary among moose herds depending upon snow accumulation, temperature, and summer precipitation, and thus to influence forage quality and availability, with consequences for recruitment of young. From the NDVI time-series data, we computed three NDVI metrics that reflected spring plant phenology using the program TIMESAT (Jönsson and Eklundh 2004) for seasonal ranges within each herd. We calculated the date of onset of spring to represent when quality forage became available in spring, and the length of spring, which represented the number of days between the onset of spring and peak NDVI, thereby indicating how long growing vegetation was available (Pettorelli et al. 2005). We calculated the rate of spring green-up based on the rate of increase in NDVI between the onset of spring and the plateau in NDVI (Pettorelli et al. 2005). Rate of spring green-up was highly correlated ($r = 0.91$) with maximal increase in NDVI in any two-week period during spring, a similar metric to that used to represent rate of spring green-up in other studies (Pettorelli et al. 2007). We also calculated integrated NDVI, which provides an index to net primary productivity (Pettorelli et al. 2005). Nevertheless, we chose not to use integrated NDVI in subsequent modeling because it was positively correlated with rate of green-up ($r = 0.60$), positively correlated between years ($r = 0.85$), and is a metric that may be less relevant for a concentrate selector such as a moose (McArt et al. 2009; 2007; Pettorelli et al. 2005).

Statistical analysis

Our overall approach to statistical analyses was to (1) evaluate temporal trends in climate and plant phenology and the relationships between them, (2) model recruitment of young as a function of weather and plant phenology, and (3) evaluate whether the relationships identified in (2) remained in de-trended recruitment rates. We identified temporal trends in average temperature and cumulative

precipitation within seasons, and for annual plant phenology metrics using separate linear mixed models (PROC MIXED; SAS Institute, Cary, NC, USA), with a random intercept for herd unit, year as a fixed effect, and each environmental variable as the response variable. We used simple linear regression to evaluate relationships between principal component variables that reflected weather patterns and metrics of plant phenology.

We assumed that survey data were representative of the variation in demography of moose populations, and that the trends were biological rather than a result of measurement error. We believe the consistent methods of data collection employed by each State agency upholds these assumptions, but we also recognize that long-term datasets that were collected under basic monitoring protocols rather than designed for statistical hypothesis testing are subject to variation and errors (White 2000). Because population size and survey efforts were variable among herd units, we estimated the variance in each recruitment estimate (Czaplewski et al. 1983). We then used simple linear regression, weighted by the inverse of the variance in each estimate, to identify temporal trends in recruitment separately for each herd unit. In this way, estimates with greater confidence (lower variance) were allocated more weight in our analysis than those with less confidence (higher variance). We considered herd units to have declining recruitment rates if the coefficient for time was negative and if $P < 0.10$; we considered all others to be stable.

We modeled recruitment of young as a function of seasonal weather patterns or plant phenology during both the year that a cohort of young was raised and the preceding year. We included environmental covariates from the preceding year because recruitment could be affected either by nutritional carryover from the previous year (Monteith et al. 2013) or by environmental effects of the previous year on fecundity (Testa and Adams 1998). We used linear mixed models (PROC MIXED; SAS Institute), weighted by the inverse of the variance in each recruitment estimate, to model annual recruitment as a function of weather or plant phenology. We conducted two separate modeling efforts because metrics of plant phenology were correlated with weather patterns, and weather and plant phenology have the potential to cause different nutritional and physiological constraints on recruitment of young. We included herd unit as a random effect to help account for unbalanced sample sizes among herds, and because we expected some level of unobserved heterogeneity and lack of independence within each herd unit (Gillies et al. 2006). We included principal components representing weather and metrics of plant phenology as fixed effects because we were interested in the marginal population-level response to those covariates.

We used an information-theoretic approach to evaluate the importance of predictor variables. In both analyses (i.e., weather and plant phenology), we evaluated all possible combinations of predictor variables that we hypothesized would influence recruitment of young (Arnold 2010; Doherty et al. 2010). Variables that were correlated ($r > 0.50$) were not allowed to enter the same model. For each model, we calculated Akaike's information criterion adjusted for a small sample size (AIC_c), ΔAIC_c, and the Akaike weight (w_i). We then calculated model-averaged parameter estimates and the associated 90 % CI, based on unconditional SEs. We determined if model-averaged parameter estimates differed from zero based on whether their 90 % CIs overlapped with zero, and used importance weights to evaluate their relative importance (Arnold 2010). We calculated importance weights as the sum of w_i across all models that contained that particular variable (Arnold 2010). We standardized all variables so that estimates of coefficients could be interpreted as the relative magnitude of the effect of each variable on the response variable.

