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Research Article

Predicting Mule Deer Recruitment From Climate Oscillations for Harvest Management on the Northern Great Plains

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ABSTRACT We analyzed a unique 51-year time series for a population of mule deer in the North Dakota badlands, USA to examine the effects of seasonal weather on autumn recruitment. Winter weather recorded prior to birth of fawns and weather conditions recorded during spring the previous year (lagged effect), but not during spring or summer after birth, were related to observed patterns in autumn recruitment. When deer density was low (approx. 1 deer/km^2) during the 1960s, fawn/female ratios were high ranging from 1.1 to 1.4 when minimum temperatures during the prior winter averaged -16° C and -8° C, respectively. Likewise, during the 2000s, when deer density was high (approx. 3 deer/km^2), fawn/female ratios ranged from 0.6 to 0.9 when minimum daily temperatures during the previous winter were -16° C and -8° C, respectively. Large-scale Pacific-based climatic indices (>2,000 km to the Pacific coast) were correlated with local weather and helped explain variability in autumn recruitment. Higher values of the multivariate el niño southern oscillation and Pacific decadal oscillation were correlated with warmer and drier winters in the North Dakota badlands, whereas the North Pacific Index was correlated with colder and snowy winters. The ability to predict recruitment from local weather or from broad-scale climate indices (oscillations) provides greater opportunities for conservation and management, such as adjusting harvest quotas prior to autumn harvest.

KEY WORDS aerial survey, harvest management, mule deer, multivariate el niño southern oscillation, North Pacific index, Pacific-based climate, Pacific decadal oscillation, recruitment, survival, weather.

Variation in climate is an important driver of environmental stochasticity affecting fluctuations in ungulate populations for temperate systems (Sæther 1997, Gaillard et al. 1998, Mysterud et al. 2001). Seasonal fluctuations in climate can affect recruitment, which is a key vital rate in population dynamics (Sæther 1997; Gaillard et al. 1998, 2000), with its influence being most profound during the following 3 periods: 1) pre-birth (maternal) period, in which the mother's body condition is expected to affect the likelihood of a successful pregnancy (e.g., Bishop et al. 2009), 2) birth to weaning in summer (e.g., Hurley et al. 2011), and 3) autumn to first offspring's winter (e.g., Bergman et al. 2014). Knowing recruitment rates is especially important for managing hunted populations because license numbers often must be set months before this information is available. The ability to predict recruitment from seasonal weather has the potential to assist managers with adjusting harvest quotas before the beginning of the hunting season.

Continental climates in the interiors of continents are characterized by having large variances in temperature and precipitation with extreme weather commonly recorded in winter and summer. Variability in winter conditions has the potential to influence population dynamics of herbivores through an effect on mortality (Bartmann and Bowden 1984, Sæther et al. 1996, Mysterud et al. 2001, Hurley et al. 2011) or body condition (Sæther and Gravem 1988, Monteith et al. 2013). Harsh winters can aggravate the effects of competition for available food and negatively affect vital rates (Forchhammer et al. 2001, Bishop et al. 2009, Hurley et al. 2011). In contrast, climate can have a major influence on the quantity and/or quality of summer forage available to herbivores based largely on rainfall and temperature (Sæther 1985, Post and Stenseth 1999, Hurley et al. 2011). Positive effects of summer precipitation on ungulate survival and reproduction can sometimes balance the negative effects of harsh winter conditions (Grotan et al. 2008).

The mule deer, *Odocoileus hemionus*, is a large herbivore that occurs throughout western North America from Alaska and

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Western Canada through the Rocky Mountains and Western Plains States of the United States south to the Peninsula of Baja California and Northwestern Mexico. The northern Great Plains are characterized by relatively cold and long winters where deer are typically in negative energy balance during winter because metabolic requirements cannot be met by foraging alone (Wallmo 1981; Torbit et al. 1985*a*,*b*; Parker et al. 1996; Bishop et al. 2009; Monteith et al. 2014). The nutritional condition of mule deer is, therefore, linked to seasonal availability of food resources with seasonal limitations in food resources being a major cause of mortality for fawns (Bishop et al. 2009, Hurley et al. 2011, Forrester and Wittmer 2013). Mule deer are highly selective feeders that depend on high-quality forage (Wallmo 1981), and annual weather effects on the progression of vegetative growth and quality are expected to affect year-to-year mule deer population dynamics (Parker et al. 2009, Forrester and Wittmer 2013).

Recent studies have demonstrated the predictive power of broad-scale climate indices to predict recruitment in ungulates (Stenseth et al. 2003; Hegel et al. 2010*a*,*b*), and it has been suggested that biological effects may be related more strongly to global indices than to any single local climate variable (Stenseth et al. 2003). If this is true, the use of large-scale indices as proxies of local weather has the potential to shed further light on our understanding of the relationships between climate and population dynamics (Stenseth et al. 2003). In western regions of Europe and eastern North America, the North Atlantic Oscillation (NAO) index predicts ungulate dynamics better than local weather because the index integrates variation and interactions from multiple variables across temporal and spatial scales (Stenseth et al. 2003, Hallett et al. 2004, Stenseth and Mysterud 2005). Relationships between local weather patterns or broad climatic indices with ungulate population dynamics ultimately depend on the spatial and temporal scale of the process in question. Broad-scale climate indices are likely better suited for large-scale studies with scattered and discontinuous local weather data (assuming geographic stationarity, which may not hold at large scales), whereas local weather data (e.g., a single weather station) could be enough to predict population dynamics for small-scale studies. Large-scale indices also are retrospectively available back to the early 1900s, freely available online, and can be the only available weather proxies for those areas where local weather stations and historical data are sparse. Whether the Pacific-based climate fluctuations can influence local weather in continental areas, such as the North American Great Plains where the distance from the Pacific Ocean may exceed 2,000 km, is not well documented. Only a few studies have used Pacific-based climate fluctuations to predict ungulate dynamics in North America (Hebblewhite 2005; Hegel et al. 2010*a*,*b*), and these studies were mainly limited to areas closer to the Pacific coast (e.g., Marshal et al. 2002, Stenseth et al. 2003). The multivariate el niño southern oscillation index (MEI; also known as el niño-la niña fluctuations) has been correlated with terrestrial vertebrate population dynamics in North America (Marshal et al. 2002). Recently, 2 additional Pacific-based indices have been implicated as influencing population-growth rate, survival, fertility, and other life-history characteristics in North America—the North Pacific index (NPI; also known as North Pacific Patterns NP) and the Pacific decadal oscillation (PDO; Hebblewhite 2005, Morrison and Hik 2007, Hegel et al. 2010*a*).

