2024

Population Growth Rates of Pronghorn: Influence of Temporally and Spatially Explicit Conditions, Density Dependence, and Scale

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Abstract

Density-independent and density-dependent population regulation has long been a subject of investigation. We examined density-dependent and density-independent factors on growth rates of pronghorn (*Antilocapra americana* (Ord, 1815)) using a retrospective analysis of population survey data. Across Idaho, we found that as the proportion of the subpopulation harvested the previous year increased, growth rates increased. Similarly, as fawn recruitment increased, growth rates increased. We also found when the growth rate in the previous year increased, the growth rate the subsequent year decreased. When subpopulations were examined independently, we found that in a low-elevation desert subpopulation, growth rates were influenced by growth the previous year. In an agricultural-dominated site, growth rates were influenced by fawn recruitment in the current year and maximum temperature the previous fall. Growth rates in a mid-elevation shrub–steppe site were influenced by drought severity prior to parturition and the growth rates from the previous year. Growth rates in two mountain valley subpopulations were influenced by measures of vegetative greenness. At the statewide scale, while managers may strive for increased numbers of pronghorn, density dependence will limit the ability for a region-wide numerical response. On the localized scale, drivers of growth were temporally and spatially explicit, and biologists must consider site-specific actions.

Key words: *Antilocapra americana* (Ord, 1815), density dependence, environmental conditions, growth rates, pronghorn, scale

Introduction

Monitoring population trends and demographics of large ungulates is fundamental to species management and conservation (DeCesare et al. 2012). Ungulate populations may be driven by both density-independent and density-dependent factors, often with site-specific consequences (Owen-Smith 2014). Growth rates of ungulate populations may be affected by a multitude of factors, including habitat changes, severe weather (e.g., deep snow), starvation, disease, predation, human hunting, competition with other ungulates (native and domestic), changes in sex and age structure, density dependence, and interacting combinations of these factors (e.g., Sinclair 1979; Mech et al. 1987; McRoberts et al. 1995; Ballard et al. 2001; Byers and Dunn 2012). In general, density-dependent and density-independent factors can influence ungulate population growth rates directly or indirectly, either alone or in combination (Eberhardt 2002; Williams et al. 2002; Ayotte et al. 2020; Jesmer et al. 2021; Peláez et al. 2022). In addition, the shape of the functional relationship between population growth rate and population density has im-

portant consequences for population dynamics (Hassell 1975; May 1981).

Density dependence is the outcome of the effects of changes in population abundance on the vital rates of the individuals constituting the population (Owen-Smith 2014; Pearce-Higgins et al. 2015). Eberhardt (1977, 2002) suggested that for large mammals (e.g., ungulates), increased population density negatively affects juvenile survival, the age at which females first reproduce, adult fecundity, and adult survival. Juvenile survival tends to be widely variable and responsive both to changing density and to changing resource supplies, while adult survival tends to be more stable and resistant to environmental variability (Gaillard et al. 1998, 2000).

Density-independent factors (i.e., environmental or abiotic) include climatic conditions such as timing and amount of precipitation, and temperature. The degree of influence that environmental factors have on the population growth rate of ungulates does not depend on population density but rather on the severity of the climatic change (e.g., drought), the age class of the individual, and the nutritional condition of the

individual (Owen-Smith 2014; Gedir et al. 2015; Koons et al. 2015; Rattenbury et al. 2018; Yalcin and Leroux 2018). As the knowledge base of population dynamics widens, studies have indicated that some amount of interaction or combination of density-dependent factors and density-independent environmental factors can drive population dynamics (Bonenfant et al. 2009; Koons et al. 2012, 2015; Zubillage et al. 2018; Hansen et al. 2019; Hurley et al. 2020; Jesmer et al. 2021).

Pronghorn (*Antilocapra americana* (Ord, 1815)) are a small ruminant with a limited ability to digest plants with high amounts of fiber (e.g., graminoids; Hofmann 1989). Their diets are diverse and vary with the palatability, availability, succulence, and nutritional gains present in the plant species available in their environment (Yoakum 2004*a*). Additionally, pronghorn are thought to align closely with the income-breeding strategy (Clancey et al. 2012), meaning reproduction is fueled by fat reserves and energy as it is acquired (Stephens et al. 2009) and the quality and palatability of forage, as directly influenced by environmental conditions, may directly influence pronghorn population growth rates. Forage quality influences the nutritional condition of pregnant female pronghorn and subsequent birth weights and survival of their fawns (Panting et al. 2021). Coincidentally, increased forage height provides vertical structure for pronghorn neonates to hide and serves as potential thermal cover (Bodie 1979; Gregg et al. 2001; O'Gara 2004*a*; Yoakum 2004*b*; Smyser et al. 2006; Simpson et al. 2010; Bender et al. 2013; Gedir et al. 2015; Heffelfinger et al. 2018; Michel et al. 2018).

Historically, pronghorn were found throughout the central plains, western grasslands, and deserts of North America. Pronghorn are viewed as an iconic symbol of the deserts and plains of the United States and are a valued game animal for hunters. In Idaho, estimates of pronghorn numbers peaked in the late 1980s (Rachael et al. 2010). The increased abundance of pronghorn created increased crop depredations by pronghorn on local farms. Pronghorn depredation on agricultural fields led to the herds being heavily harvested to reduce numbers (Rachael et al. 2010). Since the reduction in pronghorn populations, Idaho has yet to see pronghorn numbers return to pre-control levels (Rachael et al. 2010). Gese et al. (2023) found that at mountain valley sites, survival of pronghorn fawns through the summer was reliant upon the quality of vegetation the lactating female was exposed to. Fawn recruitment at lower elevation sites was driven by several environmental conditions (i.e., normalized difference vegetation index (NDVI), drought severity, minimum and maximum temperatures, forb, and grass cover) during late gestation that would affect fawn birth weights and subsequent fawn survival. Fawn recruitment at intermediate elevation sites showed mixed results during late gestation with fawn recruitment at one site influenced by low temperatures and the other by drought severity. These differences were not due to elevation per se but were likely a result of the timing of arrival into these sites and the timing of snow melt and subsequent green-up of vegetation.

To assess why pronghorn populations across Idaho remain low, the objectives of this paper were to (1) investigate the role that density dependence plays on population growth rates (λ) of pronghorn statewide, and (2) assess how density-dependent and density-independent environmental factors influenced pronghorn population growth rates across five subpopulations, using a retrospective analysis of 31 years of survey data. We hypothesized that growth rates of pronghorn could be affected by density-independent factors (i.e., habitat, climate, nutrition, and hunting) and density dependence. In addition, recent studies have reported how the variability in climate and plant phenology influenced recruitment and adult survival in ungulates (e.g., DeMars et al. 2021; Jesmer et al. 2021); thus, we hypothesized that the predictability or variation in the climatic and environmental variables could similarly affect pronghorn population growth rates.