We predicted that the effects of climate and plant phenology may differ between herds with declining trends in recruitment and those that are stable. We evaluated expected interactions among predictor variables using the global model before modeling all possible combinations of predictor variables. Interaction terms with CI that overlapped with zero and failed to improve model fit ($<2\ \Delta AIC_c$) were excluded from further modeling because their inclusion can alter model-averaged estimates of the independent counterparts of those terms (Arnold 2010). To best depict relationships between a specific predictor variable and a response variable in figures, we used the best model ($\Delta AIC_c = 0$) of all possible combinations of variables and modeled expected effects (y-axis) of the variable of interest (x-axis) within the observed range while holding all other variables constant at their means.

In some instances, relationships between a biological factor, such as recruitment, and a climatic covariate may be an artifact of a co-occurrence of similar linear trends through time (Grosbois et al. 2008). Consequently, recruitment could be a function of some other overlooked causal factor rather than climate (i.e., a lurking variable). To minimize the potential of such spurious results, we evaluated the relationship between climate or plant phenology variables within our best models ($\Delta AIC_c = 0$) identified in previous analyses and the residuals from a regression between year and recruitment rate. The residual analysis allowed us to determine whether variation in de-trended recruitment rates was still accounted for by climate or plant phenology covariates (Grosbois et al. 2008).

Results

Recruitment rates of Shiras moose during 1980–2009 across 18 herds in the Rocky Mountains averaged 46.7 (SE = 0.81) and ranged from 15 (Jackson, 2008) to 100 young per 100 adult females (North Park, 1985 and Snowy Range, 2003). We identified eight herds with declining recruitment rates (Table 1); those units occurred in northwestern Wyoming, northeast Utah, and the sole herd in Colorado (Fig. 1). The other ten herds all had negative coefficients for the time trend; however, their slopes were not different from zero (Table 1; Fig. S2 in the ESM). No herds exhibited an increasing trend in recruitment, significant or otherwise.

Seasonal weather patterns were described adequately by three principal components (PCs), all of which had eigenvalues >1 and accounted for 75.6 % of the total variation [eigenvalues (% variance explained): PC1 6.11 (45.1 %), PC2 1.89 (18.2 %), PC3 1.08 (12.3 %)]. PC1 represented annual temperature patterns contrasting relatively cool years (negative PC1) with relatively warm years (positive PC1). PC2 was related positively to spring–summer precipitation, opposing dry spring–summers with wet spring–summers. PC3 corresponded positively to autumn–winter precipitation, opposing dry autumn–winters with wet ones.

Table 1 Temporal trends in annual recruitment rates (midwinter number of young per 100 adult females) for 18 herd units in Rocky Mountains, USA, 1980–2009

Herd unit	Slope	r^2	P value	n	Status
North Slope Daggett[a]	−1.53	0.28	0.10	10	Declining
Jackson[a]	−1.04	0.64	<0.001	29	Declining
Targhee[a]	−0.77	0.37	0.006	19	Declining
Morgan Rich[a]	−0.59	0.31	0.074	11	Declining
Sublette[a]	−0.56	0.45	<0.001	30	Declining
Uinta[a]	−0.54	0.20	0.10	15	Declining
Chalk Creek[a]	−0.50	0.33	0.051	12	Declining
North Park	−0.46	0.14	0.091	21	Declining
Snowy Range	−2.42	0.24	0.18	10	Stable
North Slope Summit[a]	−0.74	0.22	0.11	13	Stable
Kamas	−0.58	0.08	0.41	11	Stable
Cache	−0.50	0.11	0.30	12	Stable
Ogden[a]	−0.49	0.10	0.34	11	Stable
South Slope	−0.36	0.14	0.28	10	Stable
Lander	−0.33	0.07	0.15	30	Stable
Lincoln[a]	−0.11	0.02	0.51	27	Stable
Bighorn	−0.07	0.00	0.83	27	Stable
Dubois	−0.02	0.00	0.94	23	Stable

[a] Herd units identified as established before the early 1970s (Brimeyer and Thomas 2004; Kufeld and Bowden 1996; Wolfe et al. 2010)