We related a 51-year time series of mule deer autumn recruitment in the North Dakota badlands, which host a population of mule deer that is one of the most distant populations from the Pacific Ocean (Forrester and Wittmer 2013). We had 3 major hypotheses. First, we postulated that variation in weather during fawn growth would affect mule deer recruitment; therefore, we would see differences in recruitment depending on the strength of seasonal weather conditions. We expected that unfavorable weather conditions recorded before (winter: Nov–Mar), during (spring: Apr–May), and after (summer: Jun–Sep) the birth of fawns would negatively affect fawn survival and, consequently, we would observe low fawn recruitment in October. Specifically, we expected harsh winter conditions to weaken female body condition with consequences to their reproductive success (Wallmo 1981; Torbit et al. 1985*a*,*b*; Parker et al. 1996; Bishop et al. 2009). Snowy and cold spring weather can debilitate body condition of female mule deer at the end of the winter season when fat reserves are reduced (Monteith et al. 2013, 2014). During springs with cold weather, snow may persist for long periods delaying green-up. If 75–80% of the fetal growth occurs during the last trimester as in white-tailed deer (*Odocoileus virginianus*; Armstrong 1950), then delay of green-up could affect fawn recruitment. Hot and dry summers are expected to reduce food quality and availability during weaning and reduce fawn survival (Hurley et al. 2011).

Second, we hypothesized that adverse weather conditions (e.g., harsh winters, snowy and cold springs, and/or hot and dry summers) would affect female body condition and, thus, recruitment in the following year. We predicted that adverse weather conditions in year t-1 would result either in a negative or a positive effect on recruitment in year t. A 1-year lag effect of unfavorable weather conditions recorded in 1 or more seasons is expected to diminish female body fat over the next year and negatively affect conception and fawn recruitment. Alternatively, adverse weather conditions in year t-1 may cause fawn mortality and reduce female's energy expenditure (no weaning), leading to enhanced female body condition that would actually improve survival of fawns in year t.

Finally, we predicted that Pacific-based climate indices (MEI, NPI, and PDO) would be correlated with local weather in the Upper Great Plains. We tested the efficacy of these ocean proxies in predicting mule deer recruitment compared to local weather data. If this is true, managers can use ocean climate proxies when local weather data are not available.

STUDY AREA

We performed our study in southwestern North Dakota. The primary range of North Dakota's mule deer population (7,327 km^2) is restricted to the badlands within the drainage system of the Little Missouri River (Fig. 1). Elevation ranged from a low of 615 m above sea level in the Little Missouri River bottoms to a high of 913 m at plateau tops.

This region encompasses abrupt changes in substrate, slope, and soils. Badlands are a type of dry terrain where clay-rich soils and softer sedimentary rocks have been widely eroded by wind and water. They are characterized by steep slopes, minimal vegetation, and high drainage density. Native prairie is generally the main habitat on shallow slopes. Pine forest (Ponderosa pine [*Pinus ponderosa*]) is a unique

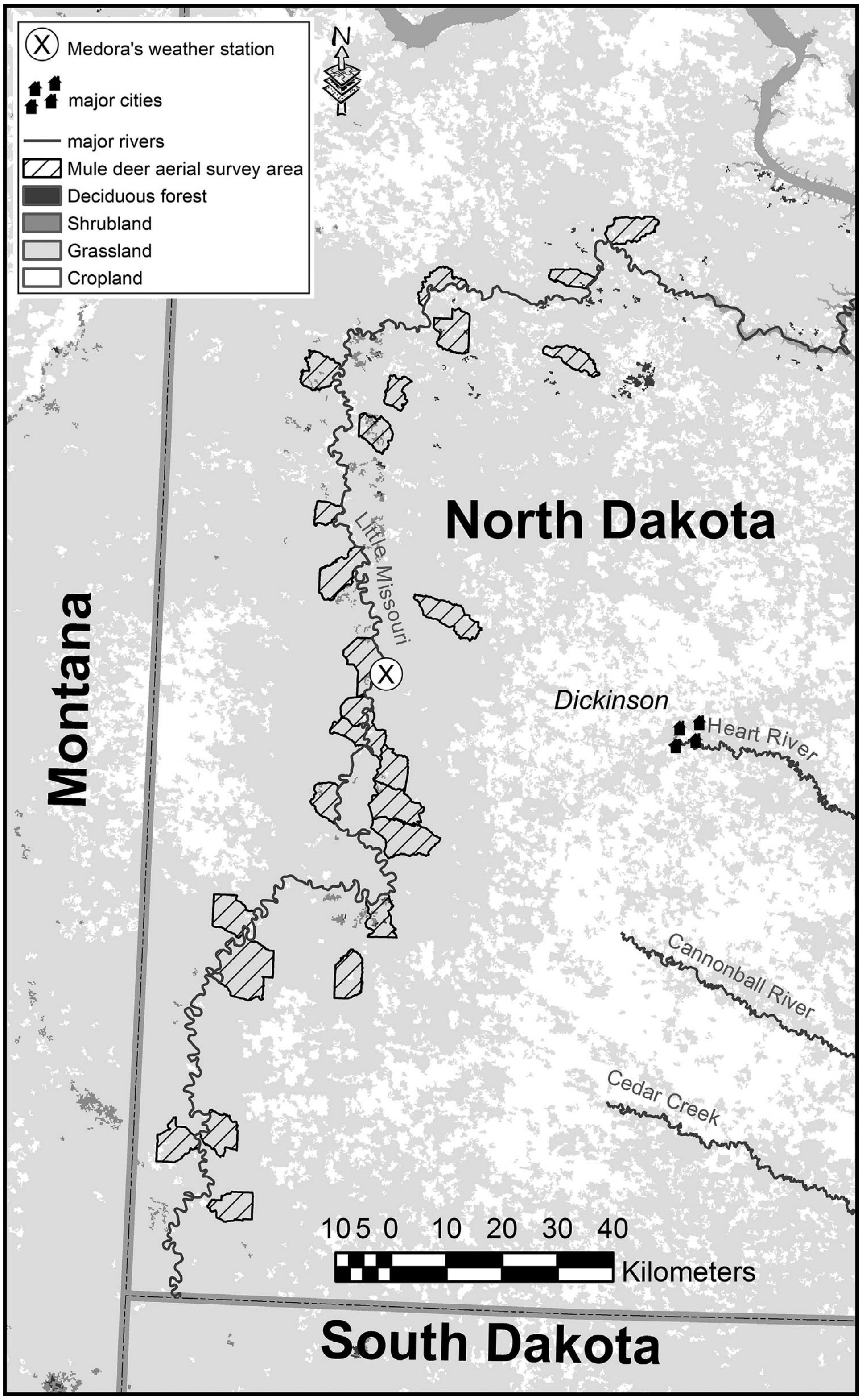

Figure 1. Map of the mule deer study area located along the Little Missouri River, North Dakota badlands, where surveys were flown from 1962 to 2012. Location of the Medora weather station is indicated in the map (latitude: 46.96°; longitude: −103.50°; elevation: 686 m a.s.l.).

habitat representing up to 35 km^2 of the southern half of the badlands. Rocky Mountain juniper (*Juniperus scopulorum*) dominates much of the rest of the badlands, occupying about 2,500 km^2.