Materials and methods

Study areas

We examined population growth rates in five pronghorn subpopulations from 1988 to 2018 across Idaho including Camas Prairie, Jarbidge, Little Wood, Little Lost–Pahsimeroi, and Lemhi–Birch Creek (Table 1), and these sites represented the majority of pronghorn habitats and population productivities in southern Idaho (Smyser 2005). The area used by the Camas Prairie subpopulation was dominated by private, agricultural lands planted primarily with alfalfa (*Medicago sativa* Urb.), barley (*Hordeum* spp. Linneaus), grasses (*Poa* spp. Linneaus), and wheat (*Triticum* spp. Linneaus; Kinder 2004) with the remaining agricultural lands in pasture or enrolled in the Conservation Reserve Program (Smyser 2005). In Camas Prairie, major cover types consisted of forbs and grasses (48% ± 3% SD), while shrubs covered 19% ± 3%, with little annual change. Camas Prairie received an average annual precipitation of 41.64 cm with a mean annual maximum and minimum temperature of 14 and −0.23 °C, respectively (Thornton et al. 2019); see Smyser (2005) for a complete description of all sites.

The area used by the Jarbidge pronghorn subpopulation was located on mostly federal land dominated by basin and Wyoming big sagebrush (*Artemisia tridentata tridentata* Osterh. and *Artemisia tridentata wyomingensis* Beetle & A.L. Young); some patches of crested wheatgrass (*Agropyron cristatum* (Linneaus)) were established as fire remediation tools to combat cheatgrass expansion and to provide forage for domestic cattle. Other vegetation found in the Jarbidge area included low sagebrush (*Artemisia arbuscula* Nutt.), antelope bitterbrush (*Purshia tridentate* (Pursh)), rabbitbrush (*Chrysothamnus* spp. Nutt.), and perennial grasslands (Smyser 2005). The Jarbidge area consisted of 46% ± 4% forbs and grasses, and 14% ± 4% shrubs; again, with little annual change in these cover types. The Jarbidge area received an average annual precipitation of 37.64 cm and experienced a mean annual maximum and minimum temperature of 15.46 and 1.40 °C, respectively (Thornton et al. 2019).

The area used by the Little Wood subpopulation typified native shrub–steppe habitat located north of the Snake River Plain (Whitehead 1992) in the Little Wood River drainage. Basin and Wyoming sagebrush covered a majority of the area, with limited pasture and irrigated agriculture land for

Table 1. Mean elevation, primary habitat, area, and number of survey years examined for five subpopulations of pronghorn *Antilocapra americana* in Idaho.

Subpopulation	Mean elev. (m)	Primary habitat	Area (km²)	Survey years (available/used[1])
Camas Prairie	1552	Agriculture	750	23/22
Jarbidge	1552	Desert	2996	31/25
Little Wood	1726	Sagebrush steppe	472	27/24
Little Lost–Pahsimeroi	1897	Mtn sagebrush	962	12/9
Lemhi–Birch Creek	2018	Low sagebrush	1347	13/10

[1]Number of survey years used in subpopulation models.

alfalfa (Smyser 2005). In the Little Wood site, major cover types consisted of forbs and grasses (48% ± 3%) and shrubs (22% ± 3%) with little annual change. The area received an average annual precipitation of 40.02 cm and experienced a mean annual maximum and minimum temperature of 13.56 and −1.19 °C, respectively (Thornton et al. 2019).

The area used by the Little Lost–Pahsimeroi pronghorn subpopulation was located mostly on federal lands in mountain valleys dominated by native vegetation, including low and mountain big sagebrush (*A. t. vaseyena* Rydb.; Smyser 2005; Panting et al. 2021). In the Little Lost–Pahsimeroi site, forbs and grasses comprised 34% ± 2% of the area and shrubs comprised 17% ± 2%, with little annual change. The Little Lost–Pahsimeroi area received an average annual precipitation of 33.02 cm. The mean annual maximum and minimum temperature in the area was 12.45 and −2.39 °C, respectively (Thornton et al. 2019).

The area used by the Lemhi–Birch Creek subpopulation was also located in mountain valleys dominated by native vegetation, including low, mountain, basin, and Wyoming big sagebrush with limited agricultural fields in the valley bottoms (Smyser 2005). The Lemhi–Birch Creek study area consisted of 40% ± 2% forbs and grasses, and 20% ± 2% shrubs, with little annual change in cover types. The Lemhi–Birch Creek study area received an average annual precipitation of 39.80 cm with a mean annual maximum temperature of 11.36 °C and a mean annual minimum temperature of −2.74 °C (Thornton et al. 2019).

Survey data

We examined formal and informal reports from Idaho Department of Fish and Game (IDFG) to obtain yearly pronghorn aerial and ground surveys conducted in the five subpopulations from 1988 to 2018, for a total of 31 survey years (Table 1). For ground surveys, herd composition surveys were conducted by IDFG personnel in late August to early September by driving a standardized route sampling most of the pronghorn habitat in the study site. If road conditions precluded the survey from being completed along the fixed route, we censured that count from analysis as it would be an underestimate of population size. Aerial surveys involved IDFG personnel obtaining counts of pronghorn from either a helicopter or fixed-wing aircraft following line transects covering the study site. Aerial surveys were conducted in the same time period and were predominantly used in open habitat (i.e., Jarbidge study area), while ground surveys were conducted in the remaining four study areas. The surveys were

considered an estimate of relative abundance. Reports provided the number of does, bucks, and fawns counted in the survey, and the number of pronghorn (bucks and does) harvested in the fall hunting season. We used the fawn:doe ratio as a measure of fawn survival through the summer and was considered a proxy of fawn recruitment to August. The percent of the subpopulation harvested was the number of animals harvested that fall hunting season divided by the total number of animals counted during the August survey of the same year.

We defined the population growth rate (λ) as the change in the survey count from year (t) to year ($t + 1$) for each subpopulation. Any year with $\lambda \geq 2$ was considered an anomaly and censured from analysis (Gedir et al. 2015) and were generally attributed to a change in the survey method (e.g., used a helicopter 1 year), route, or timing of the survey. Some subpopulations (e.g., Camas Prairie) were consistently surveyed by the same observers, while in other sites the observers conducting the survey varied between years. To identify the boundaries for each subpopulation, we used an area that encompassed the summer range and the area surveyed each year.

