

Effects of climate change on long-term population growth of pronghorn in an arid environment

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Abstract. Climate often drives ungulate population dynamics, and as climates change, some areas may become unsuitable for species persistence. Unraveling the relationships between climate and population dynamics, and projecting them across time, advances ecological understanding that informs and steers sustainable conservation for species. Using pronghorn (*Antilocapra americana*) as an ecological model, we used a Bayesian approach to analyze long-term population, precipitation, and temperature data from 18 populations in the southwestern United States. We determined which long-term (12 and 24 months) or short-term (gestation trimester and lactation period) climatic conditions best predicted annual rate of population growth (λ). We used these predictions to project population trends through 2090. Projections incorporated downscaled climatic data matched to pronghorn range for each population, given a high and a lower atmospheric CO₂ concentration scenario. Since the 1990s, 15 of the pronghorn populations declined in abundance. Sixteen populations demonstrated a significant relationship between precipitation and λ , and in 13 of these, temperature was also significant. Precipitation predictors of λ were highly seasonal, with lactation being the most important period, followed by early and late gestation. The influence of temperature on λ was less seasonal than precipitation, and lacked a clear temporal pattern. The climatic projections indicated that all of these pronghorn populations would experience increased temperatures, while the direction and magnitude of precipitation had high population-specific variation. Models predicted that nine populations would be extirpated or approaching extirpation by 2090. Results were consistent across both atmospheric CO₂ concentration scenarios, indicating robustness of trends irrespective of climatic severity. In the southwestern United States, the climate underpinning pronghorn populations is shifting, making conditions increasingly inhospitable to pronghorn persistence. This realization informs and steers conservation and management decisions for pronghorn in North America, while exemplifying how similar research can aid ungulates inhabiting arid regions and confronting similar circumstances elsewhere.

Key words: *Antilocapra americana*; climate change; density dependence; integrated Bayesian population models; large herbivores; population dynamics; rainfall effects; southwestern United States; standardized precipitation index.

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INTRODUCTION

Variations in climate affect the growth, development, fecundity, and demographic trends in ungulates, thereby driving their population dynamics (Sæther 1997, Post and Stenseth 1999). Unravelling such relationships between species and climate provides critical information for advancing ecological understanding and targeting management actions. Ecologically, as climates change, some areas may become unsuitable for species that historically inhabited them (Luo et al. 2015). These species must move elsewhere or perish (see Minter and Collins 2010). Therefore, understanding the relationships between climate and a species' ecology helps wildlife managers formulate conservation strategies. For example, any resources put towards conserving a species in an area that is projected to become unsuitable, may only delay the inevitable population declines, thereby risking unwise conservation investments. Sustainable approaches would focus effort on the locations where habitat conditions will remain viable, or where new habitats may arise (or could be restored), to ensure that enough, quality habitat persists for the species. By doing so, the conservation and management strategies that biologists pursue, and the locations where they work, align with the climatological, and hence ecological, trajectory of a site. Clearly, identifying which climatic drivers affect populations most, and resolving how and where they operate now and into the future, will provide ecologists and management professionals the necessary information to inform and steer species conservation.

Biologists have already documented the effects of climate change on ungulates. In northern Europe, increasingly warm and wet winters led to a decrease in body mass of red deer (*Cervus elaphus*), reducing their survival and reproductive success (Post et al. 1997). In Alaska, earlier onset of plant emergence from warmer springs reduced calving success in caribou (*Rangifer tarandus*), due to trophic and spatial asynchrony (Post et al. 2008). Adult survival rates in moose (*Alces alces*) decreased with increasing ambient temperatures, resulting in lower moose densities, and ultimately, a northward shift in the southern boundary of their distribution (Lenarz et al. 2009, Dou et al. 2013). Lastly, in a study encompassing

16 populations of seven ungulates, Post and Stenseth (1999) revealed that large-scale climatic variability influenced growth, development, and fecundity of these species, which led to declines in 14 of the populations.

Most studies investigating climatic effects on ungulates occurred in northern and temperate climates. Ungulates in southern climates face unique challenges, especially across the arid southwestern United States (hereafter the "Southwest"), where density-independent factors drive ungulate populations (Hailey et al. 1966, Beale and Smith 1970, Bright and Hervet 2005, Marshal et al. 2009). Indeed, it is widely recognized that climate in this region is growing warmer, and in some areas drier (Garfin et al. 2013), which reduces quality and quantity of forage, thereby exacerbating ungulate declines. Here, the pronghorn (*Antilocapra americana*), a native ungulate representing a unique genus, serves as an ideal ecological model for investigating impacts of climate change on ungulate population dynamics. Pronghorn inhabit diverse environments spanning 23° latitude (Wildlife Management Institute 2001), with their populations often exhibiting large fluctuations (Nelson 1925, Trippensee 1948, Yoakum 1986) due to climatic and habitat variability (especially severe droughts and winters; O'Gara 1999), and a high reproductive capacity (Canon et al. 1997, O'Gara 1999), which enables pronghorn to rebound from significant population reductions. Despite this, pronghorn numbers have declined since the 1980s (Yoakum et al. 1999, O'Gara 2000, Wildlife Management Institute 2001). In part, their population declines appear to correspond with pronghorn requiring a high-quality diet (Hofmann 1985). Hence, pronghorn populations are sensitive to even slight changes in forage conditions (Brown et al. 2006), which as above, are climatically induced (Prato 2009).

In the Southwest, mean annual temperature increased 1.6°C from 1901 to 2010, and paleoclimatic reconstructions suggest that since 1950, temperatures are warmer than any other period in the past 600 years (Garfin et al. 2013). Although the Southwest experienced little change in annual precipitation in the past century, spatial extent of drought over this region from 2001 to 2010 was the second largest observed for any decade since 1901 (Garfin et

al. 2013). Such climatic changes can alter hydrologic, nutrient, and carbon cycles, changing the availability of water, energy, and nutrients, and thereby altering the forage base for animals (Prato 2009). Previously, such effects have been demonstrated with populations of desert bighorn sheep (*Ovis canadensis*) and pronghorn in the Southwest (McKinney et al. 2006, Simpson et al. 2007, McKinney et al. 2008, Marshal et al. 2009).

Our study had two objectives. First, we identified and quantified relationships between past trends in pronghorn populations and climate at a local scale (i.e., population level). We used a Bayesian approach to analyze long-term data from 18 pronghorn populations spanning the Southwest, to identify which climatic factors predicted the annual rate of population growth. Our approach focused on temporal changes in temperature and precipitation, and incorporated key periods in the annual female reproductive cycle (e.g., lactation, gestation). Our results identified the extent of population increases and declines for pronghorn in the Southwest, and the causal, climatic factors that best explain them. Second, we coupled these models of pronghorn population growth with downscaled projections of the explanatory climate variables to forecast long-term population trajectories for each of these populations over the coming century. With the exception of Wang et al. (2002), we are unaware of other studies that modeled the effects of long-term inter-annual variability in temperature and precipitation on ungulate populations, and then incorporated climate projections to estimate their future populations.

Our approach places individual population management in context with abiotic changes occurring at a landscape scale. By examining multiple sites, we identified commonalities and differences between pronghorn population trajectories and the explanatory factors driving these populations throughout the Southwest. This process allowed us to identify which pronghorn populations are likely to remain sustainable over time, and which are predicted to experience rapid declines culminating in extirpation.

METHODS

Study area

The study area was in the southwestern United States in Utah, Arizona, New Mexico, and western Texas, encompassing a total area of about 1.1 million km². Approximately 300,000 km² are considered pronghorn range, which is characterized by short to mixed grass, mixed grass-shrub, and desert habitats (Yoakum 1972), at elevations between about 1,000 and 2,500 m (Yoakum 2004a:417). Climate in the study area is semi-arid to arid with mean annual precipitation ranging from 310 mm in Utah to 456 mm in west Texas, with the majority of precipitation occurring in winter and summer (National Oceanic and Atmospheric Administration 2014). Mean annual temperature in the study area ranges from 9.2°C in Utah to 18.0°C in west Texas, with mean winter temperatures between -2.1°C and 8.8°C, and mean summer temperatures between 20.9°C and 27.3°C. Temperatures in the Southwest commonly reach below 0°C in winter and above 40°C in summer.