Significant changes in seasonal weather patterns and plant phenology were evident across the range of Shiras moose we studied. During 1980–2009, average daily temperature during winter, spring, summer, and autumn increased at a region-wide average of 0.5–0.6 °C per decade (Table S1 in the ESM), whereas spring and summer precipitation declined at an average of 1.0 and 0.6 cm per decade, respectively (Table S1 in the ESM). The characteristics of spring green-up also changed significantly from 1989 onwards; start of spring and length of spring decreased by ~3 days per decade, while spring green-up became more rapid (Table S2 in ESM). Metrics of seasonal plant phenology were correlated with the climatic variables PC1 (onset of spring: $r = -0.46$, $P < 0.001$; days of spring: $r = -0.13$, $P = 0.013$; rate of green-up: $r = 0.38$, $P < 0.001$) and PC2 (onset of spring: $r = 0.52$, $P < 0.001$; days of spring: $r = 0.02$, $P = 0.66$; rate of green-up: $r = -0.14$, $P = 0.006$). We assessed the relationship between recruitment and plant phenology separately from climate because those variables were correlated, and to avoid truncating our dataset when evaluating the effects of climate because NDVI data were not available prior to 1989.

Our evaluation of the effects of seasonal weather patterns indicated that recruitment rates were associated mostly with PCs that reflected annual temperature ($PC1_{t-1}$) and spring–summer precipitation ($PC2_{t-1}$) from the year before a cohort of young was born (Table 2). Nevertheless, there was a significant interaction between $PC1_{t-1}$

Table 2 Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from models of the effect of principal component (PC) variables during the current and preceding year on annual recruitment rates (midwinter number of young per 100 adult females) of Shiras moose ($n = 304$) for 18 herd units in the Rocky Mountains, USA, 1980–2009

Parameter	Estimate	90 % CI		Importance weight
		Lower	Upper	
PC1	−0.85	−2.69	0.99	0.82
PC2	0.15	−0.67	0.96	0.66
PC3	0.36	−0.55	1.27	0.71
$PC1_{t-1}$	−0.50	−3.50	2.49	1.00
$PC1_{t-1}$ × status[a]	−8.97	−12.74	−5.20	1.00
$PC2_{t-1}$[a]	3.33	4.54	2.12	1.00
$PC3_{t-1}$	0.24	−0.76	1.24	0.70

Principal components corresponded to annual temperature (PC1), spring–summer precipitation (PC2), and autumn precipitation (PC3). Status distinguishes herd units that exhibited declines in calf recruitment during 1980–2009 (coded as 1) from those that did not (coded as 0). Covariates were standardized ($\bar{x} = 0$, SD = 1)

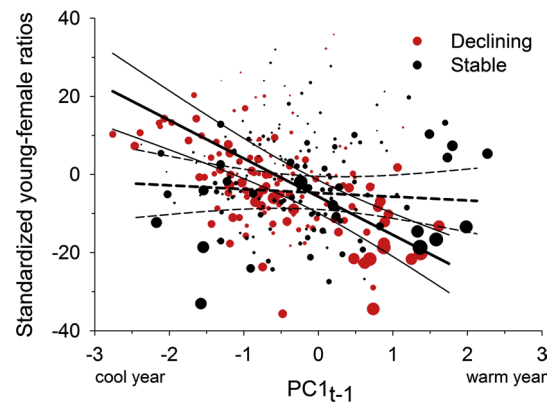[a] The 90 % CI for the corresponding parameter estimate does not overlap with zero

Fig. 2 Predicted relationship (±95 % CI) between annual recruitment rates (midwinter number of young per 100 adult females) of Shiras moose and a metric representing annual temperature during the preceding year for populations with declining (*solid line*) and stable (*dashed line*) trends in recruitment for 18 herds in Rocky Mountains, USA, 1980–2009. The size of *each point* represents the inverse of the variance in each recruitment estimate, which was used as a weighting term in predictive models

and herd status, indicating that there was a negative effect of temperature during the preceding year among herds that exhibited declining trends in recruitment (Table 2). Recruitment rates decreased as $PC1_{t-1}$ increased in herds with declining recruitment ($\beta = -8.97$), but $PC1_{t-1}$ did not influence recruitment in herds with stable recruitment rates ($\beta = -0.50$; Fig. 2). In contrast, recruitment increased similarly among herds with declining and stable recruitment rates with rises in spring–summer precipitation the preceding year (Fig. 3). Standardized parameter estimates indicated an ~3× larger effect size of temperature compared with spring–summer precipitation.