Model variables

For each individual subpopulation, we examined environmental variables that could potentially influence population growth rate, including minimum and maximum temperature, precipitation, NDVI, and drought severity (Palmer drought severity index (PDSI); Palmer 1965; Dai 2011). We calculated the mean, standard deviation, and cumulative values, where appropriate, for each variable for each year across five time periods (1 and 2 months pre- and post-parturition, and the previous breeding season). We examined the standard deviation of each environmental variable for each year within each time period because the variability of environmental conditions has been shown to influence pronghorn adult mortality (Reinking et al. 2019) and fawn summer survival (Gese et al. 2023). We assumed that the average parturition date for Idaho pronghorn was 20 May (Folker 1956; Bodie 1979; McNay 1980; Bender et al. 2013; Panting et al. 2021; Gese et al. 2023), while the breeding season in northern pronghorn occurred during mid-September into October (O'Gara 2004c). We also explored potential lag effects of the previous year's breeding season variables on the following year. Additionally, we examined variables such as elevation, total shrub cover, and the combined cover of forbs and grasses for each year for each of the five pronghorn subpopulations. We also examined density-dependent variables

for each subpopulation for each survey year. We considered density-dependent variables to be the population growth rate in the prior year, fawn survival from the prior year, fawn survival during the current year, and the proportion of the subpopulation harvested the prior year. In total, we examined 12 variables from five environmental factor groups, including NDVI (27 variables), precipitation (15 variables), maximum and minimum temperature (10 variables each), the PDSI (8 variables), plus 7 variables not associated with any temporal data set (Appendix 1). Time periods of pre- and post-parturition, and the previous breeding season, were examined for each environmental group independently (i.e., univariate models) to determine the time period most influential on population growth rates.

The NDVI is a measure of photosynthetic activity of vegetation indicating "greenness" that ranges from −1 (indicating no vegetation) to +1 (indicating healthy vegetation) and is a proxy for vegetative health (Jensen 2007). It has the ability to indicate the rate and timing of spring green-up in temporally consecutive, remotely sensed imagery, which can directly influence female adult ungulate nutrition throughout gestation and lactation, and subsequent fawn survival (Christianson et al. 2013; Caltrider and Bender 2018). We examined NDVI values for each year in each site to determine whether the greenness of vegetation influenced population growth rates in the five pronghorn subpopulations in Idaho. The NDVI values were obtained from Landsat surface reflectance data that had been atmospherically corrected; Landsat records NDVI values every 14 days at 1 km resolution. We conducted NDVI extractions in Google Earth Engine (Vermote et al. 2014; Gorelick et al. 2017), interpolated missing NDVI values (i.e., missing days) using the "interpolation" command in the impute time series library (imputeTS; Moritz and Bartz-Beielstein 2017), and standardized the values to a minimum of −1 and a maximum of 1 to facilitate comparison across subpopulations and years. We used a weighted Whittaker smoothing process (Eilers 2003; Atzberger and Eilers 2011) to remove inherent noise in NDVI data (Zeng et al. 2020). All NDVI interpolations, standardizations, and smoothing processes were conducted in R (R Core Team 2020). We obtained percent cover of the combined forb and grass cover and total percent shrub cover from the Rangeland Analysis Program (https://rangelands.app; resolution is 30 × 30 m), which provided vegetation data across the western United States from 1984 to 2020 (Allred et al. 2021), to examine the influence of vegetation composition on population growth rates within each subpopulation.

We obtained measures of precipitation, minimum temperature, and maximum temperature for each subpopulation for each survey year to assess the influence of climate conditions on population growth rates from the Daily Surface Weather and Climatological Summaries database (Midwestern Regional Climate Center 2019). This database is a 1 km² gridded estimate of daily weather across the United States (Thornton et al. 2019). All temperature (°C) and precipitation (mm) extractions were conducted in Google Earth Engine (Gorelick et al. 2017).

We examined the PDSI, an index of atmospheric moisture conditions, to assess whether drought conditions influenced population growth rates across the five pronghorn subpopulations (Dai 2011). This index ranges from −10 to 10 (extreme dryness to extreme wetness), with values less than −3 indicating extreme drought (Dai 2011). We obtained the PDSI for all surveyed years for each of the subpopulations based on the 4 km daily Gridded Surface Meteorological dataset (Abatzoglou 2013) in Google Earth Engine (Gorelick et al. 2017).

Model evaluation

We investigated pronghorn population growth rates at two scales, with all subpopulations combined (i.e., statewide) and each subpopulation independently. For the statewide scale, we examined the correlation between the population growth rate in the current year with (a) the percent of the subpopulation harvested the previous fall, (b) the population growth rate the previous year, (c) the summer survival rate of fawns from the previous year, and (d) the summer survival rate of fawns in the current year.

We examined each subpopulation individually based on previous research in Idaho, which found that the influence of environmental variables on fawn recruitment was site-specific (Gese et al. 2023). Conducting our analyses at both the statewide and subpopulation scales allowed us to examine location-specific drivers or mechanisms influencing spatially heterogenous population dynamics (Owen-Smith 2014) and regional effects across the state. Our analysis at the subpopulation level also reflected the area at which management objectives are identified and management actions would be implemented, and provided an analysis of how scale might influence ecological processes and subsequent management decisions.

Subpopulation sample sizes limited us to conducting linear models (Zar 1996) rather than linear mixed models with subpopulation as a random variable. We used a three-step phased modeling evaluation process (Symonds and Moussalli 2011; McLaughlin et al. 2014; Anderson-Cook et al. 2015) to examine the factors influencing subpopulation growth rates. This approach also enabled us to accommodate the number of variables we assessed (Appendix 1). All models were ranked based on Bayesian information criteria (BIC; Schwarz 1978) where the highest ranked model most closely matched how the response variable was generated (Cruyff et al. 2021). In step 1, we generated models for each site and ranked all univariate models within each variable across different time periods (see Appendix 1): NDVI (27 models), precipitation (15 models), maximum temperature (10 models), minimum temperature (10 models), and PDSI (8 models). For each variable, models with BIC weight ≥0.10 or the highest ranked model after the null model advanced to step 2. Our null model was population growth rates as the response variable.