North Dakota's climate is continental and is characterized by large variances in temperature, both on a seasonal and daily basis. Temperatures range from a mean daily high of 30.8° C in July (1962–2012: range 23.5–34.5° C) to a mean daily low of −16.1° C in January (range −24.9° C to −6.5° C). Snow cover typically occurs between November and April. Snow cover is variable and often sparse, with cover maintained throughout the winter only in shaded areas. Pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and a small herd of elk (*Cervus elaphus*) share the mule deer range. Coyote (*Canis latrans*), golden eagle (*Aquila chrysaetos*), and more recently mountain lion (*Puma concolor*) are the major natural predators of mule deer (Seabloom 2011).

Harvest management is regulated by the North Dakota Game and Fish Department through harvest quota set on a yearly basis (since late 1950s). The footprint of energy development (particularly oil) has increased significantly in the Dakota badlands over the last 30 years, especially in the last decade with energy development growing rapidly because of the use of fracking extraction techniques.

METHODS

Mule Deer Aerial Surveys

From 1962 to 2012, mule deer surveys were flown by staff of the North Dakota Fish and Game Department during October on as many as 26 (17 ± 5, mean ± SD) survey units within the study area (Fig. 1) to estimate deer recruitment rates. The aerial survey design employed a census (100% coverage per unit). A total of 54,744 mule deer were counted by age and sex class over the monitored period (total males: 9,362, yearly mean ± SD: 183 ± 115; total females: 22,699, yearly mean ± SD: 445 ± 237; total fawns: 22,683, yearly mean ± SD: 444 ± 187). We defined recruitment recorded in October as the fawn/female ratio observed in the entire region. From 1962 to 2012, the fawn/female ratio ranged from 0.59 to 1.52 (mean ± SD: 1.07 ± 0.22).

During the same 51-year period, spring surveys were flown during April to estimate deer density in the region. These surveys were flown on as many as 26 survey units within the study area (average number of survey units surveyed each year ± SD: 19 ± 6; deer density range: 0.89–3.56 deer/km^2). Deer density recorded in spring is expected to reflect density-dependent effects on females during pregnancy and weaning; effects on physical condition and fecundity (Stewart et al. 2005) and eventually on recruitment are recorded in the fall. The spring mule deer population of the North Dakota badlands has tripled in size (approx. 1 deer/km^2 in the 1960s vs. approx. 3 deer/km^2 in 2000s), whereas fall recruitment rate has almost halved (approx. 1.3 fawns per female in the 1960s vs. approx. 0.7 fawn per female in 2000s). This suggests an overall density-dependent regulatory effect of deer density on fall recruitment that we further investigated in our recruitment models (see below). Our observational study did not employ animal handling and adhered to relevant regulations and guidelines regarding the ethics of animal welfare of animals. Procedures were part of a study plan approved by the North Dakota Game and Fish Department, Bismarck, North Dakota, USA.

Local Weather Data and Pacific-Based Climate Indices

Local weather data, including daily precipitation (mm), snowfall (mm), snow depth (mm), and maximum and minimum temperatures (°C), were collected at the Medora weather station (station id: Medora, ND, US; elevation 686.1 m a.s.l.; latitude 46.966°; longitude −103.500°) centrally located in the mule study area (Fig. 1). Data are freely available online from the National Oceanic and Atmospheric Administration (NOAA; www.noaa.gov). Daily data can be accessed through a geographic information system (GIS) viewer available at the following website:

http://gis.ncdc.noaa.gov/map/viewer/#app=cdo&cfg=cdo&theme=daily&layers=111&node=gis. Although we collected fawn recruitment data in the period 1962–2012 ($n = 51$), a continuous time series in weather data were available at the Medora station since 1956 ($n = 57$). We used this extended time series to describe local weather and its relationship with Pacific-based climate indices.

Based on our knowledge of the ecology of mule deer and available literature (Forrester and Wittmer 2013), we defined 3 seasons when weather conditions were expected to affect female reproductive success and fawn survival, and in turn, recruitment recorded during October (Fig. 2). Fall green-up is not a significant phenomenon in this region (W. F. Jensen, North Dakota Game and Fish Department, personal communication). Radiocollared female mule deer were observed to feed in brush complex types in the fall, with

Figure 2. Diagram depicting seasonal intervals at which local weather and Pacific-based climate covariates were computed as predictors of mule deer fawn recruitment in the North Dakota badlands, 1962–2012. We considered seasons before, during, and after the birth of fawns, as well as those seasons when weather was expected to affect body condition of females on the long term (1-year lag).

the tendency to use steeper slopes with a northerly aspect and to avoid grasslands (Jensen 1988), suggesting that browse and forbs compose the majority of the fall diet. Northerly slopes, with slightly moister microclimates, support a higher percentage of browse and forbs, and were among the last areas for plants to enter senescence in fall (Jensen 1988). Based on these observations, we did not consider fall as a single season, and assigned fall months to either summer or winter seasons consistent with their weather characteristics. We included September in summer (average max. temperature: 24.1° C, range: 15.8–28.8° C); November can be harsh (average snowfall: 105.3 mm, range: 0–376 mm, average min. temperature: $-7.4°$ C, range: $-13.9°$ C to $-2.6°$ C) and we included it in winter (Fig. 2).

We estimated average local weather covariates for each season, except for snow metrics, which we did not consider for summer (Jun–Sep). We estimated a winter severity index (WSI) using data from the Medora weather station and a well-established protocol where we accumulated 1 point for each day when mean ambient temperature was $\leq -7°$ C, and we accumulated an additional point for each day in which snow depth was ≥ 35 cm (Brinkman et al. 2005). We computed WSI for winter (Nov–Mar) and spring (Apr–May) of each year.

We considered the following 3 Pacific-based climate indices: 1) PDO (data were available at http://www.esrl.noaa.gov/psd/data/climateindices/list/); 2) NPI (available at https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter); and 3) MEI (available from http://www.esrl.noaa.gov/psd/enso/mei/#data). El Niño occurs when MEI values are high, whereas La Niña occurs when MEI values are low. We averaged all monthly Pacific-based indices seasonally (see Fig. 2 for season classification).

Data Analyses

Our primary objective was to relate local weather and Pacific-based indices (same set of data available for the North American continent) to fall fawn recruitment in the North Dakota badlands. We modeled the time series of fawn recruitment collected from 1962 to 2012 using as a response variable of the total number of fawns counted in the entire study area divided by total number of females counted in the same region each year. We did not attempt to test for the effect of local variation of weather conditions on fawn recruitment across different survey units of the study area (Fig. 1) because multiple weather stations with consistent reporting were not available in the area and the weather within this region was generally similar.

