



Research Article

# Intrinsic, Environmental, and Anthropogenic Factors Related to Pronghorn Summer Mortality

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**ABSTRACT** Pronghorn (*Antilocapra americana*) are an iconic wildlife species of sagebrush (*Artemisia spp.*) and grassland ecosystems in western North America. Over 50% of pronghorn have historically occurred in Wyoming; however, these populations have declined by nearly 30% in <2 decades, concurrent with expanding energy development and prolonged drought. Research suggests adult female pronghorn, unlike other temperate ungulates, are more likely to die in summer, when body condition is lower from extreme energetic demands of reproduction, which are higher for pronghorn than other ungulates. To evaluate the potential effects of intrinsic, environmental, and anthropogenic factors on summer mortality risk, we monitored 114 adult female pronghorn equipped with global positioning system transmitters in the Red Desert region of south-central Wyoming, USA between 2013 and 2015. We modeled mortality risk using Cox's proportional hazards regression. Summer mortality risk was influenced by intrinsic and environmental factors; mortality risk increased when individuals were in poorer body condition entering the previous winter and when they experienced greater variation in average daily snow depth during the previous winter. We did not detect an effect of the distance to and density of roads, oil and gas wells, or fences on pronghorn summer mortality. During years of increased winter severity with deep and fluctuating snow depths, managers may observe higher winter mortality and higher mortality the following summer, likely as a consequence of the energetic expense associated with winter survival and spring reproduction for female pronghorn. © 2018 The Wildlife Society.

**KEY WORDS** *Antilocapra americana*, body condition, climate variability, energy development, income survivalist, pronghorn, snow depth variability, summer mortality risk, Wyoming.

Most ungulate species in temperate ecosystems are considered capital breeders, with reproduction largely fueled by fat reserves (Jönsson 1997, Andersen et al. 2000, Stephens et al. 2009). Pronghorn (*Antilocapra americana*), however, may align more closely with income breeders along the income-capital breeder spectrum (Clancey et al. 2012), suggesting that their reproduction is fueled by fat reserves and by energy as it is acquired (Stephens et al. 2009). Other income-breeding ungulates (e.g., roe deer [*Capreolus capreolus*]) time their reproduction to coincide with periods of spring green-up, whereas energy reserves stored by capital-breeding ungulates

serve as insurance against inconsistent nutritional availability across the landscape (Parker et al. 2009). Although this distinction in breeding strategy serves as an economic metaphor for the balancing act between acquired energy and the costs of reproduction (Stephens et al. 2009), it is closely tied to the strategies employed to ensure survival (Parker et al. 2009). For example, Arctic reindeer (*Rangifer tarandus tarandus*) finance their survival and reproduction using fat reserves, thus employing a capital strategy in both instances (Barboza and Parker 2008). If pronghorn rely more heavily on the immediate acquisition of energy relative to other ungulates, the link between adult survival and reproduction and surrounding environmental conditions may be even stronger for pronghorn compared with other species. Although pronghorn may align more closely with ungulates employing

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an income strategy, fat reserves still play an important role in their seasonal survival (O'Gara and Yoakum 2004).

Pronghorn in the northern portions of the species' range face increased thermoregulatory and locomotive costs during winter (Parker et al. 1984, Byers 1997), equating to net energy loss and declining body condition (Bear 1971, Byers 1997). Therefore, after experiencing the depletion of fat reserves common to temperate ungulates during winter (Mautz 1978, Monteith et al. 2013), pronghorn are often in poor condition prior to parturition. Pronghorn invest more highly in reproduction than all other ungulate species, expending substantial energetic reserves during prenatal and postnatal phases of offspring development (Robbins and Robbins 1979, Byers 1997, O'Gara and Yoakum 2004). For example, the length of pronghorn gestation is roughly 8 months, which is longer than other ungulates of a similar body size (O'Gara and Yoakum 2004), and the weight of pronghorn offspring at birth constitutes 15.5% of maternal weight, making the ratio of offspring to adult female weight higher for this species than all other ungulates (Robbins and Robbins 1979). Prior research reported fat levels in adult female pronghorn to be at their lowest in June (Bear 1971), largely because of the high energetic costs associated with late gestation and lactation (Smyser et al. 2005, Dunn and Byers 2008, Clancey et al. 2012). Female pronghorn were the only sex and species to experience higher mortality rates in summer than winter compared to 87 other species of wild ruminants kept in zoos (Carisch et al. 2016). Furthermore, Bender et al. (2013) reported that 73% of adult female pronghorn mortality in New Mexico occurred in summer months between parturition and weaning. Although ungulate demographic trends can be influenced by juvenile survival (Raithel et al. 2007), adult survival also has the potential to be a strong influence on population growth (Gaillard et al. 2000). Given the potential increase for mortality rates in adult female pronghorn during summer and the important role that adult survival can play in population dynamics, it is crucial to understand what factors contribute to female pronghorn mortality risk during that season.