Step 2 was conducted as an additional elimination process in which the highest ranked models from step 1 were ranked with univariate models for elevation, total shrub cover, combined grass and forb cover, proportion of the subpopulation harvested the previous fall, the population growth rate the prior year, and the recruitment rates for the previous and current years. Performing step 2 reduced the number of

Fig. 1. (A) Influence of the proportion of the subpopulation harvested the previous year, (B) population growth rate in the previous year, (C) summer fawn survival (recruitment) in the previous year, and (D) summer fawn survival (recruitment) in the current year, on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the five subpopulations combined, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.
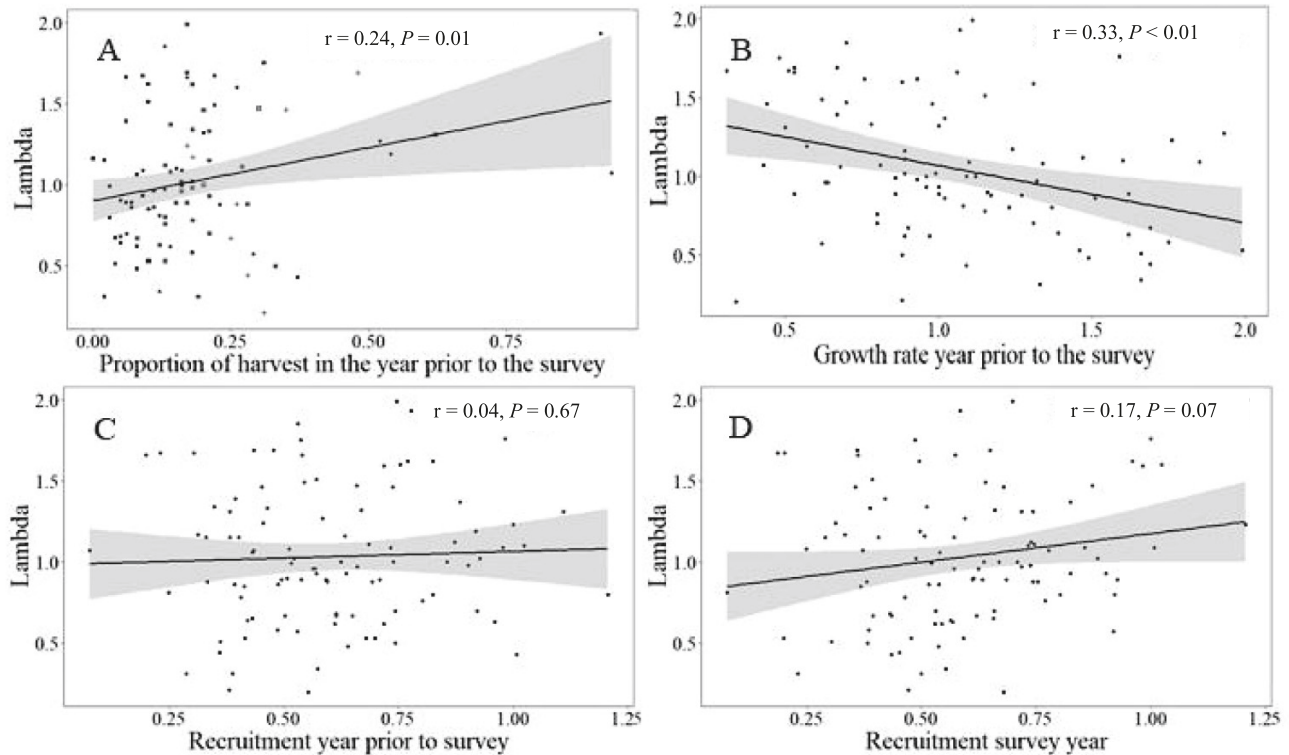
possible additive models that could be generated during step 3. We assessed assumptions of linear regression (e.g., linearity, normality, and heteroscedasticity) of the top-ranked models in step 2 in R. Models with a BIC weight ≥0.10, or the highest ranked model following the null model, were carried forward to step 3.

In step 3, we generated additive models from the univariate models that met our criteria from step 2. We assessed correlations of these additive models via Pearson's correlation tests in R using the corr.test command in the psych package (Revelle 2019), and variables with a correlation coefficient ≥0.60 were not allowed to occur in the same multivariate model (Richard 1990). Step 3 model determination was not conducted for high-elevation sites due to correlations above our criteria. We compared the highest ranked multivariate models using BIC weights and tested them for variance inflation in R with the vif.mer command in the VIF package (Dongyu et al. 2011). We used $\alpha = 0.10$ for all statistical tests.

Results

Statewide

The statewide pronghorn growth rate averaged 1.04 (range = 0.56–1.51). The proportion of the subpopulation harvested the previous fall positively influenced population growth rates (Fig. 1A), while the previous year's growth rate negatively influenced the current year's growth rates (Fig. 1B). Fawn survival in the previous year did not influence current year's population growth rates (Fig. 1C), while fawn survival in the current year positively influenced population growth rates (Fig. 1D).

Camas Prairie

The mean population growth rate for pronghorn in the Camas Prairie subpopulation was 1.15 (range = 0.43–1.93). The highest ranked model influencing growth rates in the current year was the recruitment rate during the current year followed by the null, the mean maximum temperature during the previous breeding season, and the additive model of mean maximum temperature during the previous breeding season plus recruitment in the current year (Table 2). The three top-ranked models, excluding the null model, carried 73% of model weight and all were found to positively influence growth rates (Figs. 2A–2C).

Jarbidge

Mean population growth rate for the Jarbidge subpopulation was 1.03 (range = 0.31–1.75). The previous year's population growth rate was the top-ranked model at 94% of the model weight (Table 2) and negatively influenced the current year's growth rate (Fig. 3). No environmental variables were found to influence growth rate in the Jarbidge subpopulation.

Table 2. Top-ranked models with a BIC weight ≥0.1 examining factors influencing growth rates of five subpopulations of pronghorn *Antilocapra americana* in Idaho, 1988–2018.

Study area	Model	BIC weight	df	Variable	Estimate	Standard error	t value	P
Camas Prairie	Fawn recruitment in current year	0.29	3	Recruitment	0.75	0.41	1.81	0.08
	Null	0.26	2		1.15	0.09	13.16	<0.01
	Mean maximum temperature during previous breeding season	0.25	3	MaxTemp	0.08	0.05	1.73	0.10
	Mean maximum temperature during previous breeding season + fawn recruitment in current year	0.19	4	MaxTemp	0.07	0.05	1.42	0.17
				Recruitment	0.62	0.41	1.52	0.14
Jarbidge	Growth rate in previous year	0.94	3	Lambda_prior	−0.70	0.16	−4.30	<0.01
Little Wood	STD of PDSI 2 months pre-parturition + growth rate in previous year	0.55	4	SdPDSI60PR	−0.61	0.24	−2.58	0.02
				Lambda_prior	−0.46	0.18	−2.55	0.02
	STD of PDSI 1 month pre-parturition + growth rate in previous year	0.13	4	SdPDSI30PR	−1.31	0.69	−1.89	0.07
				Lambda_prior	−0.39	0.20	−1.99	0.06
	STD of PDSI 2 months pre-parturition	0.10	3	SdPDSI30PR	−0.66	0.26	−2.51	0.02
	Growth rate in previous year	0.10	3	Lambda_prior	−0.50	0.20	−2.48	0.02
Little Lost–Pahsimeroi	STD of minimum temperature 1 month pre-parturition	0.32	3	SdMinT30PR	−0.29	0.09	−3.32	0.01
	STD of NDVI 1 month pre-parturition	0.22	3	SdNDVI30PR	27.37	8.81	3.11	0.02
	Cumulative daily rate of change in NDVI 1 month pre-parturition	0.20	3	CDRC30PR	10.04	3.31	3.04	0.02
	Mean daily rate of change in NDVI 1 month pre-parturition	0.13	3	MDRC30PR	265.51	100.24	2.65	0.03
Lemhi–Birch Creek	Cumulative NDVI 2 months post-parturition	0.69	3	CNDVI60PS	0.26	0.06	4.23	<0.01
	Cumulative NDVI 1 month post-parturition	0.15	3	CNDVI30PS	0.46	0.14	3.34	0.01