We modeled fall recruitment (hereafter referred to as recruitment) as a function of spring mule deer density (hereafter referred to as deer density) and 1 or more seasonal weather covariates (x_i) using generalized additive models (Wood 2006, 2011) withance σ^2.

$$\text{Recruitment}_i = a + f_1(\text{Deerdensity}_i) + f_2(x_i) + \ldots + \varepsilon_i \quad (1)$$

where $\varepsilon_i \sim N(0, \sigma^2)$.

In additive modeling, we used a smoothing function to link the response variable recruitment to deer density f_1(Deer density$_i$) and the seasonal weather covariates $f_2(x_i)$ to allow for non-linear relationships (Wood 2006). In practice, the additive model fits a smoothing curve through the data. The amount of smoothing was not fixed to a present value; hence, we used cross-validation that automatically determines the optimal amount of smoothing (Wood 2006). We inspected normality of residuals using quantile–quantile plots. We screened independence of residuals using the autocorrelation function (Venables and Ripley 2002).

Year of study was collinear with spring deer density (Pearson correlation: $r_p = 0.83$, $P < 0.001$); therefore, they could not be included in the same models. Models including year as a predictor (not shown in this paper) were characterized by lower uncertainty compared to models including deer density as a predictor, with no temporal autocorrelation issues. However, deer density recorded in spring is expected to be related to food availability to females during pregnancy and weaning, with the potential to affect fall recruitment via density-dependent regulatory effect (Stewart et al. 2005). Thus, we used mule deer density as a predictor in our models because it was better justified biologically. This choice introduced a 1-year time lag autocorrelation in the residuals of our models, as expected because next year's population size is directly a consequence of this year's population size. This autocorrelation does not bias the estimate of the coefficient for density, but it causes an underestimate of the variance, that is, increasing the likelihood of a Type I error. This did not affect model-selection because deer density was included in all models to account for the density-dependent regulatory effect (Bergman et al. 2015). However, we avoided making any inferences on the *P*-values recorded for the effect of deer density on deer recruitment. To select the best seasonal predictors of fawn recruitment among local weather covariates, which usually are collinear ($|r_p| > 0.7$) within the same season, we fitted a series of generalized additive models (Equation (1)) with only 1 weather covariate. We ranked model support using the Akaike's Information Criterion corrected for small sample size (AIC$_c$). We selected the covariate included in the models with the lowest AIC$_c$ values as the best local weather predictors in fawn recruitment.

Pacific-based climate indices are metrics that oscillate over time and are strictly inter-related among each other. Specifically, MEI and PDO values are positively correlated with each other, and negatively correlated with NPI values (Table S1). We fitted Principal Component Analyses (PCAs; Crawley 2012) on the 3 Pacific-based climate indices to compute principal components of the first axis (PC1s) derived for each season (winter, spring, and summer) and PCIs for 1-year lags of weather variables for each season (Figs. S1, S2, and S3). Following the same procedure used to select best local seasonal weather predictors, we fitted a series of generalized additive models (Equation (1)) with only 1 climate covariate, and we selected Pacific-based climate indices or PCI covariates included in the models with the lowest AIC_c values as the best climate predictors in fawn recruitment. Next, we fitted 2 a priori sets of generalized additive models using the top 1) local weather covariates from each season and 2) Pacific-based climate indices from each season as predictors of fawn recruitment. We included seasonal covariates that reflected weather and climate conditions for the current year (t) and the previous year (t-1). A priori models were alternative and plausible (biologically motivated) models supported by our knowledge of the species and previous literature (Table S2). Pacific-based climate indices can be collinear ($|r_p| > 0.7$) among different seasons, even among consecutive years. We did not include collinear first principal components (including 1-year lags) in the same model.

For all sets of models, we performed model selection using AIC_c (Burnham and Anderson 2002). Because there was not enough support for a single best model, we reported a confidence set of models ($w_i > 0.90$; Burnham et al. 2011). We used model averaging to calculate the relative importance of each explanatory variable as a sum of Akaike weights across all models in the confidence set that contained that variable (Burnham and Anderson 2002). We included interactions between deer density and weather recorded in winter_t, that is, when cumulative food limitations imposed by deer density and snow cover are expected to interact in affecting female body condition and eventually recruitment. We analyzed relationships between observed and predicted recruitment in top-ranked models with the Pearson correlation coefficients to quantify how well the models fit the data.

We analyzed linear relationships between local weather covariates, Pacific-based climate indices, and first principal components PC1s using the Pearson's correlation coefficient. We performed all analyses in R 3.0.2 (R Development Core Team 2011).

RESULTS

Weather and Climate Predictors of Fawn Recruitment

Based on the AIC_c of generalized additive models (Equation (1)) fitted with only 1 weather covariate, the best local weather predictors of fawn recruitment were the average minimum temperature recorded in the previous winter ($\mathrm{AIC}_c = -32.07$), and the average maximum temperature recorded during spring ($\mathrm{AIC}_c = -30.46$) and summer ($\mathrm{AIC}_c = -30.42$). These temperatures were highly correlated with the other weather covariates recorded in the same season (Table 1). Therefore, we used average minimum temperature as our winter covariate (for both winter_t and $\mathrm{winter}_{t\text{-}1}$) and average maximum temperature as our spring and summer covariates (for year_t and $\mathrm{year}_{t\text{-}1}$) when modeling fawn recruitment.

Pacific-based climate indices were strongly correlated (Table S1). Multivariate ENSO index (MEI) was positively correlated with PDO index, whereas MEI and PDO were negatively correlated with NPI (Table S1). First principal components (PC1s) resulting from the Principal Component analysis carried out on the 3 Pacific-based climate indices explained approximately 70% of variance in winter and spring (Figs. S1 and S2), and approximately 55% of variance during summer (Fig. S3). MEI and PDO always had positive loadings on the first principal component, whereas NPI had a negative loading on it. Principal components PC1s generally performed better than single Pacific-based climate indices in predicting fawn recruitment based on AIC_c values of generalized additive models (Equation (1)) fitted with only 1 climate covariate (winter PC1 $\mathrm{AIC}_c = -34.22$, spring PC1 $\mathrm{AIC}_c = -28.32$, summer PC1 $\mathrm{AIC}_c = -27.16$). Therefore, we used seasonal PC1s as candidate predictors (for both year_t and $\mathrm{year}_{t\text{-}1}$) in fawn recruitment modeling.

Relationships of Pacific-Based Climate and Local Weather Covariates

During winter (Nov–Mar), PDO and PC1 values were positively correlated with warmer weather in the North Dakota badlands (Table 2). The NPI index values were strongly and positively correlated with colder winters with more snow. Pacific-based indices were not correlated with winter severity index (WSI) values (Table 2). During spring (Apr–May), higher MEI and PC1 values were observed during drier weather in the North Dakota badlands (Table 3). The PDO and PC1 values were positively correlated with warmer weather, and PDO values were negatively correlated with the seasonal index harshness (winter severity index computed over the period Apr–May; Table 3). During summer (Jun–Sep), correlations between Pacific-based

Table 1. Correlation coefficients between the best seasonal local weather predictors of mule deer fawn recruitment (rows: average min. temperature recorded in winter, and max. temperature recorded in spring and summer) and the other local weather covariates recorded during the same seasons. Data were collected by the Medora weather station (1956–2012), North Dakota, centrally located in the mule deer study area. Among local weather covariates, best seasonal predictors of fawn recruitment (rows) were those that were included in the generalized additive model with the lowest Akaike's Information Criterion corrected for small sample size (AIC_c) values.