Population data

Long-term data from annual aerial surveys of 18 pronghorn populations were analyzed (Table 1). Based on availability and resolution of population survey data, modeled populations were delineated by single survey units in New Mexico ($n = 6$), single wildlife management units in Utah ($n = 5$), and amalgamations of game management units in Arizona ($n = 5$; Fig. 1). Arizona game management units were consolidated according to physical barriers (e.g., rivers, canyons, mountain ranges, interstate highways, etc.), variation in precipitation patterns, and/or availability of population data. Currently, Texas pronghorn are separated into two disjunct populations.

Annual rate of population growth (λ) was calculated as the response variable. This is a useful metric for evaluating population performance because it summarizes survival and recruitment rates and can be used for open populations (Nichols and Hines 2002). When population-specific harvest and translocation data were available, population estimates for calculating λ were adjusted according to the following equation:

Table 1. Modeled pronghorn populations in the southwestern United States.

Population	Survey period†	Population range	Area (km ²)	Population change (%)‡
Utah				
Northwest	1977–2011	64–584	779	–68
West	1978–2013	130–2034	5,425	+58
East	1977–2013	133–929	1,884	–28
Southeast	1977–2013	49–197	420	–44
South-central	1977–2013	512–2232	911	–12
Arizona				
Northwest	1976–2013	74–619	3,816	–34
Central	1961–2013	1,663–5,802	22,355	–55
East-central	1961–2013	391–2,808	13,714	–27
Southeast–N10	1961–2013	29–314	1,365	–69
Southeast–S10	1961–2013	13–420	1,044	–50
New Mexico				
Northeast	1992–2008	1,327–2,828	797	–27
East	1985–2009	64–239	816	+99
East-central	1980–2005	90–423	384	–38
West-central	1993–2011	210–576	802	–15
South-central	1994–2014	49–506	1,469	–80
Southwest	1990–2011	86–240	469	–33
Texas				
Trans-Pecos	1977–2013	2,751–17,226	21,780	–79
Panhandle	1977–2013	2,568–12,809	45,334	+324

† Population surveys conducted in summer in Arizona and Texas, in spring in New Mexico, and in winter in Utah. New Mexico switched to summer composition surveys in 2010. Utah switched to spring surveys in 2009.

‡ Period from early 1990s to start of population projections.

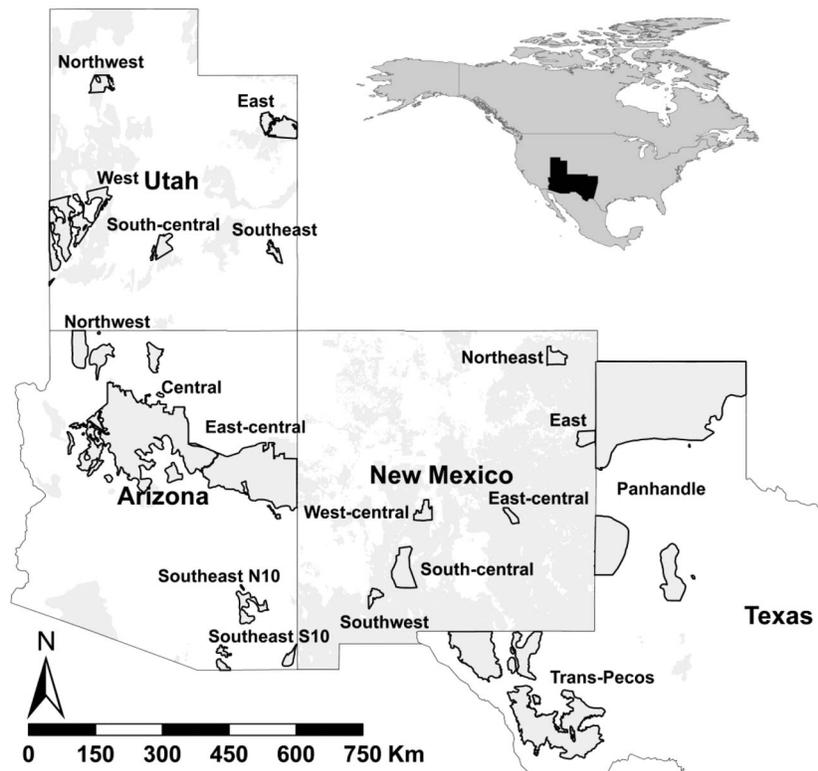


Fig. 1. Pronghorn range (grey shading) and populations modeled in the southwestern United States. Pronghorn ranges do not appear continuous across state borders because they were estimated separately by each state agency.

$$\lambda_t = \frac{N_t}{N_{t-1} - h - r + a} \quad (1)$$

where λ_t is population change from time $t - 1$ to t , N_t and N_{t-1} are population estimates from current and previous surveys, respectively, h is number of pronghorn harvested, and r and a are number of individuals removed from and released into the population, respectively, through translocations. Only population estimates from surveys conducted in consecutive years were used to calculate λ . If $\lambda \geq 2$, the associated surveys were removed from analyses because λ would be considered to be derived from unreliable or unstandardized population estimates, resulting in biologically unrealistic population growth rates. With the exception of New Mexico South-central, population-specific harvest and translocation data were not available for New Mexico, and thus, were unaccounted for in these models.

Climate data

Monthly climate data (precipitation [mm/day] and mean temperature [°C]) were derived from historical and future simulations from the World Climate Research Programme's Coupled Model Intercomparison Project phase 5 (CMIP5) Global Climate Models (GCM) subset from the National Center for Atmospheric Research Community Climate System Model version 4 (Maurer et al. 2014). Comparisons of GCM historical simulation results with observations often show biases, which may vary by location and/or season. A monthly bias-correction and spatial disaggregation (BCSD) statistical downscaling technique was used to correct for such biases (Wood et al. 2004, Maurer 2007). Model evaluations demonstrated that results from downscaling algorithms were in good agreement with observations, with precipitation and average surface temperature biases of ± 0.04 mm/day and $\pm 0.05^\circ\text{C}$, respectively, for all values for all time steps and grid cells (Brekke et al. 2013). These climate data have a 14×14 km grid resolution, and within each population, data were collected only from grids that overlap pronghorn range. Means across these grids were calculated to obtain monthly values of precipitation and temperature.

The aim was to compare two realistic future global climate situations; an optimistic lower atmospheric CO_2 concentration (ACDC) scenario

and a pessimistic high ACDC scenario. Therefore, our climate projections were modeled with data derived from the BCSD CMIP5 Representative Concentrations Pathways (RCP) 4.5 and 8.5 (Moss et al. 2010, van Vuuren et al. 2011). These scenarios attempt to account for external factors that have affected climate in the past, since GCMs calculate their own internal patterns of natural variability. External factors include the forcing of greenhouse gases, aerosols, and reactive species from anthropogenic emissions, changes in solar output, particulate emissions from volcanic eruptions, and changes in tropospheric and stratospheric ozone (Hayhoe and Stoner 2014). The RCP8.5 pathway represents a comparatively high ACDC scenario of continued global dependency on fossil fuels, whereby ACDC approaches 2.5 times current levels by 2100 (Riahi et al. 2011). The RCP4.5 pathway represents a lower ACDC scenario, whereby there is an increase of about 60% in ACDC by mid-century, followed by a decline to near 1990 levels by 2100 (Thomson et al. 2011).