Note: STD = standard deviation; PDSI = Palmer drought severity index; NDVI = normalized difference vegetation index.

Little Wood

The mean population growth rate for the Little Wood subpopulation was 1.03 (range = 0.50–1.99). The standard deviation of drought severity during the 2 months pre-parturition plus the population growth rate the previous year was the highest ranked model influencing the population growth rates in the current year with 55% of the model weight (Table 2, Fig. 4A). The other three top-ranked models had similar weights between 10%–13%, while the four top-ranked models combined carried 88% of the model weight. All four models negatively influenced the population growth rate of the Little Wood subpopulation (Figs. 4A–4D).

Little Lost–Pahsimeroi

The mean population growth rate for pronghorn in the Little Lost–Pahsimeroi subpopulation was 0.97 (range = 0.31–1.34). The highest ranked model was the standard deviation of the minimum temperature 1 month pre-parturition followed by the standard deviation of NDVI values 1 month pre-parturition, then the cumulative daily rate of change in NDVI 1 month pre-parturition, and lastly the mean daily rate of change in NDVI values 1 month pre-parturition. These four top-ranked models combined carried 87% of model weight (Table 2). The standard deviation of minimum temperature 1 month pre-parturition negatively influenced the popula-

tion growth rate (Fig. 5A), while all measures of NDVI positively influenced population growth rate (Figs. 5B–5D).
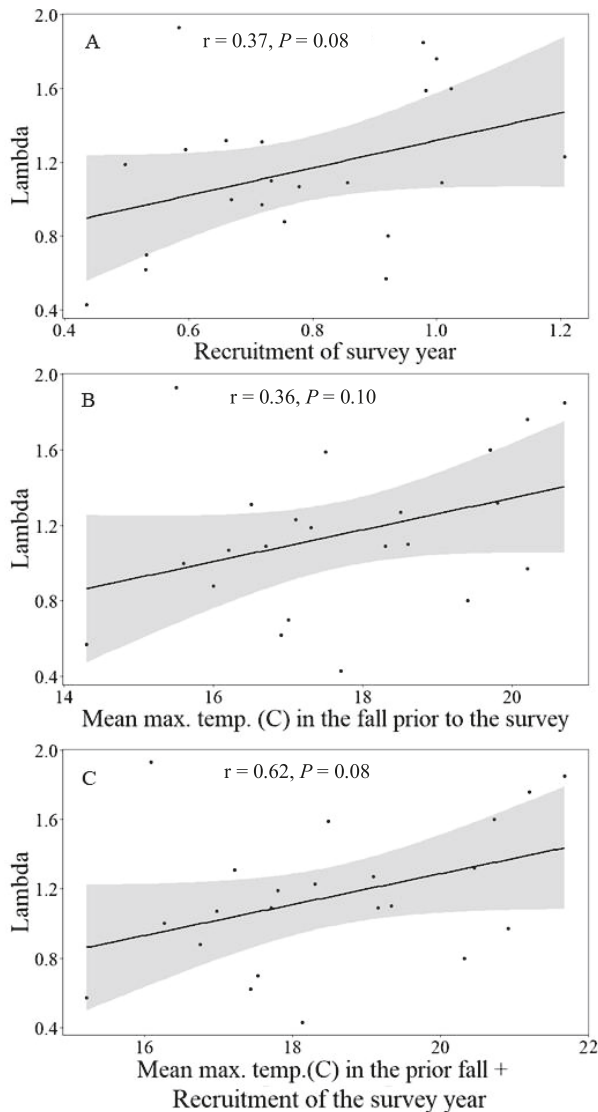
Lemhi–Birch Creek

The mean population growth rate for pronghorn in the Lemhi–Birch Creek subpopulation was 0.96 (range = 0.21–1.69). The univariate models with BIC weights ≥0.10 from step two included the cumulative NDVI values during 1 and 2 months post-parturition with these two top-ranked models carrying 84% of model weight (Table 2). Both variables positively influenced the population growth rate (Figs. 6A–6B).

Discussion

We designed our analyses to determine the variables influencing pronghorn growth rates at two scales (i.e., statewide and subpopulation). We found density-dependent variables influenced population growth rates of pronghorn across Idaho. As the proportion of individuals harvested in the subpopulation during the previous hunting season increased, population growth rates in the subsequent year increased (Fig. 1A), indicating that hunting positively influenced populations growth rate in a density-dependent manner. Harvest likely resulted in decreased intraspecific competition among pronghorn for food resources. We also found density dependence with high growth rates in 1 year resulted in low growth
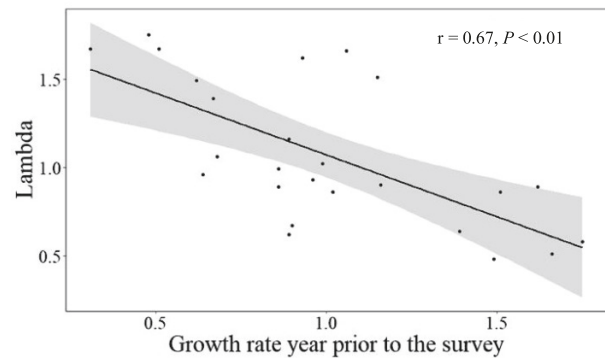
Fig. 2. (A) Influence of summer fawn survival (i.e., recruitment) in the current year, (B) mean maximum temperature in the prior breeding season (fall), and (C) mean maximum temperature in the prior breeding season (fall) plus summer fawn survival (recruitment) in the current year, on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the Camas Prairie subpopulation, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.