Season	Covariate	Average min. temperature (°C)	Average max. temperature (°C)	Average precipitation (mm)	Average snowfall (mm)	Average snow depth (mm)	WSI^{a}
Winter	Average min. temperature °C		0.79*	−0.28*	−0.41*	−0.58*	−0.75*
Spring	Average max. temperature °C	0.52*		−0.45*	−0.46*	−0.48*	−0.44*
Summer	Average max. temperature °C	0.44*		−0.45*	^{b}	^{b}	^{b}

[a] Winter severity index (computed over the period Nov–Mar for winters, Apr–May for springs).

[b] Snowfall never occurs from July to August and was a rare event in June and September.

[*] Indicates significant Pearson correlations ($P < 0.05$).

Table 2. Correlation coefficients between Pacific-based climate predictors (rows) and local weather covariates (columns) during winter. Local weather data were collected by the Medora weather station, North Dakota (1956–2012), centrally located in the mule deer study area.

Climate index[a]	Average min. temperature (°C)	Average max. temperature (°C)	Average precipitation (mm)	Average snowfall (mm)	Average snow depth (mm)	WSI[b]
MEI	0.24	0.19	−0.14	−0.14	−0.05	−0.01
NPI	−0.38*	−0.35*	0.24	0.30*	0.14	0.10
PDO	0.29*	0.14	0	0	−0.09	−0.07
PC1	0.36*	0.27*	−0.15	−0.17	−0.11	−0.07

[a] MEI, multivariate ENSO index; NPI, North Pacific index; PDO, Pacific decadal oscillation; PC1, first principal component resulting from the principal component analysis carried out on MEI, NPI, and PDO Pacific-based climatic indices.

[b] Winter severity index (computed over the period Nov–Mar).

* Indicates significant Pearson correlations ($P < 0.05$).

indices and local weather covariates were weaker compared to other seasons. The MEI and PC1 values were correlated with precipitation (Table 4).

Modeling Fawn Recruitment From Local Weather and Pacific-Based Climate Indices

Based on relative importance in the confidence set of generalized additive models ($w_i > 0.90$) of the effect of seasonal local weather on fawn recruitment (Table 5), deer density, winter$_t$ average minimum temperature, and spring$_{t\text{-}1}$ average maximum temperature had the strongest relationship with mule deer fawn recruitment. Mule deer density recorded in spring was inversely related to fawn recruitment recorded in fall (Fig. 3a).

Predicted recruitment recorded during the 1960s (low mule deer density, approx. 1 deer/km^2) ranged from approximately 1.1 fawn per female, when temperature recorded during the winter prior to the birth of fawns was lower than −16° C, to 1.4 fawns per female when winter temperatures were at least 4° C warmer (Fig. 3b). Recruitment recorded during the early 2000s (high mule deer density, approx. 3.2 deer/km^2) ranged from 0.6 to 0.9 fawns per female when temperatures recorded during the winter prior to the birth of fawns were −16° C and −8° C, respectively. This suggests a weak interaction between winter harshness and deer density that was retained by the second-ranked model ($\Delta\text{AIC}_c = 2.40$), but not by the top-ranked one. The lowest recruitment rates were predicted when cold winters prior to the birth of fawns (winter$_t$) and cold springs 1 year earlier (spring$_{t\text{-}1}$) were recorded (Fig. 4). Weather conditions recorded in the other seasons (year$_t$ and year$_{t\text{-}1}$) had little importance on the confidence set of models and weak effects on fawn recruitment (Table 5).

The AIC$_c$ of the most parsimonious model using Pacific-based climate predictors ($\text{AIC}_c = -34.22$; Table 6) was more than 10 AIC$_c$ points larger than the top-ranked model using local weather covariates ($\text{AIC}_c = -45.36$; Table 5). This indicates that local weather is a better predictor of deer recruitment compared to Pacific-based climate. However, at more than 2,000 km from the Pacific coast, large-scale Pacific-based climatic indices remarkably explained a substantial proportion of the variability in recruitment. The Pacific-based climate index that had the strongest relationship with mule deer fawn recruitment was the one recorded during the winter prior to the birth of fawns (winter$_t$ first principal component PC1; Table 6). Similar to when using local weather predictors, deer density was related to recruitment, and its interaction with winter harshness was included in the second ranked model ($\Delta\text{AIC}_c = 1.06$). Fawn recruitment in October increased when April deer density decreased (Fig. 5), as well as when winter$_t$ PC1 increased. Increased winter$_t$ PC1 corresponds to higher MEI and PDO and lower NPI values, that is, warmer, drier, and less snowy winters. Pacific-climate indices recorded in the other seasons (Table 6) had little importance on the confidence set of models and weak effects on fawn recruitment.

Autocorrelation plots for the residuals of top-ranked models revealed 1-year time lag autocorrelation in the residuals of our models (Fig. S4). We inspected relationships between observed and predicted mule deer recruitment in

Table 3. Correlation coefficients between Pacific-based climate predictors (rows) and local weather covariates (columns) during spring. Local weather data were collected by the Medora weather station, North Dakota (1956–2012), centrally located in the mule deer study area.

Climate index[a]	Average min. temperature (°C)	Average max. temperature (°C)	Average precipitation (mm)	Average snowfall (mm)	Average snow depth (mm)	WSI[b]
MEI	0.15	0.22	−0.27*	−0.03	−0.06	−0.11
NPI	−0.12	−0.18	0.25	0.13	−0.05	0.05
PDO	0.22	0.26*	−0.25	0.06	0.05	−0.27*
PC1	0.20	0.27*	−0.31*	−0.04	0.01	−0.17

[a] MEI, multivariate ENSO index; NPI, North Pacific index; PDO, Pacific decadal oscillation; PC1, first principal component resulting from the principal component analysis carried out on MEI, NPI, and PDO Pacific-based climatic indices.

[b] Winter severity index (computed over the period Apr–May).

* Indicates significant Pearson correlations ($P < 0.05$).

Table 4. Correlation coefficients between Pacific-based climate predictors (rows) and local weather covariates (columns) during summer. Local weather data were collected by the Medora weather station, North Dakota (1956–2012), centrally located in the mule deer study area.

Climate index[a]	Average min. temperature (°C)	Average max. temperature (°C)	Average precipitation (mm)
MEI	0.18	−0.11	0.29*
NPI	−0.16	−0.02	0.01
PDO	0.19	−0.02	0.22
PC1	0.23	−0.07	0.27*

[a] MEI, multivariate ENSO index; NPI, North Pacific index; PDO, Pacific decadal oscillation; PC1, first principal component resulting from the principal component analysis carried out on MEI, NPI, and PDO Pacific-based climatic indices.