Although the high energetic cost of reproduction can contribute to body condition degradation in pronghorn, other external factors may play a role as well. Environmental disturbances provoke risk-averse behaviors in many ungulate species, potentially depleting energy reserves by reducing foraging opportunities (Lima 1998, Winnie and Creel 2007). It has been hypothesized that animals perceive anthropogenic activities on landscapes as a source of risk (Frid and Dill 2002), a subject that has been increasingly studied considering the worldwide growth in energy resource demand (e.g., Buchanan et al. 2014). Such development can cause increased stress for wildlife, and associated infrastructure may directly inhibit their ability to move to areas of improved resource quality, as is frequently demonstrated by the barrier effect of roads and fences (Sheldon 2005, Sawyer et al. 2013). In many areas, flat, sagebrush (*Artemisia* spp.) environments preferred by pronghorn are ideal locations for energy development, and these environments are projected to continue experiencing increased

disturbance because of energy extraction efforts (Copeland et al. 2009).

Historically, Wyoming, USA has provided habitat to  $\geq 50\%$  of all pronghorn worldwide (Yoakum and O'Gara 2000), where they are emblematic of state culture and are popular with big game hunters. State-wide pronghorn populations have declined by nearly 30% since reaching estimated population highs during the mid-2000s (Wyoming Game and Fish Department [WGFD] 1995–2015). At the same time, Wyoming has experienced an increase in severe droughts (National Oceanic and Atmospheric Administration [NOAA] 2017), which have the potential to negatively affect wildlife by limiting forage availability and body condition, potentially resulting in decreased productivity and survival (Beale and Smith 1970, Dunn and Byers 2008). Wyoming also has experienced some of the greatest increases in energy resource extraction in the United States and ranks as the leading producer of federal onshore natural gas (Bureau of Land Management [BLM] 2012). Such infrastructure may affect wildlife by altering movement patterns, resource selection, behavior, and demography (Sawyer et al. 2005, Dzialak et al. 2011, Beckmann et al. 2012, Buchanan et al. 2014, Gregory and Beck 2014). Increasingly, energy development has become the focus of management and conservation efforts for an array of Wyoming's wildlife. To manage pronghorn populations and provide effective mitigation for risks to survival, practitioners need scientifically rigorous information regarding stressors for pronghorn. Understanding elements contributing to adult female mortality, particularly during summer, improves our ability to understand key demographic factors influencing pronghorn populations.

Pronghorn populations in the Red Desert region have experienced declines of 15–30% over the last 20 years, and show little to no recovery (WGFD 1995–2015). Congruent with these declines, the region also has experienced rapid increases in oil and conventional and coalbed methane natural gas extraction (Wyoming Oil and Gas Conservation Commission [WOGCC] 2016) coupled with 11 of 20 years characterized as drought, and 5 of 20 years described as extreme drought between 1996 and 2015 (NOAA 2017).

We evaluated mortality of adult females in the Red Desert of south-central Wyoming from 2013 to 2015. Our objectives were to identify the role of intrinsic, environmental, and anthropogenic stressors on summer mortality risk of adult female pronghorn. Given the role that individual characteristics can play in risk of death (Gaillard et al. 2000, Parker et al. 2009), we predicted that intrinsic factors including older age and poorer body condition entering winter would increase likelihood of death in summer for adult female pronghorn. Given the strong link between pronghorn survival and their environment, we predicted that poorer climate and land cover conditions, such as decreased summer precipitation or greater distance to water, would increase mortality risk (Yoakum et al. 2014). We predicted that anthropogenic features like roads, wells, and fences, would negatively influence survival, because disturbance associated with oil and natural gas extraction has been

reported to negatively affect the physiology, behavior, and survival of pronghorn and other ungulate species (Sawyer et al. 2006, Dzialak et al. 2011, Wasser et al. 2011, Beckmann et al. 2012, Northrup et al. 2015). Furthermore, anthropogenic features such as roads and fences have been reported to be a source of direct and indirect mortality for pronghorn (O’Gara and Yoakum 2004, Harrington and Conover 2006, Kolar et al. 2012, Taylor et al. 2016), and can alter pronghorn movement and behavior (Sheldon 2005, Gavin and Komers 2006, Gates et al. 2012, Sawyer et al. 2013, Yoakum et al. 2014).