Fig. 3. Influence of the growth rate in the previous year on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the Jarbidge subpopulation, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.

elevation. Changes in growth rates were not due to elevation per se but were the result of the timing that pronghorn arrived at their summer range, as well as the climatic variability (i.e., timing of snow melt-off and subsequent vegetation green-up) and the concomitant major ecotype at that elevation (i.e., desert, sagebrush steppe, and high mountain valley). At lower elevation sites (i.e., Camas Prairie and Jarbidge) population growth rates were influenced by both environmental factors and density-dependent variables, while at higher elevations (i.e., Little Lost–Pahsimeroi and Lemhi–Birch Creek) population growth rates were influenced by environmental variables (Table 2). Interestingly, at the intermediate elevation site (i.e., Little Wood), pronghorn population growth rates were influenced by a combination of density dependence and environmental factors.

We found that density-dependent and density-independent environmental variables influenced the low elevation subpopulations' growth rates. When comparing these two sites, the Camas Prairie subpopulation growth rate was positively influenced by the current year's recruitment and the mean maximum temperature during the previous breeding season (Fig. 2), while the Jarbidge subpopulation was entirely influenced by density dependence where the previous year's growth rate negatively influenced the current year's growth rate (Fig. 3). The inclusion of the mean maximum temperature during the previous breeding season demonstrated a density-independent positive influence on pronghorn in the Camas Prairie site, which may be extending the duration of quality forage available to female pronghorn into the fall. The influence of forage quality is important because recent investigations found that Camas Prairie pronghorn had some of the highest measures of ruminant nutrition (i.e., 2,6-diaminopimelic acid (DAPA) and fecal nitrogen) of these five subpopulations during the breeding season (Bleke 2022). That nutrition prior to winter likely positively influenced the current year's fawn recruitment as maternal condition during the breeding season has been shown to influence offspring prenatal growth rates (Clancey et al. 2012), gestation length and birth weights (Byers and Hogg 1995), and subsequent fawn survival (Fairbanks 1993; Panting et al. 2021). Panting et

rates the following year (Fig. 1B). The actual mechanisms driving the density-dependent relationship for pronghorn in Idaho is presently unknown but likely contained elements of reduced survival as population growth rates and subsequent density increased. Density-dependent changes may be a product of increased ungulate density on population parameters such as an initial decrease in individual body mass, followed by delayed primiparity, reduced fawn survival, and finally adult survival (Eberhardt 2002; Bonenfant et al. 2009).

Similar to findings influencing recruitment of pronghorn fawns in Idaho (Gese et al. 2023), population growth rates across the five subpopulations were loosely associated with

Fig. 4. (A) Influence of the standard deviation of the PDSI during 2 months pre-parturition plus the growth rate in the prior year, (B) the standard deviation of the PDSI during 1 month pre-parturition plus the growth rate in the prior year, (C) the standard deviation of the PDSI during 1 month pre-parturition, and (D) the growth rate in the previous year, on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the Little Wood subpopulation, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.
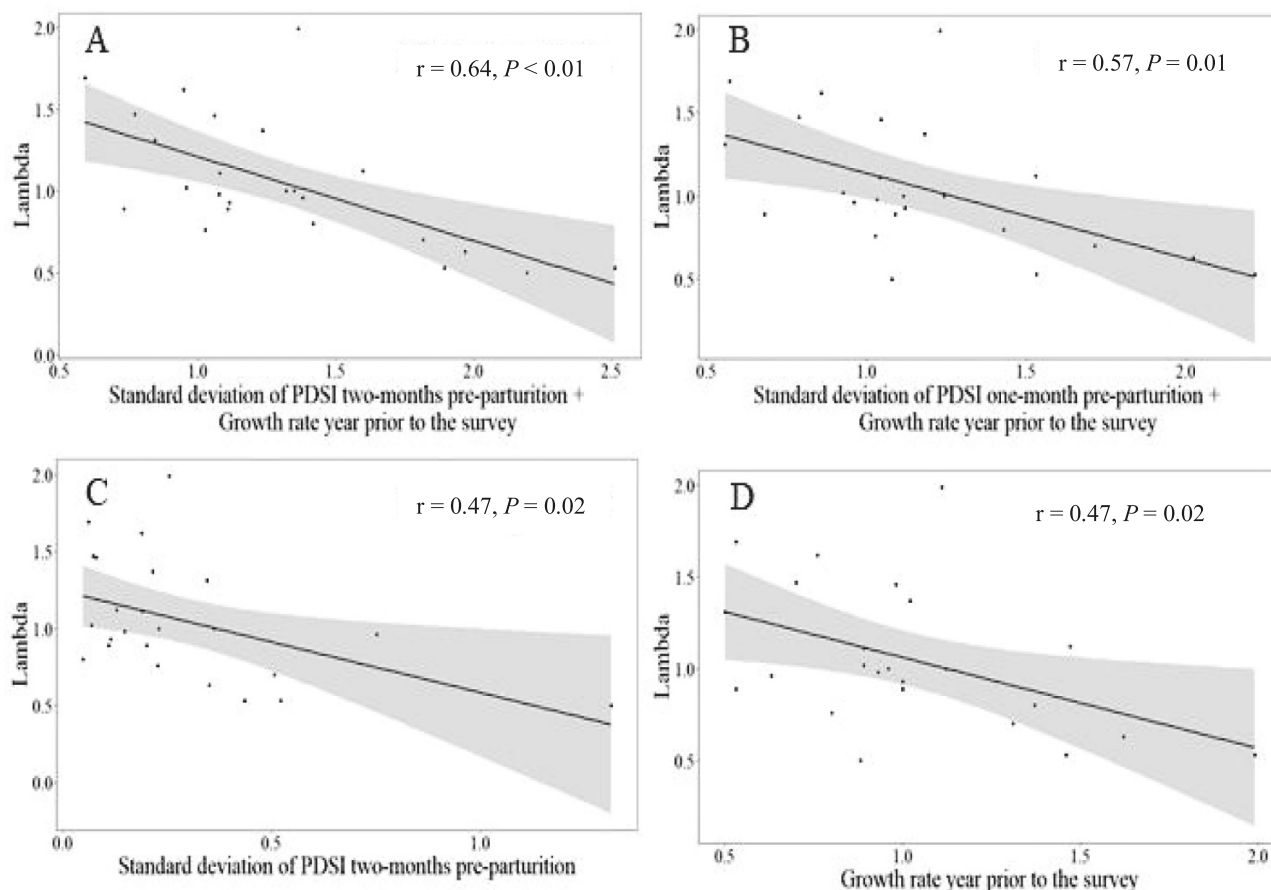
al. (2021) found pronghorn fawn birth weights and survival rates to be highest within the Camas Prairie subpopulation of those studied. Interestingly, Camas Prairie pronghorns' summer range is an agricultural-dominated landscape and yet a majority of their seasonal dietary protein intake was from native forbs (Bleke et al. 2023).