* Indicates significant Pearson correlations ($P < 0.05$).

top-ranked models to verify goodness of fit in our models (Fig. S5). Generalized additive models fit the data well with predicted and observed recruitment rates highly correlated (model fit with local weather data: $r_p = 0.83$, $P < 0.001$; model fit with Pacific-based climate: $r_p = 0.71$, $P < 0.001$).

DISCUSSION

We found evidence for a density-dependent regulatory effect of fawn recruitment in the North Dakota badlands, with deer density recorded during female pregnancy being inversely related to fall recruitment. Density-dependent effects are expected to be manifested principally through intraspecific competition, body condition, and fecundity of females (Stewart et al. 2005, Bergman et al. 2015). Using deer density to control for the density-dependent effect, we were able to examine how seasonal weather relates to fawn recruitment. Our first hypothesis related to the differential effects of weather in different seasons on mule deer recruitment was supported. We found that winter weather recorded prior to the birth of fawns (winter$_t$) was a factor related to autumn fawn/female ratios. Weather conditions recorded during (spring$_t$) and after (summer$_t$) birth were found to have no significant effect. Our second hypothesis relating to the time-lag effects of weather on recruitment also was supported, with conditions recorded during the spring 1 year prior to births (spring$_{t-1}$) likely affecting female body conditions and eventually recruitment.

Surprisingly, Pacific-based climate indices were correlated with local weather even in this area of the Great Plains >2,000 km distant from the ocean, supporting our third hypothesis. Finally, Pacific-based climate had the ability to predict recruitment, even though its predictive ability was lower compared with local weather data. This suggests that broad-scale indices may provide a good alternative to predicting fawn recruitment when local weather data are not available.

Mule deer occur across much of North America, ranging from the northern Yukon Territory of Canada to central Mexico and from the 100th Meridian west to the Pacific coast (Forrester and Wittmer 2013). The species occupies a wide range of habitats including prairie in the east, woodlands and all forest types of the Rocky Mountains in the northwest, and the desert scrub in the southwest (Wallmo 1981). Mule deer habitats generally are characterized by early stages of plant succession, mixed plant communities and available browse (Baker et al. 1979, Carpenter et al. 1979, Wallmo 1981). Forage species may suffer from summer drought with consequences on fawn survival at least in the southern and western areas of mule deer range (Hurley et al. 2011). However, according to our results, summer drought does not seem to be a limiting factor for mule deer in the North Dakota badlands. Recent research has suggested that high winter snowfall can lower winter fawn survival across almost the entire mule deer range (Forrester and Wittmer 2013), with little evidence that summer precipitation affects survival in the following year; this also may suggest that increases in summer forage

Table 5. Confidence set of generalized additive models (cumulative weight: $w_i > 0.90$) predicting the effect of seasonal local weather on mule deer fawn recruitment in the North Dakota badlands (1962–2012) obtained from a starting set of 35 a priori models (including a null model: $\text{AIC}_c = -4.37$, $\Delta\text{AIC}_c = 41.0$). Our representative covariate for winter was average minimum temperature and our representative covariate for spring and summer was average maximum temperature. We investigated seasonal weather covariates from the current year (t) and the previous year (t-1). Models are ordered according to the corrected Akaike's information criterion (AIC$_c$) with the most parsimonious model at the top. We also report degrees of freedom (df); AIC$_c$ difference between a given model *i* and the top ranked model (ΔAIC$_c$); Akaike weights (w_i); evidence ratio (ER), that is, a measure of how much more likely the best model is than model *i*; and adjusted R-squared (adj R^2).

Model structure[a]	df	AIC$_c$	ΔAIC$_c$	w_i	ER	adj R^2
Spring$_{t-1}^*$ + winter$_t^*$ + deer density*	9.3	−45.36	0	0.56	1	0.64
Spring$_{t-1}^*$ + (winter$_t$ × deer density)*	9.5	−42.96	2.40	0.17	3.3	0.63
Winter$_{t-1}$ + spring$_{t-1}^*$ + winter$_t^*$ + deer density*	10.6	−42.39	2.97	0.13	4.4	0.64
Winter$_{t-1}$ + spring$_{t-1}^*$ + winter$_t^*$ + summer$_t$ + deer density*	11.2	−41.48	3.88	0.08	7.0	0.64
Spring$_{t-1}^*$ + summer$_t$ + deer density*	7.4	−41.03	4.33	0.06	8.7	0.58

[a] Relative variable importance ($\Sigma\, w_i$):
Mule deer density: 0.83
Average min. temperature (winter$_t$): 0.77
Average min. temperature (winter$_t$) × mule deer density: 0.17
Average max. temperature (spring$_{t-1}$): 1
Average min. temperature (winter$_{t-1}$): 0.21
Average max. temperature (summer$_t$): 0.14

* Significance of smooth terms ($P < 0.05$).

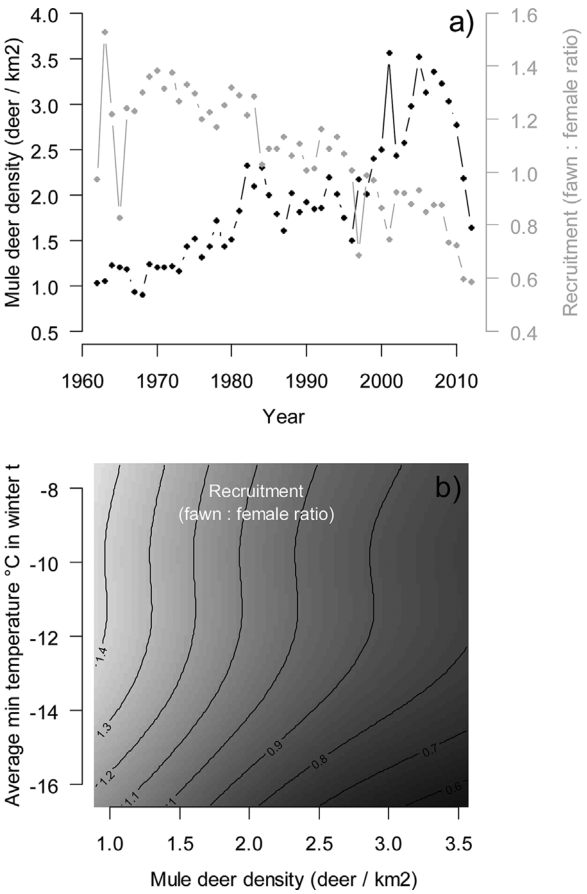

Figure 3. a) Mule deer density (deer/km^2) and fawn recruitment (fawn/female ratio) recorded by aerial surveys in the North Dakota badlands from 1962 to 2012. Deer density estimates were recorded during spring (Apr) surveys, and recruitment was estimated during fall (Oct) surveys. b) Effect of mule deer density (deer/km^2, *x*-axis) and average minimum temperature recorded during winter$_t$ (i.e., during female pregnancy prior to the birth of fawns; °C, *y*-axis) on fall fawn recruitment as predicted by the most-supported generalized additive model. Model terms not shown in the plot were kept to mean values.