## STUDY AREA

The Red Desert region in south-central Wyoming, USA extends from the Wyoming–Colorado border to north of Interstate 80 near Atlantic City, Wyoming and the southern portion of the Wind River Mountain Range, and east to west from Rawlins to Rock Springs, Wyoming (Fig. 1). We designated 4 study areas within the Red Desert encompassing 13,626 km<sup>2</sup>. We defined study area boundaries using a 100% minimum convex polygon around locations of pronghorn captured primarily within 5 WGFD Antelope Hunt Areas. The Baggs area was based in Hunt Areas 53 and 55, Bitter Creek in Hunt Area 57, Red Desert in Hunt Area 60, and Continental Divide–Creston (CDC) in a portion of Hunt Area 61 constricted by the BLM’s CDC Environmental Impact Statement (EIS) area (Fig. 1). Environmental characteristics, ownership, and levels of anthropogenic development varied across study areas, providing an opportunity to evaluate pronghorn mortality risk in response to a range of conditions (Table 1). We used infrared traffic monitors (Model TM1550, TrailMaster, Lenexa, KS, USA) to evaluate annual road traffic in Baggs and Bitter Creek to better understand vehicle volumes on lower and higher traffic

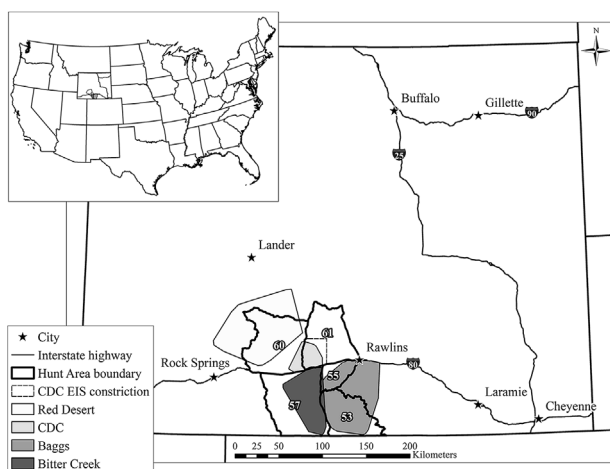
roads in study areas with low and high oil and gas development, respectively. On lower traffic roads, there was an average of 7.7 vehicles/day (range = 0.8–21.2) in Baggs and 25.2 (range = 15.5–36.8) in Bitter Creek. On higher traffic roads, there was an average of 285.7 vehicles/day (range = 56.6–482.0) in Baggs and 490.2 (range = 43.4–1981.0) in Bitter Creek.

Study areas were dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*) communities interspersed with an herbaceous understory of perennial grasses and forbs. Black greasewood (*Sarcobatus vermiculatus*) and Gardner’s saltbush (*Atriplex gardneri*) dominated low-lying areas with alkaline or saline soils. Higher elevations were dominated by mountain big sagebrush (*A. t. vaseyana*), mixed shrub communities, and aspen (*Populus tremuloides*) stands. Common mammalian species included elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed jackrabbit (*Lepus townsendii*), and common avian species included common raven (*Corvus corax*), greater sage-grouse (*Centrocercus urophasianus*), and sage thrasher (*Oreoscoptes montanus*). Topography ranged from sand deserts and gently rolling hills to badlands and buttes. Oil and natural gas extraction, livestock grazing, and big game hunting were predominant land uses. Big game hunting license quotas for female or fawn pronghorn remained low across study areas throughout the monitoring period, and did not have the potential to cause summer mortality given fall hunting season dates. In most Red Desert Hunt Areas, 25 or fewer female or fawn licenses were allotted in the 2013 and 2014 hunting seasons, with quotas for some areas increasing to as many as 100 female or fawn licenses in the 2015 hunting season (including private-lands-only hunts), after those areas experienced slight pronghorn population growth in 2014 (WGFD 1995–2015).

## METHODS

### Capture and Handling

We contracted to capture pronghorn using helicopter net-gunning (Native Range Capture Services, Ventura, CA, USA) in November 2013 and 2014. To reduce capture-related mortality rates, which can be high in pronghorn compared with other wild North American ungulates (Yoakum et al. 2014), we followed guidelines by Jacques et al. (2009a). Additionally, we administered a cold-water enema to animals whose rectal temperature approached or exceeded 40°C (Jacques et al. 2009a). We weighed each female to the nearest 0.1 kg and collected biological samples for lab analyses. We estimated age of individuals based on tooth eruption and wear (Lubinski 2001). We also developed a correction factor for age (corrected age = 0.786 × estimated age + 2.009;  $r^2 = 0.69$ ) by regressing ages for 18 dead pronghorn determined via cementum annuli analysis (WGFD Forensic Laboratory, Laramie, WY) on estimated age at death based on estimated age at capture. We fitted animals with store-on-board global positioning system (GPS; model G2110D, Advanced Telemetry Systems, Isanti, MN, USA) necklace transmitters with a uniquely



**Figure 1.** Location of the Red Desert, Continental Divide–Creston (CDC), Baggs, and Bitter Creek study areas used to evaluate adult female pronghorn summer mortality risk in the Red Desert, south-central Wyoming, USA 2013–2015. Study areas were based on 5 Wyoming Game and Fish Department pronghorn Hunt Areas and 1 Bureau of Land Management (BLM) Environmental Impact Statement (EIS) area. We delineated study area boundaries using a 100% minimum convex polygon encompassing the pronghorn locations recorded within each study area.