Rates of green-up during both the current and preceding year had importance weights of >0.90, and displayed a similar negative relationship with recruitment rates (Table 3). Only the parameter estimate for rate of green-up during the year of birth differed from zero. The effect of rate of green-up on recruitment of young was similar for herd units with declining and stable recruitment rates, indicating that a more rapid rate of spring green-up reduced recruitment the following winter (Fig. 4).

After accounting for a linear trend in recruitment through time, the outcomes from previous analyses held, with slight decreases in effect size. Annual temperature during the preceding year for herds with declining recruitment rates remained negative ($\beta = -4.96$, 90 % CI = −8.08 to −1.85), and the effect of spring–summer precipitation during the preceding year remained positive ($\beta = 2.22$, 90 % CI = 1.03 to 3.41). Likewise, the negative effect of rate of spring green-up persisted with detrended recruitment rates ($\beta = -1.77$, 90 % CI = −3.35 to −0.19). Both analyses indicate that the patterns of climate
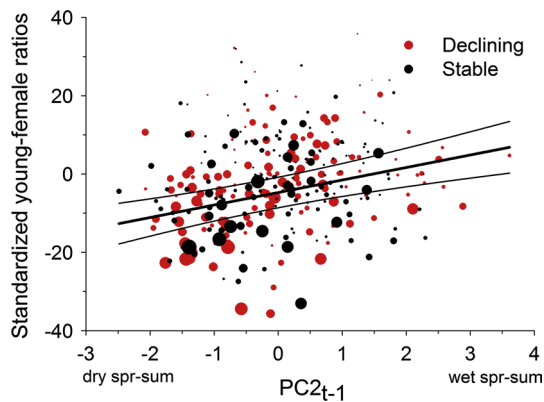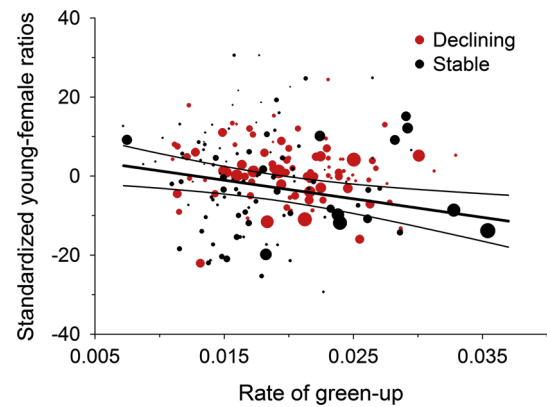
Fig. 3 Predicted relationship (±95 % CI) between annual recruitment rates (midwinter number of young per 100 adult females) of Shiras moose and a metric representing spring–summer precipitation during the preceding for year populations with declining and stable trends in calf recruitment for 18 herds in Rocky Mountains, USA, 1980–2009. The size of *each point* represents the inverse of the variance in each recruitment estimate, which was used as a weighting term in predictive models

Fig. 4 Predicted relationship (±95 % CI) between annual recruitment rates (midwinter number of young per 100 adult females) of Shiras moose and rate of spring green-up for populations with declining and stable trends in calf recruitment for 18 herds in Rocky Mountains, USA, 1980–2009. The size of *each point* represents the inverse of the variance in each recruitment estimate, which was used as a weighting term in predictive models

Table 3 Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from models of the effect of plant phenology metrics during the current and preceding year on annual recruitment rates (midwinter number of young per 100 adult females) of Shiras moose ($n = 199$) for 18 herd units in the Rocky Mountains, 1980–2009

Parameter	Estimate	90 % CI Lower	90 % CI Upper	Importance weight
Onset of spring	0.0001	−0.018	0.019	0.15
Rate of green-up[a]	−2.25	−4.04	−0.45	0.97
Length of spring in days	−0.032	−0.087	0.023	0.31
Onset of spring$_{t-1}$	−0.0005	−0.017	0.016	0.15
Rate of green-up$_{t-1}$	0.11	−1.11	1.34	0.72
Length of spring$_{t-1}$ in days	−0.0012	−0.023	0.020	0.16

Covariates were standardized ($\bar{x} = 0$, SD = 1)

[a] The 90 % CI for the corresponding parameter estimate does not overlap with zero

and plant phenology associated with recruitment of young were not merely an artifact of a co-occurrence in linear changes though time, but that climate and plant phenology did indeed affect annual variation in recruitment.