following high snowfall years do not compensate for lower survival in high snowfall winters. Our models indicate that there is no detectible relationship between summer conditions and fall fawn recruitment, even when considering 1-year time lags. North Dakota badlands host one of the mule deer populations most distant from the Pacific Ocean, where long and harsh winters appear to be the most limiting season in the mule deer biological cycle; at least concerning fawn recruitment. Harsh winter conditions likely weaken female body condition in this region prior to birth. Reproductive performance of females can be strongly influenced by their physical condition and nutritional status during gestation, with potential consequences on post-partum survival of fawns (e.g., reduced fawn physical condition at birth, low quality of mothers' milk), as has been suggested for other North American populations (Torbit et al. 1985*b*, Parker et al. 1996, Bishop et al. 2009, Monteith et al. 2013, Monteith et al. 2014). Additionally, we documented a clear relationship between weather during the spring 1 year before the birth and fawn recruitment. Harsh springs (time lag year t-1) could be critical because they may make the winter much longer and further weaken females that face the next winter (the one just prior to birth) with reduced body condition. Poor nutrition or body condition in ungulates can negatively affect hypothalamic–pituitary function (Schillo 1992, Wade et al. 1996), inhibit ovulation (Tanaka et al. 2003), reduce pregnancy rates (Folk and Klimstra 1991, Tanaka et al. 2003, Bishop et al. 2009), increase probability of terminating pregnancy after breeding (Sosa et al. 2004), and reduce production of offspring (Adamczewski et al. 1998, Russell et al. 1998, Cook et al. 2004).

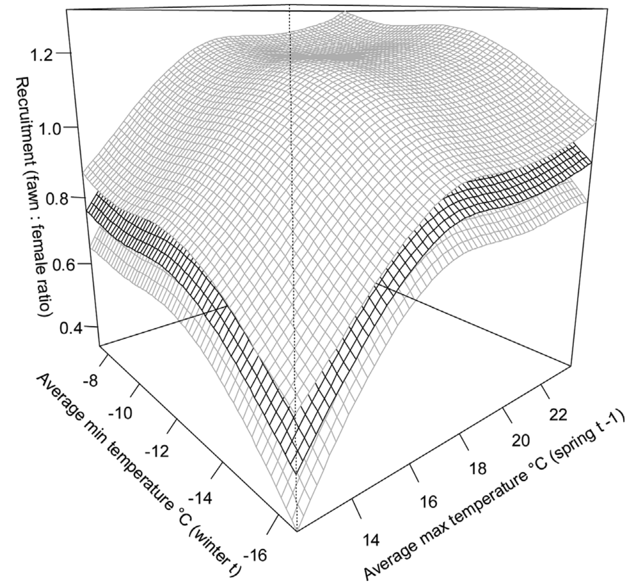

Figure 4. Effects of local weather covariates recorded during spring$_{t-1}$ (i.e., 1 year prior to the birth of fawns) and winter$_t$ (i.e., during female pregnancy) on fall mule deer fawn recruitment (fawn/female ratio) in the North Dakota badlands (1962–2012) as predicted by the most supported generalized additive model. Model terms not shown in the plot were kept to mean values. Gray surfaces are standard errors.

Interestingly, we did not find negative effects of 2 harsh winters in a row on fawn recruitment. Most likely, the first of 2 harsh winters (year t-1) negatively affects fawn recruitment, as confirmed by our analyses. This suggests compensation, for example, females that did not give birth to a fawn or lost it because of weakened body condition after the first adverse winter (year t-1), supposedly reduced their energy expenditure (no weaning) and were in a better condition to face the second harsh winter (year t). This compensation could be the reason why our analyses did not detect any cumulative effect of 2 consecutive adverse winters. In white-tailed deer, when does lost their fawns shortly before or after parturition, they quickly regained top physical condition and exhibited higher subsequent fecundity than does suckling young (Verme 1969, Mansell 1974).

Temperatures captured more variability in fawn recruitment than other metrics of local weather, such as snowfall or even more comprehensive covariates like the winter severity index. For subpopulations spread over such a large area, as is the case in our study area, 1 single weather metric (e.g., snow depth) derived from a single local weather station may not

Table 6. Confidence set of generalized additive models (cumulative weight: $w_i > 0.90$) predicting the effect of seasonal Pacific-based climate on mule deer fawn recruitment in the North Dakota badlands (1962–2012) obtained from a starting set of 29 a priori models (including a null model: AIC$_c = -4.37$, ΔAIC$_c = 29.86$). Our representative covariate for all seasons was PC1, which was generated by a principal components analysis fitted on Pacific-based indices (multivariate ENSO index, North Pacific index, and Pacific decadal oscillation). We investigated seasonal weather covariates from the current year (t) and the previous year (t-1). Models are ordered according to the corrected Akaike's information criterion (AIC$_c$) with the most parsimonious model at the top. We also report degrees of freedom (df); AIC$_c$ difference between a given model *i* and the top ranked model (ΔAIC$_c$); Akaike weights (w_i); evidence ratio (ER), that is, a measure of how much more likely the best model is than model *i*; and adjusted *R*-squared (adj R^2).

Model structure[a]	df	AIC$_c$	ΔAIC$_c$	w_i	ER	adj R^2
Winter$_t^*$ + deer density*	4.6	−34.22	0	0.20	1	0.48
(Winter$_t$ × deer density)*	4.0	−33.16	1.06	0.12	1.7	0.48
Winter$_t^*$ + spring$_t$ + deer density*	5.4	−33.02	1.20	0.11	1.8	0.48
Spring$_t$ + (winter$_t$ × deer density)*	5.4	−32.75	1.48	0.10	2.1	0.47
Winter$_{t-1}$ + winter$_t^*$ + deer density*	5.7	−32.38	1.84	0.08	2.5	0.48
Winter$_t^*$ + summer$_t$ + deer density*	6.0	−32.34	1.88	0.08	2.5	0.48
Spring$_{t-1}$ + winter$_t^*$ + deer density*	5.7	−32.08	2.14	0.07	2.9	0.47
Summer$_t$ + (winter$_t$ × deer density)*	5.6	−31.69	2.53	0.06	3.5	0.47
Winter$_{t-1}$ + winter$_t^*$ + spring$_t$ + deer density*	6.6	−31.05	3.18	0.04	4.9	0.48
Winter$_{t-1}$ + (winter$_t$ × deer density)*	5.0	−30.76	3.47	0.04	5.6	0.45
Spring$_{t-1}$ + (winter$_t$ × deer density)*	5.0	−30.70	3.52	0.03	5.8	0.45
Winter$_{t-1}$ + spring$_t$ + (winter$_t$ × deer density)*	6.0	−30.34	3.88	0.03	6.9	0.46
Winter$_{t-1}$ + winter$_t^*$ + summer$_t$ + deer density*	7.1	−30.34	3.88	0.03	6.9	0.48
Winter$_{t-1}$ + winter$_t^*$ + summer$_t$ + spring$_t$ + deer density*	8.0	−29.41	4.81	0.01	11.1	0.48

[a] Relative variable importance ($\Sigma\, w_i$):
Mule deer density: 0.63
PC1 (winter$_t$): 0.63
PC1 (winter$_t$) × mule deer density: 0.37
PC1 (spring$_t$): 0.30
PC1 (winter$_{t-1}$): 0.23
PC1 (summer$_t$): 0.18
PC1 (spring$_{t-1}$): 0.10

* Significance of smooth terms ($P < 0.05$).