**Table 1.** Landscape characteristics of study areas where summer mortality risk for 114 adult female pronghorn was evaluated in the Red Desert, south-central Wyoming, USA, 2013–2015.

Landscape characteristic	Study area			
	Baggs	Bitter Creek	CDC <sup>a</sup>	Red Desert
Size (km <sup>2</sup> )	4,665	2,435	878	5,648
Elevation (m)				
$\bar{x}$	2,256	2,068	2,074	2,140
Range	1,915–3,287	1,850–2,413	1,968–2,215	1,966–2,646
30-yr precipitation (cm) <sup>b</sup>				
$\bar{x}$	45.8	25.4	19.7	25.2
Range	23.1–94.3	19.0–39.3	18.8–22.6	17.4–36.8
Land ownership (%)				
Federal	56	70	51	83
State	9	2	0	5
Private	36	28	49	12
Well density (no./km <sup>2</sup> ) <sup>c</sup>				
$\bar{x}$	0.2	0.7	0.7	0.0
Range	0.0–3.0	0.0–5.0	0.0–4.9	0.0–0.6
Fence density (km/km <sup>2</sup> ) <sup>d</sup>				
$\bar{x}$	0.4	0.3	0.3	0.1
Range	0.0–2.1	0.0–1.7	0.0–1.9	0.0–2.0
Road density (km/km <sup>2</sup> ) <sup>e</sup>				
$\bar{x}$	0.4	0.9	1.1	0.3
Range	0.0–4.0	0.0–7.1	0.0–7.1	0.0–4.9

<sup>a</sup> Continental Divide-Creston (CDC).

<sup>b</sup> 30-yr annual precipitation (1981–2010, Prism Climate Group 2017).

<sup>c</sup> Kernel density estimate of number of oil and natural gas wells/km<sup>2</sup> as of 31 December 2015 (Wyoming Oil and Gas Conservation Commission 2016).

<sup>d</sup> Line density estimate of fences within 1-km search window (Wyoming Cooperative Fish and Wildlife Research Unit).

<sup>e</sup> Line density estimate of roads within 1-km search window (O'Donnell et al. 2014).

colored and numbered ear tag to facilitate field identification. We programmed transmitters to record pronghorn locations every 2 hours over a period of 2 years. Mortality sensors on collars were triggered after 8 hours of inactivity, and we conducted aerial surveys to locate mortalities approximately every 2–3 months.

Given capture-related mortality periods used in other pronghorn research, we considered all deaths of released animals occurring within 3 weeks of capture date to be capture-related, barring evidence indicating another fate (Amstrup et al. 1980, Grogan and Lindzey 2007, Jacques et al. 2009b). Individual pronghorn were captured, handled, and monitored in accordance with protocols approved by WGFD (Chapter 33-923 Permit) and University of Wyoming Institutional Animal Care and Use Committee (protocol 20131028JB00037).

### Mortality Risk Covariates

We assessed pronghorn mortality risk with time-independent and time-dependent covariates representing intrinsic, environmental, and anthropogenic conditions (Table 2). Intrinsic covariates were time-independent and included age and body condition metrics. Environmental covariates were time-dependent and included variables related to climate and land cover. Anthropogenic covariates were time-dependent and included total distance to and density of surrounding anthropogenic features. We performed extraction of covariate values and all other analyses using RStudio and Program R (R Version 3.4.1, www.r-project.org, accessed 31 Jul 2017) and ArcMap version 10.4.1 (Environmental Systems Research Institute, Redlands,

CA). We evaluated environmental and anthropogenic covariates at each pronghorn location, and then averaged covariates for each individual during each day. Averaging accounted for differing location frequencies for each individual that occurred as a result of infrequent GPS error. We did not include correlated covariates in the same model.

*Intrinsic covariates.*—In studies assessing the body condition of sample animals, individuals are often re-captured multiple times because condition can change drastically across seasons and years (Cook et al. 2010, Monteith et al. 2013, Aikens et al. 2017). However, the high rates of capture-related mortality observed in pronghorn (Yoakum et al. 2014) increased the risk that our previously collared animals would die if re-captured, and the potential to collect longer-term movement and survival data would be lost. Therefore, we evaluated body condition only once, at each animal's single capture. For this reason, mortality risk analysis intervals spanned only the first year after capture. During November 2013 and November 2014 capture events, we assessed body condition with palpation and ultrasonography (Ibex<sup>®</sup> Pro, E. I. Medical Imaging, Loveland, CO, USA), following protocols developed and standardized for other ungulates (Stephenson et al. 2002; Cook et al. 2007, 2010). We measured maximum depth of subcutaneous fat directly cranial to the cranial process of the tuber ischium (Stephenson et al. 2002) and assigned a leanness score associated with depth of indentation between the sacroscliotic ligament and caudal vertebrae. Higher values of the leanness score reflect animals with lower somatic reserves and thus, poorer condition compared with lower scores. This score is

**Table 2.** Predictor covariates considered in pronghorn summer mortality risk modeling using Cox proportional hazards regression in the Red Desert, Wyoming, USA, 2013–2015.