Discussion

Recruitment reflects fecundity and survival of young, and, because it is the most variable demographic rate of large ungulate populations, it determines interannual variation in population growth (Gaillard et al. 2000). Young of the year also are the age class expected to be most vulnerable to factors that affect forage quality and availability, because allocation of resources by mothers is secondary to maintenance (Monteith et al. 2013), and young lack the energetic reserves to buffer against such variation. Therefore, elucidating factors that limit production and recruitment of young for moose at the southern periphery of its range provides an indicator of how changing climatic conditions may affect the performance of Shiras moose populations. As predicted, recruitment of young was affected by ambient temperatures and spring–summer precipitation (H₁), but those effects were delayed by 1 year, indicating potential climate effects on pregnancy and nutritional carryover (H₃). Although date of spring green-up or length of spring had no apparent effect on recruitment of young, a more rapid rate of green-up during the year young were raised affected recruitment negatively (H₂).

Severe weather during winter can reduce overwinter survival and subsequent recruitment of young for temperate herbivores (Hegel et al. 2010). Nevertheless, autumn–winter precipitation did not affect recruitment of moose at the southern extent of their range, and temperature had the opposite effect expected from a context of severe winter weather (Table 2). The lack of influence of winter severity could have occurred if our data failed to capture some overwinter mortality, because recruitment surveys were conducted in midwinter. Nevertheless, moose are uniquely adapted to a northern environment, have the lowest thermal neutral zone and greatest chest height of any North American ungulate, and are capable of feeding on willows above deep snow (Renecker and Hudson 1986; Telfer and Kelsall

1984). Moose can be sensitive to snow conditions during winter (Crête and Courtois 1997; Sæther 1997), but climatic changes have resulted in milder winters in our study region (Shuman 2011), while spring and summer have become hotter and drier for this northern ungulate.

If nutrient intake is sufficiently low, reproductive females may encounter a trade-off between accumulation of fat reserves and allocation of resources to reproduction (Monteith et al. 2013). In accordance with life-history theory, females of long-lived herbivores invest in reproduction according to their nutritional state (Monteith et al. 2013; Testa and Adams 1998), because somatic losses during lactation can reduce overwinter survival and reproduction. Although early onset of spring can be critical for nutrient gain of reproductive females in late gestation (Hegel et al. 2010; Herfindal et al. 2006b), our results indicate that characteristics of the rate of green-up during spring were more important than timing of green-up for recruitment of young in Shiras moose. Diet quality and the duration of forage availability during spring and summer is a key determinant of ungulate productivity (McArt et al. 2009; Pettorelli et al. 2007), because spring is when fat accretion and energetic demands for reproduction are greatest (Monteith et al. 2013). Warm springs may lead to an earlier green-up, but cool weather that produces a slow and prolonged green-up increases the availability of high-quality forage by lengthening the temporal window (Fig. S3 in the ESM) and spatial heterogeneity in green-up (Pettorelli et al. 2007). Cool and wet weather during the growing period improves forage quality by increasing nitrogen content, whereas warm and dry spring conditions reduce nitrogen and increase fiber content and thus reduce digestibility (Lenart et al. 2002). Our results support the growing body of evidence that a longer window of access to slow-growing and highly digestible forage (as indexed by a slow rate of NDVI increase) enhances growth and recruitment of young (Ericsson et al. 2002; Hegel et al. 2010; Herfindal et al. 2006b; Pettorelli et al. 2007).

We documented delayed effects of temperature and spring–summer precipitation, but weather patterns of the current year had little detectable effect on recruitment. Those results indicate that, for ungulates that rely heavily on stored fat reserves to support reproduction, carryover in nutritional condition from the previous winter and summer can have profound effects on reproductive success (Keech et al. 2000; Testa and Adams 1998). Similarly, the productivity of other moose populations was more strongly related to weather of the preceding year than the current one (Crête and Courtois 1997; Grøtan et al. 2009; Solberg et al. 1999). Such carryover effects, which may extend for multiple years, complicate our understanding of climate-performance relationships in northern ungulates.