A drought index was also tested as an additional measure of precipitation for predicting pronghorn population dynamics; Standardized Precipitation Index (SPI; McKee et al. 1993, Guttman 1999). The SPI represents the number of standard deviations that observed cumulative precipitation deviates from the long-term climatological average. SPI for 3-, 6-, 12-, and 24-month periods were calculated from all available monthly precipitation data in the BCSD CMIP5 climate dataset using program SPI SL 6 (National Drought Mitigation Center 2014).

Monthly mean temperature, total precipitation, and mean SPI (3-, 6-, and 12-month periods) were summarized by important periods in an adult female's annual reproductive cycle relative to peak fawning (i.e., early, mid-, and late gestation [3 months each] and lactation [4 months]). Peak pronghorn fawning is usually over three weeks during the early growing season, with the majority of births occurring within a ten day period (Autenrieth and Fichter 1975). In our study area, fawning peaks in mid-April in southern Arizona, in mid-May in northern Arizona and Texas Trans-Pecos, and in late May in Utah, New Mexico, and Texas Panhandle (Buechner 1950, Larsen 1964, Canon 1993, Ticer et al. 2000, Miller and Drake 2006; J.

Weaver, *personal communication*; A. Aoude, *personal communication*). Mean temperature and total precipitation were also calculated for 12 and 24 months preceding each population survey. Climate data were summarized over several time periods (overall and in relation to reproductive seasons) to increase the likelihood of using climate covariates with the highest predictive power when projecting populations (see next section). All data were scaled prior to analysis by subtracting the mean and dividing by standard deviation (Gelman and Hill 2007).

Population models

Bayesian inference was used to estimate parameters from regressions using a Markov Chain Monte Carlo (MCMC) technique by creating models in R 3.0.2 (R Core Team 2013) and running them in OpenBUGS 3.2.3 (Lunn et al. 2009) using R2OpenBUGS (Sturtz et al. 2005). Lambda was modeled as a log-linear function with an uninformative $N(0, 100)$ prior assigned to regression coefficients and $G(0.001, 0.001)$ assigned to hyperparameters. Model convergence was assessed in OpenBUGS using the Brooks-Gelman-Rubin diagnostic tool (Gelman and Rubin 1992, Brooks and Gelman 1998) after simultaneously running two Markov chains with different initial values. For each model, 20,000 MCMC iterations were run with the initial 10,000 MCMC samples discarded as burn-in. An information-theoretic approach was used, whereby competing models were ranked by their deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC measures the fit of the model to the data, with a penalty for model complexity, and models within 2 DIC units of the most parsimonious model (i.e., the model with the lowest DIC value) are considered to have higher predictive value than those >2 DIC units from the best-fit model (Burnham and Anderson 2002, Spiegelhalter et al. 2002).

Single climate covariate models were run first to determine which of the individual precipitation and temperature covariates strongly supported these data (i.e., covariates from all models with $\Delta\text{DIC} \leq 2$). All models included a covariate for density effect (i.e., population in the previous year). Precipitation and temperature model comparison sets were run separately, and each model set included a null model (i.e., only density

covariate, no climate covariates). These top individual precipitation and temperature covariates were then combined in models (i.e., one precipitation and temperature covariate per model), and these combined models were run including a term for the interaction between precipitation and temperature (Eq. 2). Competitive models (with precipitation and temperature alone or in combination) had $\Delta\text{DIC} \leq 2$ from the model with lowest ΔDIC .

$$\ln(\lambda_t) = \beta_0 + \beta_1 X_{N[t-1]} + \beta_2 X_{prec} + \beta_3 X_{temp} + \beta_4 X_{prec \times temp}. \quad (2)$$

If the best-fit model from the individual precipitation or temperature model set was not within 10 DIC units of the best-fit model from the other individual model set, the covariate with the higher DIC was removed from further analyses and populations were projected with only one climate covariate. If there was no statistically significant relationship between any climate covariates (individually or combined) and λ_t , projection models were not run for that population.

In an effort to maximize predictive power when making pronghorn population projections, the combined model (or in some cases, single climate covariate model) with the lowest DIC was selected to embed in the projection model, even if this model performed only slightly better than the next best model. The selected model was then run with the corresponding projected climate data derived from the BCS5 CMIP5 RCP4.5 and RCP8.5 datasets to predict λ_t . Annual pronghorn population sizes to the year 2090 were then projected with λ_t using an integrated modeling approach (Schaub and Abadi 2011), whereby population projections were generated concurrently with climate parameter estimates and λ_t , such that uncertainties from these estimates were propagated into the projections. Population projection models were created in R 3.0.2 (R Core Team 2013) and run in JAGS 3.4.0 (Plummer 2003) using R2jags (Su and Yajima 2010). In the models, at each time step, the probability of population extirpation was also calculated. Population projections were made in the absence of any management intervention (e.g., harvest or translocation) and assume that pronghorn peak fawning periods will not significantly shift in response to climate change.

R 3.0.2 (R Core Team 2013) and SPSS 21.0 (IBM 2012) were used for all other statistical analyses. Means are reported with standard errors for descriptive statistics. To reduce the probability of committing a Type II error, $\alpha < 0.10$ was accepted as significant.

RESULTS

We examined how mean temperature, total precipitation, and mean SPI influenced population growth (λ) for 18 populations of pronghorn in Utah, Arizona, New Mexico, and Texas. These variables took different forms, based on time (1–2 year periods) and female reproductive periods that influenced population growth. Sixteen (89%) pronghorn populations demonstrated that precipitation was a significant predictor of annual population growth, and in 13 of these populations, temperature was also significant (Table 2). With the exception of Arizona Northwest, λ always increased with increasing precipitation. For temperature, the direction of its relationship with λ varied among populations and within periods (e.g., gestation, lactation, etc.; Table 2). Precipitation measured as a drought index (SPI) was generally a better predictor of population growth than total precipitation, appearing in 11 of the 16 significant models (Table 2). Among the precipitation covariates, seasonal precipitation seemed most important during lactation ($n = 9$), followed by early ($n = 3$), late ($n = 3$), and mid-gestation ($n = 1$; Table 2). Mean temperatures over a longer period (i.e., 12 or 24 months) were important predictors for the dynamics of five populations; however, seasonal temperatures during early ($n = 3$), mid- ($n = 2$), and late ($n = 2$) gestation, and during lactation ($n = 1$) were also important in other populations (Table 2). In Texas Trans-Pecos, total precipitation during lactation varied as a function of mean temperature over 24 months in predicting population growth (Table 2).

Climatic trends

We provide a general overview of the temperature ranges and trends spanning these populations in the Southwest. To begin, mean annual temperature was $12.0^\circ \pm 0.8^\circ\text{C}$ from 1960 to 1999. Mean temperature ranged from $4.1^\circ \pm 0.1^\circ\text{C}$ in South-central Utah to $16.3^\circ \pm 0.1^\circ\text{C}$ in Texas

Trans-Pecos. By the end of this century, mean annual temperatures are projected to rise by $2.5^\circ \pm 0.1^\circ\text{C}$ under the RCP4.5 scenario and $5.0^\circ \pm 0.1^\circ\text{C}$ under the RCP8.5 scenario (mean 2080–2099). This warming trend remains consistent across pronghorn reproductive seasons, with trends slightly greater in Utah compared to populations in the other states.