Variable class	Covariate	Description
Intrinsic		
Age	AgeEst	Estimated age at mortality risk interval
	AgeCorr	Corrected age at mortality risk interval
Body condition	Mass <sup>a</sup>	Mass (kg)
	Leanness <sup>a</sup>	Leanness score associated with depth of indentation between sacrosciatic ligament and caudal vertebrae (mm)
	MaxFat <sup>a</sup>	Maximum rump fat thickness (mm)
Environmental		
Climate		
Temp	Temp <sup>b,d</sup>	Average daily temperature (°C)
Precipitation	Prec <sup>c,e</sup>	Average daily precipitation (cm)
Snow depth	Snow <sup>b,e</sup>	Average daily snow depth (cm)
Snow days	SnowDays <sup>b</sup>	Number of days animal experienced snow depths ≥25 cm
Snow × fence	SnowFence <sup>b,g</sup>	Interaction between total snow depth and fence density
Land cover		
Distance to water	DistWater <sup>c,f</sup>	Minimum distance to water (km)
Vegetative quality	NDVI <sup>c,f</sup>	Normalized difference vegetation index (NDVI)
Anthropogenic		
Distance to		
Roads	DistRd <sup>c,f</sup>	Minimum distance to road (km)
Wells	DistWell <sup>c,f</sup>	Minimum distance to well (km)
Fences	DistFence <sup>c,f</sup>	Minimum distance to fence (km)
Density of		
Roads	DensRd <sup>c,f,g</sup>	Density of roads (km/km <sup>2</sup> )
Wells	DensWell <sup>c,f,g</sup>	Density of wells (no./km <sup>2</sup> )
Fences	DensFence <sup>c,f,g</sup>	Density of fences (km/km <sup>2</sup> )

<sup>a</sup> Estimated at time of capture.

<sup>b</sup> Assessed during previous season only.

<sup>c</sup> Assessed during previous week, month, and season.

<sup>d</sup> Estimated mean, minimum, maximum, and standard deviation.

<sup>e</sup> Estimated total, maximum, and standard deviation.

<sup>f</sup> Estimated moving weekly average and cumulative weekly average since entering the study.

<sup>g</sup> Assessed within 0.5-km, 1.0-km, 3.0-km, and 5.0-km analysis regions.

comparable to validated body condition scores developed in cervids but has not yet been validated to estimate percent body fat for pronghorn (Cook et al. 2007). Therefore, we included estimates of body mass, depth of rump fat, and a leanness score as 3 metrics of body condition in analyses.

**Environmental covariates.**—We obtained daily raster layers (250-m grid) using SnowModel to evaluate covariates related to climate (temperature, precipitation, and snow depth; Liston and Elder 2006a; InterWorks Consulting LLC, Loveland, CO). SnowModel simulates processes related to snow, including but not limited to snow precipitation, blowing snow, snow-density evolution, and snow melt. The meteorological data required by SnowModel were provided by MicroMet (Liston and Elder 2006b) and included temperature, precipitation, and other meteorological variables.

We used Landfire Existing Vegetation Type raster data (LANDFIRE 2013) to assess the minimum distance to water from each location for individual pronghorn. To evaluate vegetative quality, we assessed the Normalized Difference Vegetation Index (NDVI) at each pronghorn

location using moderate-resolution imaging spectroradiometer (MODIS) terra satellite data products, collected once every 8 days. The NDVI is often used as a proxy for forage quality because it measures vegetative greenness across the landscape (Hamel et al. 2009).

**Anthropogenic covariates.**—We used fence data obtained from the Wyoming Cooperative Fish and Wildlife Research Unit and 2009 National Agricultural Imagery Program Imagery-derived road data from the United States Geological Survey (O'Donnell et al. 2014). We obtained locations of producing oil and gas wells from the Wyoming Oil and Gas Conservation Commission (WOGCC 2016). We filtered wells by spud date (i.e., the date when drilling activity began) to ensure wells were present during the time when we recorded individual pronghorn locations. If first spud date was not available, we used the completion date (i.e., the date of the first completion report filing).