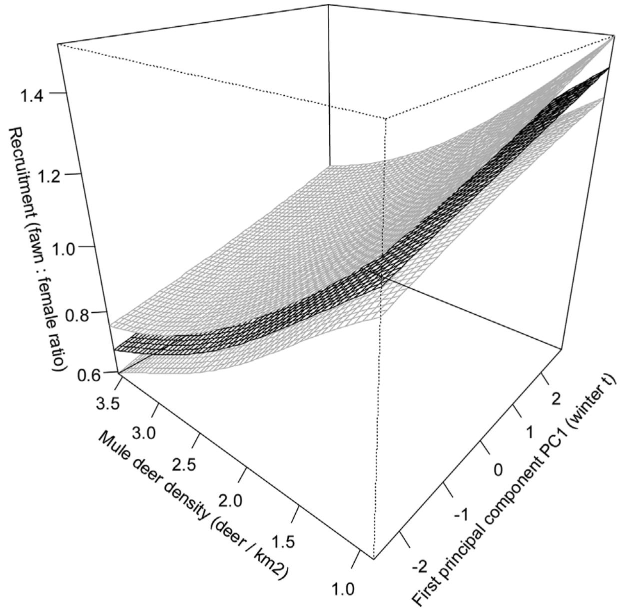

Figure 5. Effects of first principal component (PC1) computed for winter$_t$ (i.e., during female pregnancy) and mule deer density (deer/km^2) on fall fawn recruitment (fawn/female ratio) in the North Dakota badlands (1962–2012), as predicted by the most supported generalized additive model. Winter PC1 was generated by a principal components analysis fitted on winter Pacific-based indices (MEI, multivariate ENSO index; NPI, North Pacific index; PDO, Pacific decadal oscillation). Higher values of winter PC1 correspond to higher MEI and PDO values and lower NPI values, that is, warmer and drier winters. Gray surfaces are standard errors.

represent conditions experienced by all individuals. Temperature gradients are less spatially variable than snow depth or precipitation, which could be locally high at the weather station but not representative of the entire area and influenced by other parameters such as wind and freezing and thawing. Temperature gradients are better predictors of fawn recruitment, as also suggested by previous research (Melis et al. 2009; Hegel et al. 2010*a*,*b*). Bartmann and Bowden (1984) also found snow depth to have little predictive value for estimating winter mule deer mortality in Colorado, attributing this to the tempering effect of deer moving to snow-free southern slopes where forage was available. Indeed, little is known on the potential role of behavior in buffering mule deer against the effects of climate on recruitment, as suggested for other ungulate species (Long et al. 2014).

Even at more than 2,000 km from the Pacific coast, large-scale climatic indices were correlated with local weather. Pacific-based climate indices confirmed a similar scenario depicted by local weather covariates, with winter prior to birth being the limiting season that affects fawn recruitment. Although models built with ocean proxies were worse than those built with regional weather covariates, ocean proxies were able to carry the information of winter harshness that was related to mule deer recruitment in the North Dakota badlands. This opens new research and management opportunities for continental areas such as the Great Plains, where the predictive power of large-scale climate indices has been neglected because of the distance from the Pacific Ocean. Large-scale climate indices are characterized by cycles that can be predicted in advance by statistical models and can be taken into account in management plans. For example, periodic declines in carrying capacity should be anticipated by increased harvest quotas to take advantage of the interaction between density dependence and seasonal mortality (Boyce et al. 1999, Xu et al. 2005).

A typical situation in sparsely populated areas is that none or only 1 weather station may be available (Adams 2005). Pacific-based climate indices certainly open new opportunities for modeling population dynamics. On a broader perspective, large-scale climate indices can be used to anticipate the effect of weather on dynamics for those populations for which survey data are available from long-term wildlife monitoring programs (e.g., starting from the 1900s, such as in regions of US, Canada, and Europe; for Europe, see Apollonio et al. 2010), but cannot be matched with missing or incomplete local weather data. PDO metrics, for instance, are available since the year 1900. The study of the ecological effects of climate change has become a popular research topic (Both et al. 2004, Parmesan 2006), and the use of Pacific-based climate indices as predictors of climate has the potential to shed light on our understanding of the effects of climate change on large herbivores ecological patterns (Stenseth et al. 2003), including distribution and population dynamics.

Our results indicate the use of local weather data rather than ocean proxies is preferable when predicting vital rates such as deer recruitment in continental areas, especially in small-scale studies where regional weather stations can provide high-quality weather data. However, the use of ocean proxies certainly can be a new tool for managers when dealing with limited availability of local weather data. The North Dakota badlands host a continental population of mule deer that is the one of the most distant from the Pacific Ocean. Ocean proxies are expected to be increasingly more correlated with local weather moving from the Dakotas to the Pacific coast (see for instance strongly correlated Pacific-based indices with local weather in the Canadian Rockies at approx. 800 km from the Pacific coast; Hebblewhite 2005) and they can be considered a new tool accessible to managers in continental areas.

MANAGEMENT IMPLICATIONS

Being able to predict in advance the fluctuations in recruitment using local weather and/or broad-scale climate indices opens new opportunities and provides a tool for setting harvest quotas. For instance, in our mule deer study population, the North Dakota Game and Fish Department has well-established hunting units and regulates numbers of permits in each unit annually. The numbers of permits are governed by the previous years' harvest data, spring and fall aerial surveys, and estimated annual recruitment. Quotas for hunter harvest could be adjusted based on winter harshness (e.g., average minimum temperature recorded from Nov to Mar) and deer density. Such predictions could be formulated further in advance considering the degree of predictability of broad-scale climate indices. Managers might decide, for instance, to increase the number of female tags available to hunters in anticipation of a particularly harsh winter predicted to hit the deer population. We stress that conservation and management agencies should be aware of the importance of being proactive in management, of the value of maintaining long-term dataset, and the need to continually re-evaluate harvest plans, switching from a fixed to an adaptive harvest management system. Time series can be re-evaluated annually after updating with new data to anticipate future population dynamics prior to making decisions on harvest management.

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