Although warming temperatures likely had a negative effect on forage quality, the strong negative relationship between warming temperatures and recruitment of young in herds with declining recruitment suggests that thermoregulatory costs could be contributing to the reduced performance of moose populations at the southern periphery of their range (Lenarz et al. 2010; Murray et al. 2006). Moose are likely vulnerable to heat stress because they lack extensive abilities to sweat and have the lowest upper critical temperature of any northern ungulate (Renecker and Hudson 1986; Schwartz and Renecker 2007; van Beest et al. 2012). Chronic heat stress may impair reproductive performance indirectly via nutritional suppression as a result of increased metabolic costs, reduced appetite, reduced foraging time, and trade-offs in habitat selection (De Rensis and Scaramuzzi 2003; Renecker and Hudson 1986; van Beest et al. 2012). Over time, the cumulative effects of even a slight suppression of resource acquisition because of increased heat loads probably have fitness consequences, especially for females experiencing the burden of lactation. Moose alter circadian activity patterns (Dussault et al. 2004) and seek thermal refugia in response to warm temperatures (Schwab and Pitt 1991; van Beest et al. 2012). Whether such behavioral responses can compensate fully for warming thermal regimes is unclear (Bourgoin et al. 2011; Lowe et al. 2010). For example, moose in southern Norway sought thermal shelter during summer in coniferous forest, but did so at the cost of reduced accessibility of forage (van Beest et al. 2012).

Geographic variation in the population dynamics of vertebrates is common and is, in the absence of predation, underpinned by the interaction between stochastic and density-dependent factors (Sæther 1997). Temporal variation in climate can synchronize population fluctuations at a broad spatial scale (Grøtan et al. 2005) and likely was a major reason for widespread declines in the recruitment of moose in the Rocky Mountains. Despite similar changes in climate and plant phenology across our study region, however, 10 of 18 herds did not exhibit a temporal trend through time, and the effect of annual temperature regimes was not evident in herd units with stable recruitment rates (Fig. 2). Although we observed patterns among climate, plant phenology, and recruitment of young that were statistically significant, substantial variability and unaccounted-for variation existed among relationships (Figs. 2, 3, 4). These findings indicate that other local factors also are likely affecting recruitment, some of which may be modulating the effects of climate warming that we observed.

Many of the herd units for which we observed declines in recruitment have been established for the longest durations (Table 1). In particular, moose have been present in northwest Wyoming since the early 1900s (Brimeyer and Thomas 2004), and served as a source for natural dispersal

and expansion southward through western Wyoming and into northeastern Utah, where populations were established by the 1950s (Wolfe et al. 2010). With two exceptions (North Park and North Slope Summit; Table 1), most populations displaying relatively stable trends (note that all trends were negative but not significant) in recruitment were relatively new herds originating in the 1970s, compared with most of those that were well established by the late 21st century. Following introduction or expansion into a previously unoccupied range, herbivore populations often increase to peak abundance, crash, and subsequently increase to a new lower abundance (Forsyth and Caley 2006). This phenomenon, termed the irruptive paradigm, occurs as herbivore populations benefit from previously unexploited resources that become depleted by density-dependent herbivory (Forsyth and Caley 2006). We were unable to directly account for density dependence within our recruitment models because reliable population estimates were not available for most herds. Nevertheless, the commonality of declining recruitment we observed in the oldest herd units in the region is consistent with the irruptive paradigm. Furthermore, data from trend counts for herds with declining recruitment are suggestive of declining populations (Brimeyer and Thomas 2004), which would have yielded a positive relationship between population density and recruitment—a misleading result given that carrying capacity likely declined with changing climate during our study.

The regional patterns of recruitment we described may represent a novel extension of the irruptive paradigm, whereby abundant forage available to recently established populations appears to provide a nutritional buffer against depletion in critical body stores that would otherwise occur because of changing climate and plant phenology. Indeed, effects of environmental stochasticity are often stronger in populations already suppressed by density dependence or other factors (Herfindal et al. 2006a; Monteith et al. 2014). Consequently, even under the influence of climate change, habitat quality remains a key driver of population dynamics. Our results demonstrate that efforts aimed at improving forage quality and reducing inter- and intraspecific competition in populations with declining recruitment hold promise to reduce the negative effects of current changes in climate by providing a nutritional buffer against such vicissitudes. We also suspect, however, that as other populations continue to grow toward carrying capacity, and advancing plant phenology reduces carrying capacity, effects of climate will increase as their nutritional buffer is reduced. In the absence of long-term research, which rarely exists, consistent routine monitoring of population characteristics by management agencies yields long-term data that are likely our best opportunity to detect the effects of, find the tools to mitigate for, and design future studies on climate change.

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