We assessed the daily average of most land cover and all anthropogenic covariates over the previous week, month, and season (winter). We evaluated temperature and snow depth-related variables over the previous season (winter) only because these covariates were unlikely to influence summer mortality risk during other times of the year. Additionally, we evaluated the moving weekly average ( $\bar{x}$  of daily  $\bar{x}$  during the previous week for each individual since entering the study), and cumulative weekly values (sum of daily  $\bar{x}$  during the previous week for each individual since entering the study). All animals compared during a given time interval in mortality risk modeling had the same period of exposure since capture, and therefore, the use of cumulative variables was justified. We also assessed the potential influence of the density of fences, roads, and oil and gas wells across 4 spatial scales (0.5 km, 1 km, 3 km, and 5 km; Buchanan et al. 2014) for each of the 5 time periods: weekly, monthly, seasonally, moving weekly average, and cumulative weekly. We additionally evaluated the potential effect of the interaction between an environmental variable (snow depth) and an anthropogenic variable (fence density) across these 4 spatial scales.

### Mortality Risk Modeling

We used the Andersen-Gill formulation of the Cox's (1972) proportional hazards regression model with mixed effects to assess pronghorn mortality risk for summers 2014 and 2015 with the coxme package in Program R (Therneau 2015, R package version 2.2.5, www.r-project.org, accessed 1 Nov 2014). This method models mortality as intervals of risk, and allows for multiple observations and staggered entry of individuals (Cox 1972, Andersen and Gill 1982). We defined seasons based on population-averaged dates of individual seasonal movement using net squared displacement. Net squared displacement is a measure of the straight-line distance between an animal's first location and each subsequent location, and can be used to visually designate periods of migratory and non-migratory movement behavior (Bunnfeld et al. 2011). We defined summer as the period between when the individual arrived on summer range and traveled to winter range. We did not use non-migratory

individuals to determine season dates, and defined their seasonal range use periods by the mean dates of seasonal use periods of migratory individuals. Mean dates for individuals occupying summer range in 2014 and 2015 were 6 April–29 November and 22 March–24 October, respectively.

We assessed weekly mortality risk for summer 2014 and 2015 as a function of covariates related to intrinsic, environmental, and anthropogenic conditions experienced by marked adult female pronghorn (Table 2). We used locational data collected outside of the summer seasons to generate lag-time, moving average, and cumulative covariate values, but we did not include these data in our evaluation of weekly intervals of mortality risk. We right censored pronghorn that were captured in November 2013 and survived the entire study period so that mortality risk was evaluated only during the first summer after capture. We did not include in analyses any sample animals that died prior to the summer season after capture.

We first determined whether study area, individual, or year, or 2-variable combinations of these covariates would serve as the best random covariate(s) by ranking models with Akaike's Information Criterion (AIC). We considered the most predictive random effects only model to be the null model for subsequent model evaluation. We used the same technique to compare single covariate models containing each individual survivorship covariate and our best random effects only model. We retained covariates in models ranking better than the null model, and assessed only the most predictive spatial and temporal scale of each variable. We then created a global model containing all remaining covariates and the best random effect, and tested all possible combinations of non-correlated global model covariates to determine the predictive value of all possible models ( $|r| \leq 0.6$ ). We determined a top model with AIC rank, and considered models within 4  $\Delta$ AIC of the top model competitive (Arnold 2010); however, we considered covariates in competitive models to be predictive of mortality risk if they were significant at the 85% confidence level.

We evaluated final model performance using multiple techniques. We assessed Schoenfeld residuals to evaluate the assumption of proportional hazards (indicated by a trend line with a slope near zero and residuals that are randomly distributed; Schoenfeld 1982). We also evaluated a concordance ( $c$ ) index for the top model to determine its predictive

ability (Pencina and D'Agostino 2004). A maximum  $c$  index value of 1.0 indicates perfect concordance between observed and predictive responses, and  $c$  index values  $\geq 0.8$  indicate models with good predictive capabilities (Pencina and D'Agostino 2004). We calculated variance inflation factors for coefficients in the top model. Variance inflation factor values  $\leq 5$  indicate a lack of inflation resulting from collinear variables being included in the same model (Heiberger and Holland 2004).

## RESULTS

We used data from 151 adult female pronghorn captured and released during 2 events (113 adult female pronghorn in Nov 2013 and 38 in Nov 2014). We excluded 14 individuals because of cause of death (12 died as a result of capture and 2 were likely harvested illegally), and we excluded 6 because they died before the summer season. In addition, we did not relocate 5 individuals, and 11 transmitters were still deployed at the time of analysis. We excluded 1 individual because of collar malfunction. We thus evaluated mortality risk for 114 adult female pronghorn (38 from Baggs, 38 from Bitter Creek, 27 from Red Desert, and 11 from CDC) using 470,126 locations and 24 (21.1% of 114 pronghorn) mortality events. Naïve survival estimates for summer 2014 and 2015 were 80.0% (72 survived of 90) and 75.0% (18 survived of 24), respectively.