The Jarbidge subpopulation growth rate was the only subpopulation examined that was influenced solely by density dependence; as the previous year's population growth rate increased, the current year's population growth rate decreased (Fig. 3). Our findings, in combination with current fire remediation practices, which likely decreased high-quality forage for pronghorn (i.e., forbs), likely increased intraspecific competition (O'Gara 2004b) concomitantly with population size. We believe our results suggest that the Jarbidge subpopulation is near or at the ecological carrying capacity of the environment (Bowyer et al. 2014). High densities of pronghorn are also associated with higher fawn predation, starvation, fawn abandonment, and ailments such as weak fawn syndrome (O'Gara 2004a). Pronghorn fawn survival has been shown to be influenced by density (Danvir 2000) with survival being highest at lower densities in Montana (O'Gara 2004a). In

northern Utah, variability in pronghorn population sizes was positively correlated with prior-year population size (Danvir 2000).

At the mid-elevation site (Little Wood), the standard deviation of drought severity 1 and 2 months before parturition combined with the previous year's growth rate were significant negative influences on current year's growth rates of the Little Wood subpopulation (Fig. 4). Unpredictability of extreme climatic events, such as drought, likely decreased forage availability to females during the critical time of energy acquisition. The third trimester of gestation is the most metabolically demanding period of pregnancy in ungulates (Parker et al. 2009) with metabolic costs 50% higher for pregnant females compared to non-pregnant (Pekins et al. 1998) and when a majority of the fetal mass development occurs (Robbins and Robbins 1979; O'Gara 2004c; Barnowe-Meyer et al. 2011). The downstream effects of increased drought severity variability likely decreased the female's nutritional status that directly influences neonate weight and survival (Fairbanks 1993; O'Gara 2004d; Panting et al. 2021). Density dependence was also operating in this subpopulation indicating that this subpopulation is likely at

Fig. 5. (A) Influence of the standard deviation of the minimum temperature during 2 months pre-parturition, (B) the standard deviation of NDVI during 1 month pre-parturition, (C) the cumulative daily rate of change of NDVI during 1 month pre-parturition, and (D) the mean daily rate of change of NDVI during 1 month pre-parturition, on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the Little Lost–Pahsimeroi subpopulation, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.
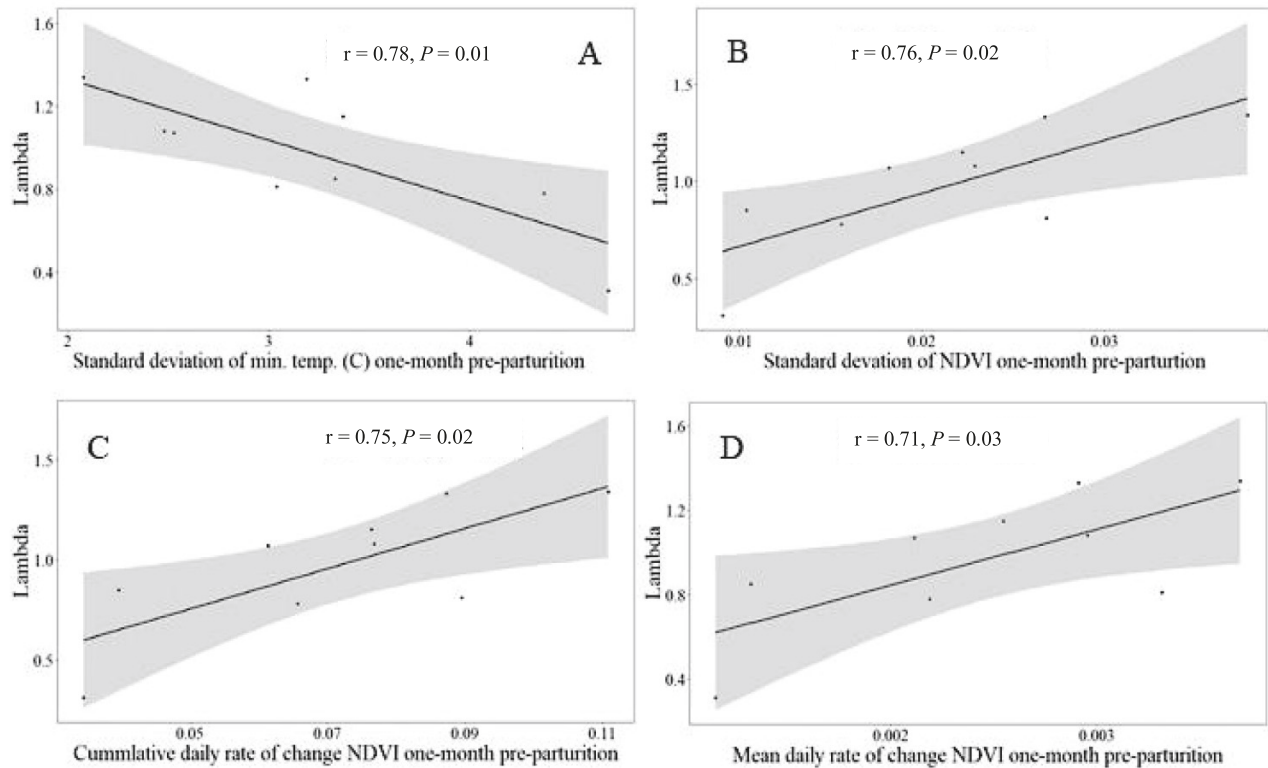
or near carrying capacity as years with high growth rates were related to lower population growth the following year (Fig. 4D).

Pronghorn growth rates in mountain valleys were positively influenced by NDVI at 1 month pre-parturition within the Little Lost–Pahsimeroi subpopulation and 1–2 months post-parturition within the Lemhi–Birch Creek subpopulation (Figs. 5 and 6). Measures of NDVI likely affected the quality of forage available to pronghorn during the metabolically demanding life history stages of late gestation and lactation. In addition to energetic demands of late gestation, the transition from pregnancy to lactation is among the most important determinants of maternal–offspring health outcomes (Dunlop et al. 2015; Prince et al. 2015; Blaser and Dominguez-Bello 2016). Lactation is the biological period when daily energetic requirements are highest for female ungulate species (Parker et al. 2009), where requirements increase by 65%–215% during the first month postpartum (Oftedal 1985; Robbins 1993), providing further support for the importance of high forage quality during lactation.