These pronghorn populations experienced a mean annual precipitation of 333 ± 19 mm for the 40-year period beginning in 1960. Precipitation ranged from 198 ± 6 mm in Utah East to 474 ± 19 mm in Texas Panhandle. Statistically, mean annual precipitation is projected to remain unchanged under both ACDC scenarios for the next century; however, this is due to the amount of annual precipitation being highly variable among these populations. Therefore, the changes projected to occur may be biologically important. For example, for each population in Utah, during the reproductive seasons most important in influencing population growth (i.e., lactation and early and mid-gestation), a negligible change in precipitation is predicted only for Northwest, whereas all other populations have projected increases of 11–28% (Table 3). In contrast, New Mexico populations are predicted to experience significant decreases in precipitation (up to 48%) during the relevant reproductive season in each population, with the exception of South-central where changes will be negligible (Table 3). In Arizona, during lactation it is expected to be drier in the south and wetter in the north, with no change in East-central, whereas central Arizona is projected to experience declines in precipitation of 24% and 36% during late gestation under the RCP4.5 and RCP8.5 scenarios, respectively (Table 3). Predicted precipitation changes on Texas pronghorn range indicate increases in Trans-Pecos of 6–15% during lactation, while conditions for the Panhandle population will be wetter (9%) under the RCP4.5 scenario and drier (12%) under the RCP8.5 scenario (Table 3).

Population predictions

Since the early 1990s, 83% ($n = 15$) of the pronghorn populations declined in abundance, whereas three populations increased in size (Table 1). Of the 16 pronghorn populations in the Southwest where climate significantly influ-

Table 2. Climate predictor regression equations used to project pronghorn populations, derived from historic climate data and pronghorn population surveys.

Population	n^\dagger	Regression equations for projections‡
Utah		
Northwest	19	$\ln(\lambda_t) = 0.04 - 0.18X_{N[t-1]} + 0.14X_{SPI03EG} - 0.06X_{TempLG}$
West	22	$\ln(\lambda_t) = 0.07 - 0.06X_{N[t-1]} + 0.09X_{SPI03MG} - 0.13X_{TempMG}$
East	23	$\ln(\lambda_t) = 0.16 - 0.09X_{N[t-1]} + 0.06X_{SPI12Lac} - 0.10X_{TempAnn12}$
Southeast	36	$\ln(\lambda_t) = -0.04 - 0.19X_{N[t-1]} + 0.11X_{PrecLac} - 0.07X_{TempAnn12}$
South-central	33	$\ln(\lambda_t) = 0.29 - 0.12X_{N[t-1]} + 0.06X_{SPI12Lac}$
Arizona		
Northwest	37	$\ln(\lambda_t) = 0.04 - 0.08X_{N[t-1]} - 0.08X_{SPI03Lac} + 0.06X_{TempAnn12}$
Central	53	$\ln(\lambda_t) = 0.13 - 0.09X_{N[t-1]} + 0.03X_{PrecLG} + 0.04X_{TempMG}$
East-central	52	$\ln(\lambda_t) = 0.19 - 0.13X_{N[t-1]} + 0.02X_{SPI03Lac} - 0.04X_{TempAnn24}$
Southeast-N10	48	$\ln(\lambda_t) = 0.06 - 0.09X_{N[t-1]} + 0.07X_{SPI06Lac} - 0.05X_{TempLG}$
Southeast-S10	48	$\ln(\lambda_t) = 0.06 - 0.11X_{N[t-1]} + 0.14X_{SPI06Lac} + 0.10X_{TempEG}$
New Mexico		
Northeast	17	$\ln(\lambda_t) = -0.02 - 0.07X_{N[t-1]} + 0.08X_{PrecLG} + 0.09X_{TempEG}$
East	17	not significant
East-central	17	$\ln(\lambda_t) = -0.04 - 0.51X_{N[t-1]} + 0.21X_{SPI03EG}$
West-central	14	not significant
South-central	19	$\ln(\lambda_t) = -0.12 - 0.28X_{N[t-1]} + 0.17X_{SPI06Lac} - 0.27X_{TempEG}$
Southwest	18	$\ln(\lambda_t) = -0.01 - 0.18X_{N[t-1]} + 0.14X_{PrecLG}$
Texas		
Trans-Pecos	36	$\ln(\lambda_t) = 0.02 - 0.14X_{N[t-1]} + 2.8X_{PrecLac} + 0.14X_{TempAnn24} - 2.8X_{PrecLac \times TempAnn24}$
Panhandle	36	$\ln(\lambda_t) = 0.09 - 0.01X_{N[t-1]} + 0.14X_{SPI12EG} + 0.08X_{TempLac}$

† Number of years modeled.

‡ Covariates used in population projection models: $N[t-1]$ = population estimate in previous year (density effect); $SPI03EG$ = Standardized Precipitation Index (SPI) over 3 months for early gestation; $TempLG$ = mean temperature during late gestation; $SPI03MG$ = SPI over 3 months for mid-gestation; $TempMG$ = mean temperature during mid-gestation; $SPI12Lac$ = SPI over 12 months for lactation; $TempAnn12$ = mean temperature over 12 months prior to population survey; $PrecLac$ = total precipitation during late gestation; $SPI03Lac$ = SPI over 3 months for lactation; $PrecLG$ = total precipitation during late gestation; $TempAnn24$ = mean temperature over 24 months prior to population survey; $SPI06Lac$ = SPI over 6 months for lactation; $TempEG$ = mean temperature during early gestation; $SPI12EG$ = SPI over 12 months for early gestation; $TempLac$ = mean temperature during lactation.

enced population growth, our models projected that nine of these will be extirpated or approaching extirpation by the end of this century from climate change under both ACDC scenarios (half of all populations; Fig. 2). In most cases, extirpation occurs within 50 years. These results are consistent across the RCP4.5 and RCP8.5 ACDC scenarios (Fig. 2). For example, among the populations predicted to disappear this century, the time step when the likelihood of extirpation exceeds the likelihood of surviving (i.e., Extirpation $P > 0.5$) occurs after an average of 54 and 48 years under the RCP4.5 and RCP8.5 scenarios, respectively. The median population trends and credible intervals tracked each other across both climatic scenarios, indicating robustness of trends irrespective of climatic severity. An exception is Arizona East-central, which will remain viable under the RCP4.5 scenario, yet under the RCP8.5 scenario, it is predicted to become extirpated (Fig. 2). Of the remaining populations, four will initially grow at the start of projections and then stabilize (Utah South-central, Arizona

Central and Southeast S10, New Mexico Northeast; Fig. 2) and two others will continue to grow through the rest of the century (Arizona Northwest, Texas Panhandle; Fig. 2).

Of the declining populations, four occur in New Mexico and Texas. Climatically, this region is generally getting hotter and drier (although this varies among the relevant precipitation variables). Increased aridity will negatively affect the significant precipitation predictors, and subsequently, population growth. In this area, New Mexico Northeast and Texas Panhandle are the only populations predicted to remain viable through the end of the century. New Mexico Northeast displayed a positive relationship with mean temperature during early gestation, and as a result, the population stabilizes under the RCP4.5 scenario (2,635 [95% credible interval 1,735–15,690] pronghorn in 2090), yet continues to increase under the RCP8.5 scenario (5,363 [2,618–44,160] pronghorn in 2090; Fig. 2). Notably, New Mexico South-central has an opposite relationship with temperature during early ges-

Table 3. Projected mean precipitation (mm; 2080–2099) under the RCP4.5 and RCP8.5 atmospheric CO₂ concentration scenarios on pronghorn range in 16 populations in the southwestern United States. Data compiled from the World Climate Research Programme's Coupled Model Intercomparison Project phase 5 Global Climate Models subset from the National Center for Atmospheric Research Community Climate System Model version 4 (Maurer et al. 2014).