### Mortality Risk Modeling

We used year as a random effect in all models because it had the lowest AIC value compared to other combinations of random effects. Seven covariates ranked above the null model in single-covariate modeling, and of these, 4 were included in the global model to be tested in all combinations because they were the best spatial or temporal scales for that covariate and were uncorrelated with other variables. Covariates included in the global model were leanness score at time of capture (leanness), cumulative total of each week's average daily distance to water, standard deviation in daily snow depth during the previous winter, and corrected age.

Results from testing all possible combinations of these 4 covariates indicated that all models were competitive (within 4  $\Delta$ AIC of top model), including the null model (Table 3). The top model contained covariates related to our intrinsic and environmental hypotheses, but none related to our

**Table 3.** Model fit statistics for models comprised of all possible combinations of non-correlated global model covariates, used to evaluate pronghorn summer mortality in the Red Desert, south-central Wyoming, USA 2013–2015. Models shown include top 3 models and the null model. All models were competitive (within 4  $\Delta$ AIC of the top model; Arnold 2010). We report the number of parameters in each model ( $K$ ), Akaike's Information Criterion (AIC), difference in AIC from the top model ( $\Delta$ AIC), AIC weights ( $w_i$ ), and log likelihood (LL).

Hypothesis testing model	$K$	AIC	$\Delta$ AIC	$w_i$	LL
Leanness <sup>a</sup> + SDSnow_Seas <sup>b</sup>	2	190.3	0.0	0.1	–93.2
Leanness <sup>a</sup> + SDSnow_Seas <sup>b</sup> + CumAvgDistWater <sup>c</sup>	3	190.6	0.2	0.1	–92.3
Leanness <sup>a</sup> + SDSnow_Seas <sup>b</sup> + AgeCorr <sup>d</sup>	3	191.5	1.1	0.1	–92.7
Null	0	194.1	3.8	0.0	–97.1

<sup>a</sup> Leanness score associated with depth of indentation between sacrosciatic ligament and caudal vertebrae at time of capture (mm).

<sup>b</sup> Standard deviation in average daily snow depth during the previous winter season (cm).

<sup>c</sup> Cumulative total of each week's average daily distance to water (km).

<sup>d</sup> Corrected age (years; based on age at time of capture).

anthropogenic hypothesis. The model best explaining summer mortality risk in adult female pronghorn in the Red Desert included leanness and standard deviation in daily snow depth during the previous winter. Although a model containing all 4 covariates was competitive, only the leanness and standard deviation in daily snow depth during the previous winter covariates were significant at the 85% confidence level. Pronghorn summer mortality risk increased by 5% for every 1-mm increase in leanness and by 19% for every 1-cm increase in standard deviation in daily snow depth during the previous winter (Table 4; Fig. 2). Average leanness score (mm) at time of capture for pronghorn that died was 1.3-times greater ( $22.1 \pm 1.8$  [SE]) compared to pronghorn that survived ( $17.5 \pm 1.1$ ). Pronghorn that died were exposed to an average standard deviation in daily snow depth (cm) during the previous winter ( $6.4 \pm 0.5$ ) 1.1-times greater than that experienced by pronghorn that survived ( $5.7 \pm 0.2$ ).

Analysis of Schoenfeld residuals revealed a trendline with a near-zero slope and randomly distributed residuals, indicating that the assumption of proportional hazards was met. The *c* index value for our best model was 0.74, indicating our model had moderate concordance between observed and predicted summer mortality risk of pronghorn. Variance inflation factor values for coefficients in the final model were  $\leq 5$ , indicating that no collinearity of coefficients in the model resulted in variance inflation.

## DISCUSSION

Risk of mortality for adult female pronghorn in the Red Desert of Wyoming in summers 2014 and 2015 was explained in part by a combination of intrinsic and environmental factors, but we did not detect an influence of anthropogenic features. Summer mortality risk was heightened by poorer early-winter body condition and by exposure to greater variation in snow depth during the previous winter. Naïve survival estimates for adult females in summers 2014 and 2015 (80% and 75%, respectively) were relatively high and consistent with survival estimates of adult female pronghorn in other areas of Wyoming (Beckmann et al. 2008).