In highly seasonal environments, like mountain valleys, spring forage conditions can have profound effects on the energy balance during late gestation and lactation. Females with access to high-quality forage during lactation could provide greater maternal care (e.g., higher milk energy output) than females on a low nutritional plane and reach sufficient

body condition in autumn to conceive again (Pettorelli et al. 2007). Digestible energy (i.e., DAPA) and diet quality (i.e., fecal nitrogen) indices were found to be important for pronghorn within these subpopulations during late gestation and lactation periods as relates to summer fawn survival (Bleke 2022). In addition, the variance of minimum temperatures negatively influenced growth rates in the Little Lost–Pahsimeroi subpopulation (Fig. 5A), likely due to the timing of green-up and the need for females to acquire quality forage during the final month of gestation. Gedir et al. (2015) found that pronghorn population growth rates increased with increased temperatures during late gestation. Studies on several species of ungulates have demonstrated that environmental factors, such as the timing and type of precipitation, temperature, and extreme weather events, influenced population growth rates (O'Gara 2004a; Bonenfant et al. 2009) and young survival (Jesmer et al. 2021).

Our results showed that density-dependent drivers influenced population growth rates at the statewide scale, while both environmental conditions and density-dependent drivers independently and in combination influenced pronghorn growth rates differently at the subpopulation scale. As Owen-Smith (2014) postulated, due to spatially heterogenous population dynamics, researchers should conduct analysis on smaller areas, rather than one large area, to tease out the variation in different regions within an overall

Fig. 6. (A) The influence of the cumulative daily rate of change of NDVI during 2 months post-parturition, and (B) 1 month post-parturition, on the population growth rate (Lambda) in the current year for pronghorn *Antilocapra americana* in the Lemhi–Birch Creek subpopulation, Idaho, 1988–2018. Shaded area represents the 95% confidence interval.
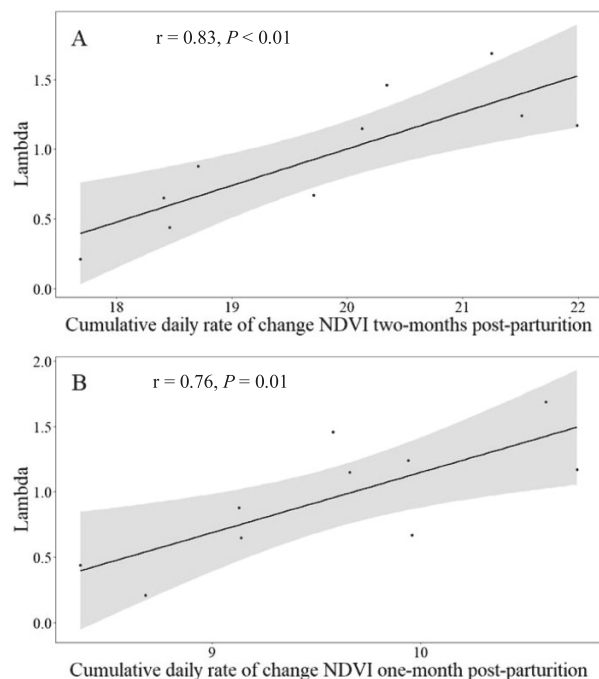
area. We concur with that statement as the drivers influencing population growth rates, both in terms of the factors involved, their variability, and the timing were dependent upon location. Simplifying such a range of temperatures, precipitation, and rate of vegetative green-up into essential information necessitates a broad generalization eliminating important subtleties driving population growth rates at the subpopulation scale (Owen-Smith 2014).

Our findings indicate that pronghorn managers consider creating management plans and enacting decisions at the scale of subpopulation given the variability of drivers and environmental conditions experienced across the state (Hoffman and Genoways 2012). For example, in the Camas Prairie site where fawn recruitment and maximum temperature were the primary drivers of population growth, management actions that increases available protein on the landscape will likely result in increased fawn recruitment (Bleke 2022). In the Jarbidge site, density dependence is driving population growth, thus managers will need to recognize that density dependence is involved and these feedbacks will limit carrying capacity of this subpopulation. Drought severity was the driver of population growth in the Little Wood subpopulation with any management action that ameliorates the negative impact of drought will need to be considered (e.g., planting patches of drought-resistant forage species). For the two mountain valley subpopulations (Little Lost–Pahsimeroi and Lemhi–Birch Creek), the variability, daily rate of change, and the cumulative effects of vegetation green-up were the principle drivers of population growth. Management actions

providing forage that will green-up and mature, thereby providing quality and nutritious forage for lactating females will need to be considered, particularly in light of possible changes in species composition and changes in plant phenology due to climate change. Continued declines in any subpopulation will require future monitoring and implementation of local management with the knowledge that density dependence may limit the ability to effect a change in carrying capacity.

Acknowledgements

Article information

History dates

Copyright

Data availability
Data are available within "Pronghorn Progress Reports" for 1983–2018 from the IDFG website https://collaboration.idfg.idaho.gov/WildlifeTechnical Reports/Forms/AllItems.aspx.

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Competing interests
The authors declare no competing or financial interests. The findings and conclusions in this publication have not been formally disseminated by the U.S. Department of Agriculture

and should not be construed to represent any agency determination or policy.

Funding information

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Appendix 1. Variables examined in relation to population growth rates for pronghorn *Antilocapra americana* in five subpopulations in Idaho, 1988–2018.

Normalized Difference Vegetation Index (NDVI, 27 variables): mean, standard deviation, and cumulative NDVI in the fall; mean, standard deviation, and cumulative NDVI 1 and 2 months pre-parturition; mean, standard deviation, and cumulative NDVI 1 and 2 months post-parturition; mean, standard deviation, and cumulative daily rate of change in NDVI 1 and 2 months pre-parturition; mean, standard deviation, and cumulative daily rate of change in NDVI 1 and 2 months post-parturition.

Precipitation (15 variables): mean, standard deviation, and cumulative precipitation in the fall; mean, standard deviation, and cumulative precipitation 1 and 2 months pre-parturition; mean, standard deviation, and cumulative precipitation 1 and 2 months post-parturition.

Maximum temperature (10 variables): mean and standard deviation of maximum temperature in the fall; mean and standard deviation of maximum temperature 1 and 2 months pre-parturition; mean and standard deviation of maximum temperature 1 and 2 months post-parturition.

Minimum temperature (10 variables): mean and standard deviation of minimum temperature in the fall; mean and standard deviation of minimum temperature 1 and 2 months pre-parturition; mean and standard deviation of minimum temperature 1 and 2 months post-parturition.

Palmer Drought Severity Index (PDSI, 8 variables): mean and standard deviation of PDSI 1 and 2 months pre-parturition; mean and standard deviation of PDSI 1 and 2 months post-parturition.

Variables without temporal variation (7 variables): proportion of subpopulation harvested the previous year; fawn survival/recruitment in the previous year; fawn survival/recruitment in the current year; population growth rate in the previous year; elevation; percent shrub cover; percent forb and grass cover combined.