Population†	Lactation ^c				Early gestation ^c				Mid-gestation ^c				Late gestation [§]			
	RCP4.5	Δ‡	RCP8.5	Δ	RCP4.5	Δ	RCP8.5	Δ	RCP4.5	Δ	RCP8.5	Δ	RCP4.5	Δ	RCP8.5	Δ
UTNW	42 (6)	13.5	56 (7)	51.4	57 (5)	-1.7	71 (8)	22.4	67 (6)	11.7	83 (10)	38.3	93 (10)	4.5	96 (7)	7.9
UTW	104 (14)	26.8	122 (11)	48.8	52 (5)	-3.7	60 (10)	11.1	51 (7)	10.9	64 (11)	39.1	74 (10)	-3.9	69 (6)	-10.4
UTE	79 (7)	11.3	86 (8)	21.1	48 (4)	-4.0	49 (7)	-2.0	39 (5)	8.3	44 (6)	22.2	59 (7)	7.3	51 (4)	-7.3
UTSE	108 (10)	17.4	117 (10)	27.2	83 (6)	9.2	73 (11)	-3.9	64 (8)	16.4	73 (12)	32.7	56 (6)	-6.7	49 (5)	-18.3
UTSC	142 (14)	22.4	148 (11)	27.6	88 (6)	10.0	88 (13)	10.0	83 (11)	16.9	98 (16)	38.0	88 (10)	-10.2	83 (7)	-15.3
AZNW	107 (12)	25.9	109 (11)	28.2	74 (8)	13.8	74 (11)	13.8	96 (14)	10.3	113 (23)	29.9	55 (8)	-19.1	54 (6)	-20.6
AZC	152 (14)	15.2	153 (13)	15.9	100 (11)	4.2	96 (14)	0.0	131 (17)	12.0	129 (25)	10.3	62 (8)	-23.5	52 (6)	-35.8
AZEC	147 (11)	8.1	136 (9)	0.0	88 (10)	-3.3	87 (12)	-4.4	72 (8)	2.9	69 (11)	-1.4	43 (5)	-17.3	33 (4)	-36.5
AZSEN10	107 (8)	-1.8	96 (7)	-11.9	125 (13)	0.8	128 (12)	3.2	81 (10)	-5.8	62 (11)	-27.9	45 (8)	-27.4	40 (8)	-35.5
AZSES10	124 (7)	-3.1	114 (6)	-10.9	154 (11)	-0.6	145 (10)	-6.5	82 (10)	-4.7	60 (9)	-30.2	45 (6)	-22.4	38 (7)	-34.5
NMNE	276 (15)	4.2	225 (13)	-15.1	54 (7)	8.0	39 (6)	-22.0	32 (3)	10.3	39 (5)	34.5	122 (8)	13.0	99 (9)	-8.3
NMEC	209 (19)	12.4	182 (15)	-2.2	48 (7)	-2.0	33 (6)	-32.7	31 (4)	10.7	29 (3)	3.6	62 (7)	14.8	41 (7)	-24.1
NMSC	168 (11)	1.8	165 (11)	0.0	53 (5)	-8.6	34 (7)	-41.4	36 (4)	-5.3	32 (5)	-15.8	22 (3)	-8.3	16 (4)	-33.3
NMSW	181 (12)	3.4	179 (12)	2.3	57 (5)	-8.1	38 (8)	-38.7	41 (5)	-6.8	39 (6)	-11.4	19 (3)	-17.4	12 (3)	-47.8
TXTP	210 (18)	14.8	194 (17)	6.0	99 (12)	2.1	86 (11)	-11.3	30 (4)	-9.1	48 (9)	45.5	42 (4)	-4.5	38 (7)	-13.6
TXPH	259 (16)	1.6	198 (20)	-22.4	71 (8)	9.2	57 (8)	-12.3	43 (5)	10.3	49 (5)	25.6	146 (12)	12.3	130 (12)	0.0

Note: Standard error of means in parentheses.

† UTNW = Utah Northwest; UTW = Utah West; UTE = Utah East; UTSE = Utah Southeast; UTSC = Utah South-central; AZNW = Arizona Northwest; AZC = Arizona Central; AZEC = Arizona East-central; AZSEN10 = Arizona Southeast-N10; AZSES10 = Arizona Southeast-S10; NMNE = New Mexico Northeast; NMEC = New Mexico East-central; NMSC = New Mexico South-central; NMSW = New Mexico Southwest; TXTP = Texas Trans-Pecos; TXPH = Texas Panhandle.

‡ Percent change from 1960–1999 period.

§ Timing of reproductive periods varies among populations; see *Methods*.

tation, and this population declines over time (a similar situation occurs in Arizona [see below]; Fig. 2). The predicted growth of the Texas Panhandle population should be viewed with caution, as the uncertainty in these projections is extremely high (Fig. 2).

In Arizona, the two populations projected to disappear (East-central [RCP8.5] and Southeast N10) differ from the other three populations, which will remain viable, in their negative relationship between temperature and λ . In East-central, the RCP4.5 scenario predicted that the population should persist through 2090,

stabilizing at a population slightly higher than the 1,153 pronghorn in 2013 (i.e., 1,366 [0–2,544] pronghorn; Extirpation $P = 0.05$), whereas the population begins a rapid decline around 2070 and decreases to 203 (0–2,910) pronghorn in 2090 with the RCP8.5 scenario (Extirpation $P = 0.23$; Fig. 2). Of the rising populations, Arizona Central actually declined by *c.* 60% since the early 1990s. Despite this, the population was predicted to double in size over the first ten years, and reach equilibrium median populations of 5,260 (3,688–8,877; RCP4.5) and 5,540 (3,707–9,707; RCP8.5) pronghorn by 2090 (Fig. 2).

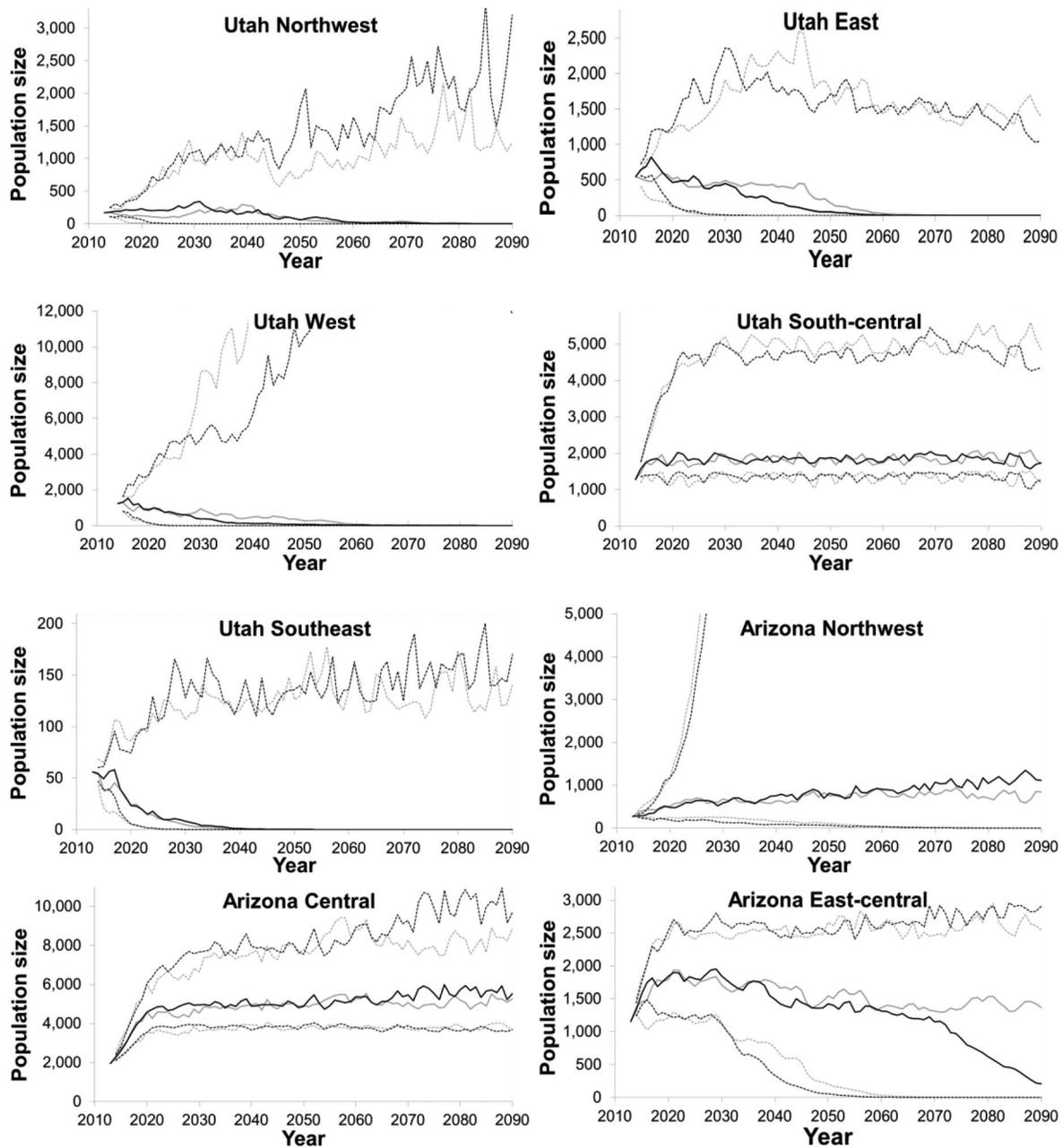


Fig. 2. Pronghorn population projections to 2090 under high (RCP8.5; black lines) and lower (RCP4.5; grey lines) atmospheric CO₂ concentration scenarios for 16 pronghorn populations in the southwestern United States. Solid lines represent estimated median populations and dashed lines represent 2.5% and 97.5% credible intervals. See Table 1 for regression equations used in these models to project populations.

Similarly, the Southeast S10 population is projected to reverse its 20-year downward trend with its population gradually increasing through the century from 192 pronghorn in 2013, to 469

(223–2,444; RCP4.5) and 850 (198–4,754; RCP8.5) in 2090 (Fig. 2).

Arizona Northwest is the only population where precipitation is negatively related to λ .

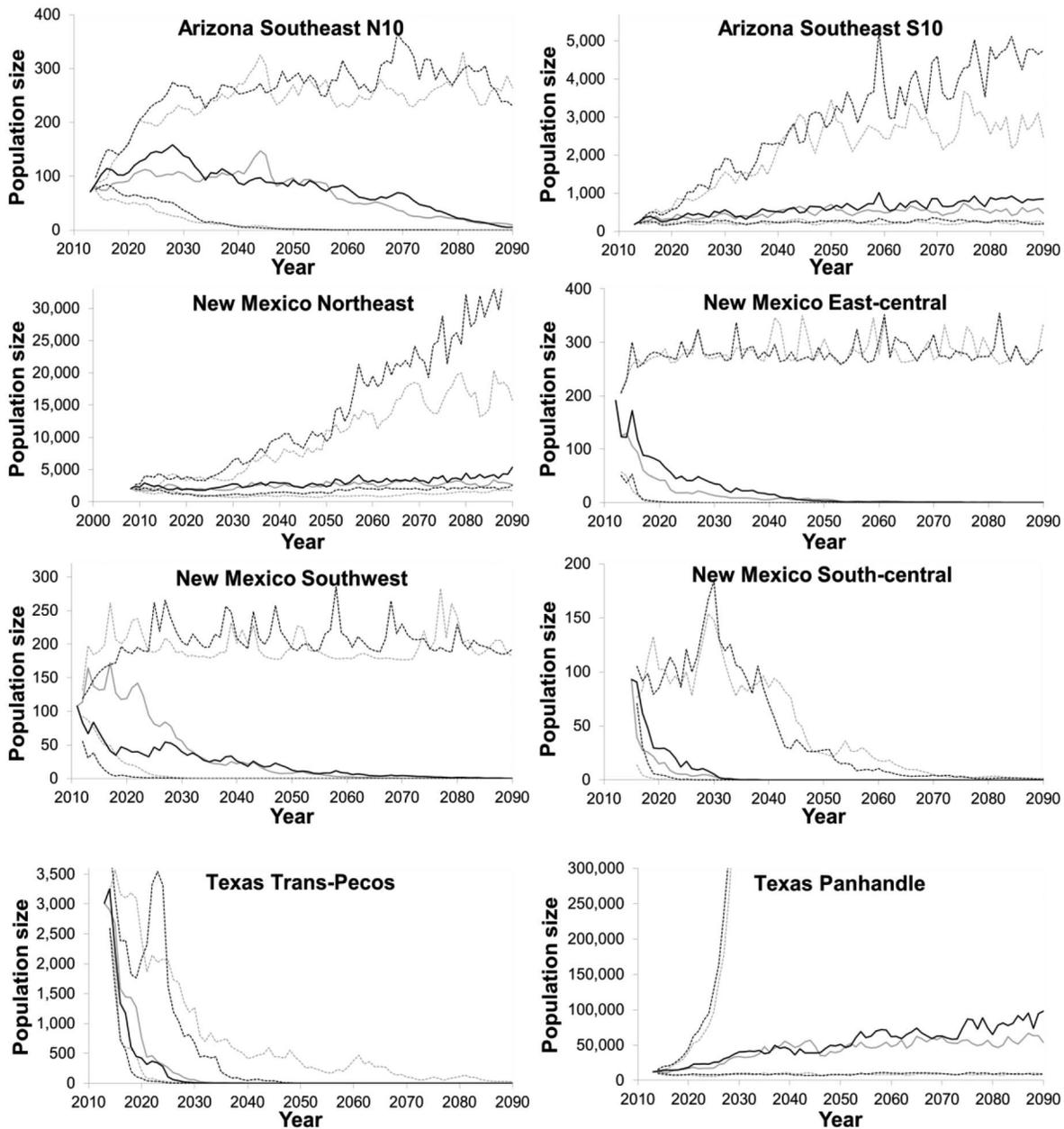


Fig. 2. Continued.

An explanation for this is not immediately apparent; however, these climate parameter estimates have high uncertainty. When these climate parameter estimates are integrated into the population projection models, very wide credible intervals around these projections result, and caution should be exercised when interpreting the predicted growth of this population (Fig. 2).

In Utah, the only population predicted to persist through 2090 was South-central. This population reached an equilibrium median population size of ~1,700 (1,197–4,849) pronghorn (initial population in 2013: 1,408 pronghorn) under both ACDC scenarios (Fig. 2). The predictive variable included a positive relationship with SPI (12 months) during lactation.

DISCUSSION

Increased temperatures and precipitation variability affect the population growth of mammals (Walther et al. 2002). Since ungulates inhabiting arid regions experience extreme climates with high inter-annual variability, they provide useful opportunities for investigating relationships between climate change and population dynamics. We focused on pronghorn, and quantified relationships between their populations and climatic variability across the southwestern United States. We found that temperature and/or precipitation influenced growth in 89% of our populations. In half of the populations, precipitation during lactation (summer) was the most important climatic variable; however, early or late gestation was also important in other populations. Temperature was an additional influence on pronghorn population growth in 81% of the significant models. The timing of temperature was typically less seasonal than precipitation, and lacked a clear pattern. In aggregate, this information leads to the conclusion that precipitation influenced the dynamics of these pronghorn populations more than temperature.

Our results correspond with previous studies involving pronghorn in the Southwest and with other ungulates elsewhere. In the Southwest, pronghorn densities were lower when spring (late gestation) precipitation was below normal (Aoude and Danvir 2002) and low summer (lactation) precipitation reduced doe abundance and fawn recruitment (Beale and Smith 1970, Brown et al. 2006, Bender et al. 2013). The most energetically demanding periods for female ungulates are late gestation and lactation (Oftedal 1985), and thus, it seems sensible that climatic factors during these periods would affect population dynamics most. Other studies on ungulate population dynamics also demonstrate the importance of precipitation during late gestation (e.g., Clutton-Brock and Albon 1989) and lactation (e.g., Milner-Gulland 1994, Solberg et al. 1999, Wang et al. 2002). Increased forage quantity and quality from increased precipitation during late gestation helps mothers meet their energy requirements during this phase of reproduction, thereby increasing the probability of birthing healthy fawns and entering lactation in good condition. More high-quality forage during lac-

tation improves female condition, which increases milk production to meet the demands of rapidly-growing neonates, and increases fawn survival. Females in better condition also have higher survival rates and are better prepared for breeding season. The lactation period is an energetically intensive season for ungulates in general, but is more pronounced in pronghorn, because they have the highest reproductive investment (i.e., proportion of neonate to adult female mass) of any ungulate species in North America (Byers and Moodie 1990). In central New Mexico, Bender et al. (2013) found that 73% of adult female pronghorn mortality occurred during lactation, and 81% of the deaths were caused by malnutrition or related digestive imbalances, which highlights the nutritional stress associated with lactation in ungulates.

Previous work also emphasizes the importance of forbs in pronghorn diets. Having a strong forb component in the vegetative mix helps sustain pronghorn populations (Yoakum 2004a), because succulent forbs during spring and summer fortify lactating females, and in turn, increase fawn survival (Ellis and Travis 1975). A limiting factor identified in much of Utah's pronghorn habitat is the lack of succulent forbs and grasses on spring and summer ranges because of xeric, low annual precipitation conditions on many of Utah's pronghorn units (Utah Division of Wildlife Resources 2009). Winter precipitation influences forb production, and pronghorn studies in Arizona and New Mexico demonstrated its importance for population growth, showing that inadequate precipitation in winter led to poor fawn recruitment (Brown et al. 2002, Bright and Hervert 2005, McKinney et al. 2008). Further, studies on other ungulates indicate a significant relationship between winter precipitation and population dynamics (e.g., Andersen et al. 1996, Aanes et al. 2000, Wang et al. 2002). Our results disagree; precipitation during mid-gestation (winter) appeared in only one of the best-fit models (Utah West). Instead, our findings suggested that precipitation in summer (lactation) had the strongest effect on pronghorn population dynamics. These are intuitive results in that, unlike in northern climates where winter severity and snow depth can be primary drivers of ungulate population dynamics (e.g., Mech et al. 1987, DelGiudice et al. 2002), summer is the more

limiting season in southern climates.

Future population trends

We coupled these model relationships between precipitation, temperature, and pronghorn population growth, with downscaled climatic predictions, to project the trajectories for 16 of these populations over the coming century. Nine of these populations declined under both ACDC scenarios, and without management intervention, are unlikely to exist past 2060 (2090 for Arizona Southeast N10). Therefore, among the projected populations, one appears to thrive (Texas Panhandle; $N > 30,000$), while six other populations remain with less than 6,000 pronghorn (with $2 < 1,000$), and the rest become extirpated (Fig. 2).

Above, we highlighted that precipitation was the important climatic factor affecting these pronghorn populations and other species inhabiting arid regions. However, our findings also indicated that when temperature was a significant predictor of annual population growth, over time its influence in the models exceeded that of precipitation. For example, all Utah populations that had a negative relationship between temperature and λ are predicted to become extirpated, despite increases in precipitation during the relevant seasons of up to 39%. In contrast, a population like Arizona Central, where precipitation during late gestation (i.e., the period that best predicts population growth) is projected to decrease 24% (RCP4.5) and 36% (RCP8.5) by the end of the century, had temperature with a significant, positive relationship with λ , and a 0% probability of extirpation. These examples demonstrate the complex interaction between temperature and precipitation in influencing ungulate population dynamics.

Increasing temperatures can have varied effects on habitat, and thus populations. For example, in autumn (early gestation) warmer temperatures can extend the growing season, while during winter (mid-gestation) when accompanied by sufficient precipitation, warming temperatures can increase winter forage and prompt earlier spring green-up; however, higher temperatures during summer (lactation) raise aridity, resulting in earlier senescence of vegetation and increases ungulate foraging time, which impacts thermoregulation strategies (e.g., Albon

et al. 1987, Langvatn et al. 1996, Wang et al. 2002). In addition to exacerbating the negative effects of changing precipitation patterns, rising temperatures can also be a direct cause of mortality, particularly in areas that experience temperature extremes. In Australian sheep (*Ovis aries*), ewes exposed to heat stress during the first 20 days of pregnancy had 100% embryo mortality (Thwaites 1967), and Wilson and Krausman (2008) found evidence suggesting that hyperthermia caused the death of some pronghorn fawns in southern Arizona.

Climate changes and population persistence

Some pronghorn populations that are projected to persist through this century (e.g., Utah South-central, Texas Panhandle, New Mexico Northeast) share a common characteristic – pronghorn range is surrounded by agricultural crops. Pronghorn often frequent these agricultural fields to the disdain of agricultural interests, and hence, local farming inadvertently subsidizes these populations with supplemental food. The climatic conditions in these populations are not markedly different from those in their surrounding populations, which are projected to decline. Hence, the conservation and management message becomes rather clear—maintaining pronghorn populations in the southwest, and delaying (or averting) their eventual extirpation, will probably involve strategies such as supplemental feeding. Indeed, restoration of the endangered Sonoran pronghorn subspecies (*A. a. sonoriensis*) in southwestern Arizona already incorporates manipulation of forage, supplemental feeding, and provision of surface water (Krausman et al. 2005). While the management intent is to supplement the population only when conditions warrant, based on the climatic projections and our results describing neighboring populations, such efforts could engender a long-term commitment.

A potential solution to the supplemental feeding issue might be achieved through improved land stewardship in areas with amenable land uses and climatic conditions. In southeast Arizona, the N10 and S10 populations, despite being adjacent to each other and predicted to experience the same temperature increases and precipitation decreases during this century, demonstrate opposite projected population trends.

This could be at least partly due to the private lands in the S10 population (predicted to increase) being managed by a landowner cooperative, whose land management practices have led to enhanced pronghorn habitat. These practices include restoration of native grassland through prescribed burning, and grass banking, whereby cattle are temporarily moved from areas experiencing severe drought to range under better environmental conditions, thereby alleviating grazing pressure on drought-stressed lands.

Generally, animals most likely affected by climate change include those with small populations and/or those limited to isolated habitats (Root and Schneider 2002). Small population sizes provide less resilience to environmental and demographic stochasticity. Seven of our modeled populations had initial sizes of less than 200 pronghorn when projections commenced, and all but one of these were predicted to disappear by the end of the century. The exception was Arizona Southeast S10 (initial population 183 pronghorn in 2013), the sole population whose growth had a positive relationship with temperature. In contrast, seven populations had more than 1,000 pronghorn at the start of projections, of which only two were predicted to fail. One of these populations (Texas Trans-Pecos: initial population size 3,016 in 2013) had already been experiencing a precipitous decline over the past six years. This suggests that a large enough population provides greater resistance to withstand extirpation when faced with a changing climate. Therefore, translocations from existing large populations might provide rescue opportunities for smaller populations. This being said, such a strategy may work now and into the near future, but as ecosystem dynamics continue shifting and habitats grow less suitable, if the forage base declines then the populations will too, irrespective of their initial size. Hence, greater population size may serve to buffer declines in the short term, but are unlikely to shield populations over the long term.

All population models included a density effect, with growth rate negatively related to population size in the previous year. Thus, pronghorn populations are driven by density-dependent and density-independent factors. Studies on other ungulates demonstrate that

these factors interact to influence demographic parameters (e.g., see Sæther 1997, Jacobson et al. 2004, Bårdsen and Tveraa 2012). In several ungulate species, the effects of climate on population dynamics occur only at high population densities (e.g., Grenfell et al. 1998, Jacobson et al. 2004). This is unsurprising, given that resource stress is the primary source of negative climatic effect on populations, and larger populations are more likely to confront resource limitations. Many of our pronghorn populations occurred at low densities (e.g., Arizona densities ranged from 0.01 to 0.40 pronghorn/km²), yet still demonstrated significant relationships between climatic factors and population growth. This suggests that resource stress may begin to manifest at lower densities in arid regions, and as such, climate change may impact these populations earlier. Further, in our study, the null models (which include only a density covariate) never outperformed any of the top models ($\Delta\text{DIC} \leq 2$) that included climate covariates. This outcome implies that within the Southwest, density-independent factors are important regulating mechanisms for pronghorn populations.

Pronghorn populations in the southwest United States are approaching the southern margin of their species range, with only 0.1% of the North American pronghorn numbers extending southward into Mexico in small, isolated populations (Gonzalez and Laffon 1993, as cited in Yoakum 2004b), Wildlife Management Institute 2001). Four of the five southernmost pronghorn populations in this study are predicted to disappear by the end of the century, and if the other small southern populations follow the same trajectory (those not modeled herein), this could essentially equate to a northward shift of the species' range. In Arizona, this could be exacerbated by the fact that a statewide evaluation of pronghorn habitat revealed that only about 1% of occupied pronghorn habitat was classified as high quality (Ockenfels et al. 1994), and it seems likely that this would diminish with climate change. This shift may not necessarily mean range contraction for pronghorn, because it could be accompanied by a shift of the northern boundary of their range as warmer temperatures make new areas suitable for pronghorn to the north. However, this may not be possible if barriers also restrict pronghorn

movements in the north, and indeed, pronghorn movements are constrained by fencing, agricultural development, and other anthropogenic activities (e.g., Hailey et al. 1966, Harris et al. 2009, Gates et al. 2012).

Climate and population data

Historic and projected climate data demonstrate the localized and highly variable patterns of precipitation, and to a lesser extent, temperature in the Southwest, highlighting the importance of using data from downscaled climate models. Among GCMs, there is consensus that temperatures will increase through this century; however, precipitation projections are much less consistent, with some GCMs predicting drier conditions and others predicting wetter conditions. This raises questions about the reliability of modeling future population dynamics based on data projected from a single climate model. The data we employed in our models came from 17 CMIP5 GCMs specific to the southwest and central regions of the United States. A more complex statistical downscaling technique was used that is capable of resolving changes in both mean values and the shape of the distribution of daily temperature and precipitation (Hayhoe and Stoner 2014). This approach has shown to significantly outperform the more simple delta downscaling method previously used (Stoner et al. 2013). These GCMs incorporated 19 ecologically-relevant bioclimate variables calculated at high spatial resolutions capable of resolving relevant scales of variability in local ecosystems (Hayhoe and Stoner 2014). Therefore, the potentially high spatial and temporal precision of the projected climate data, when combined with the integrated Bayesian approach to the modeling, minimizes the uncertainty of our projected population estimates, given the current data available.

Patterns of climate change are asymmetric, and this will undoubtedly contribute to heterogeneity in ecological dynamics across systems (Walther et al. 2002). Our study is unique in its approach by matching climate data with the specific pronghorn range in the populations investigated. Data from weather stations are highly localized (although taking means from multiple stations can help reduce this effect), whereas climate data collected from a larger-scale, more broad source,

are of low resolution and do not account for local variations in conditions. Our climate data had a 14×14 km grid resolution and was collected only on pronghorn range within the delineated populations. Therefore, our climate data corresponded with the specific area of the modeled populations, thereby increasing precision of climate relationships with specific population dynamics.

GCMs predict that variability in future climates in the Southwest will be highly seasonal, particularly in amount of precipitation and spatial distribution of precipitation events (Garfin et al. 2013). The climatic conditions in the pronghorn reproductive seasons we used agree. In all populations, precipitation predictors of λ were seasonal. Thus, when projecting populations based solely on a single seasonal climatic predictor, it is important to consider how the effect of changing conditions in one season could be offset by conditions in another season. For example, it was observed in elk (*Cervus elaphus*) that warmer, drier conditions resulting from climate change could slow population growth rates when occurring during the growing season and accelerate them when occurring during winter (Wang et al. 2002). This can result in the average annual effect being undetectable. This emphasizes the importance of how climate data are summarized, and of going beyond testing only relationships between annual precipitation and temperature, and population growth, and also examining seasons and/or biologically important periods during the year. Had we only tested annual precipitation and temperature covariates in our models, and not incorporated reproductive seasonal climate covariates, we would not have found significant relationships with λ . In contrast, other pronghorn studies in the Southwest found prolonged or severe drought (measured annually) related to increased mortality of adults and juveniles (Bright and Herver 2005). Simpson et al. (2007) found a positive relationship between long-term precipitation trends and pronghorn abundance, and short-term rainfall and fawn survival.

The predictive power of models is only as good as their data. The quality of our population data depends on standardization of survey methods, number of years, and continuity of surveys among years. For Arizona, Texas, and some Utah

populations, we analyzed over 30 years (up to 53 years) of surveys (Table 2) with few gaps in these data. In contrast, New Mexico predictions were based on < 20 years of data, often with low continuity. Consequently, New Mexico climate predictions were less consistent with the other populations, including the only two populations with non-significant relationships between climate and λ , and two of the three populations where temperature is not related to population growth. New Mexico survey data did not account for annual harvest, nor translocations (except South-central), and only allowed us to define populations based on single survey units. Pronghorn populations were often continuous across neighboring units, and thus, there was high potential for mixing of pronghorn among these units from year to year. These drawbacks likely led to diminished reliability in our λ estimates for New Mexico. Additionally, some population projections have wide credible intervals (e.g., Utah West, Arizona Northwest, Texas Panhandle), most likely due to high variability in their population data. Reducing the uncertainty in these projections would require improving pronghorn survey procedures and continuity of surveys.

Conclusions

Managing animal populations under the uncertainty of changing climates poses a daunting challenge to wildlife managers (Prato 2009). In pronghorn, the development of management plans spanning multiple populations and differing habitat conditions have mostly used inferences from single populations. Yet evidence from our work and other studies suggests that significant variation exists among the factors explaining the demography of local populations (Hoffman et al. 2010).

By examining 18 pronghorn populations across the Southwest, and using region-specific downscaled climate data aligned with the actual pronghorn ranges examined, we offered a high resolution and extensive overview that portrays and explains pronghorn population trajectories across this region. We found that while precipitation metrics formed the best predictors of population growth, temperature had the greatest influence on the future trajectory of the populations. Half of the populations were projected to

decline and become extirpated around mid-century. The climatic effects we measured are regional in scale, and experienced by the other pronghorn populations excluded from this modeling exercise. It seems reasonable then, that the relationships we uncovered between climate and λ would also apply to these populations. Hence, for many pronghorn populations, any management actions applied to avert population declines may be unsustainable over time, as climatic shifts and the habitat changes wrought, counteract human intervention. Indeed, for some of the increasing populations (e.g., in Utah, New Mexico, and Texas), growth appears to result more from unintended actions like supplemental feeding that are generally considered economically costly and problematic.

Regardless, the climatic conditions underpinning the pronghorn populations in the southwestern United States are shifting beneath them, making the ecosystems increasingly inhospitable to pronghorn persistence. Alternative management actions to enhance pronghorn habitat, such as prescribed burning and rotational livestock grazing, combined with translocations, may serve to delay pronghorn declines. However, increasingly, managers will be attempting to mitigate long-term and region-wide ecosystem changes that will be difficult, and economically challenging to forestall. Presently, there appear to be few pronghorn populations in the southwest that will persist in a natural state (i.e., lacking management intervention).

Species that are most vulnerable to extinction are those with restricted ranges, fragmented distributions, small populations, and/or those suffering population declines or habitat loss (Price et al. 2000). Such criteria describe most of the pronghorn populations in the southwestern United States examined in this study. These populations already exist in peril, at risk of local extinction even without the complexities begot from climate change. We intend for the information provided by this study, describing the effects of climate change on southwestern pronghorn, to inform decision-making for conserving and managing pronghorn in North America, and to trigger future efforts for other ungulates inhabiting arid regions and confronting similar circumstances elsewhere.

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