Although intrinsic and environmental factors influenced summer mortality risk of adult female pronghorn in the Red Desert, energy development, a common land use in the region, is a growing concern for many species worldwide. Oil and natural gas fields, particularly, pose a potential threat to the fitness of many species that spend a substantial portion of

time in sagebrush environments (Copeland et al. 2009). Such development and its associated infrastructure has, for example, caused reduced survival of adult females (Holloran 2005) and lek attendance by males (Gregory and Beck 2014) in greater sage-grouse and increased avoidance of developed areas by mule deer (Sawyer et al. 2006) and elk (Buchanan et al. 2014). Although natural gas development may have a demonstrated effect on resource selection in pronghorn (Beckmann et al. 2012, Seidler et al. 2015), like other studies (Beckmann et al. 2008, 2016), we did not detect an influence of density of or proximity to oil and natural gas wells on mortality risk of adult female pronghorn. However, any negative influences of oil and natural gas development on pronghorn fitness may lag behind the observed behavioral changes in resource selection and movement associated with this infrastructure (Beckmann et al. 2016), in which case such demographic effects would not be detected except over a longer monitoring period.

Similarly, we found no effect of density of and proximity to roads and fences on adult female pronghorn summer mortality risk in the Red Desert. In addition to the hypothesis that animals may perceive such linear features as a source of risk (Frid and Dill 2002, Gavin and Komers 2006), they can impose a strong barrier effect on pronghorn movement (Sheldon 2005, Gates et al. 2012, Sawyer et al. 2013). Fences and roads may prevent pronghorn from accessing high-quality resources, which become increasingly important during periods of high energetic demand or harsh environmental conditions (Yoakum et al. 2014). The ability to move to areas that offer better resources, such as higher quality forage, may be even more important for pronghorn, as an animal potentially employing more of an income strategy (Clancey et al. 2012), than many other ungulates in western North America that may rely more heavily on previously accrued energy reserves. Though there have been demonstrated changes in pronghorn movement behavior in relation to roads and fences (Sheldon 2005, Gates et al. 2012, Sawyer et al. 2013, Yoakum et al. 2014), and direct mortality caused by these features (O’Gara and Yoakum 2004, Gavin and Komers 2006, Harrington and Conover 2006, Kolar et al. 2012), we found no evidence of an indirect effect of roads and fences on pronghorn mortality risk.

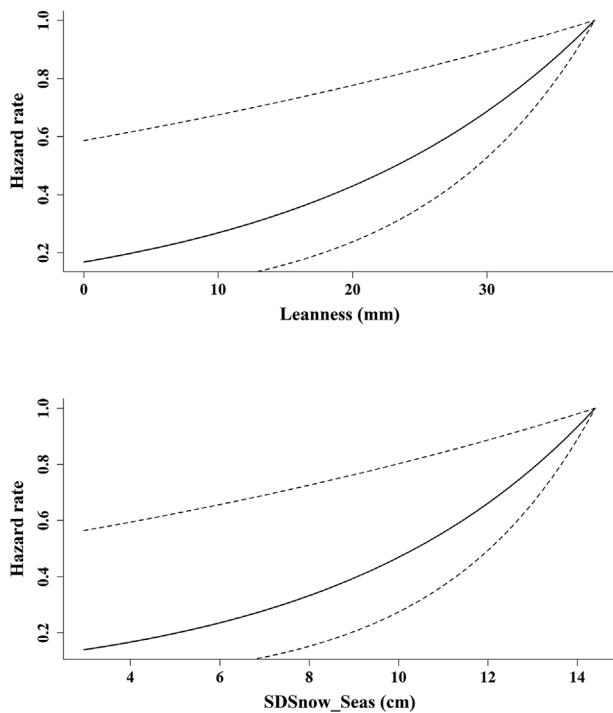
Although we found no impact of anthropogenic conditions, we found that energetic resources played an important role in risk of summer mortality for adult females in the Red Desert of Wyoming. Body condition upon entering winter may dictate an animal’s ability to survive that

**Table 4.** Parameter estimates for the top model predictive of summer mortality risk for pronghorn in the Red Desert, south-central Wyoming, USA, 2013–2015.

Variable	$\beta$	SE	Hazard ratio [exp(coefficient)]	Hazard ratio 85% CI	
				Lower	Upper
Leanness <sup>a</sup>	0.047	0.023	1.05	1.02	1.08
SDSnow_Seas <sup>b</sup>	0.172	0.085	1.19	1.07	1.31

<sup>a</sup> Leanness score associated with depth of indentation between sacrosciatic ligament and caudal vertebrae at time of capture (mm).

<sup>b</sup> Standard deviation in average daily snow depth during the previous winter season (cm).



**Figure 2.** Hazard rates for mortality factors in the final model predicting adult female pronghorn summer mortality risk in the Red Desert, south-central Wyoming, USA, 2013–2015. Hazard rates are plotted with 85% confidence intervals. Variables include leanness score associated with depth of indentation between sacrosciatic ligament and caudal vertebrae (leanness) and standard deviation in daily snow depth during the previous winter (SDSnow\_Seas). Higher leanness values indicate animals in poorer condition at the time of capture, and higher SDSnow\_Seas values indicate animals that experienced greater variability in snow depth during the previous winter.

winter season and may also affect their ability to endure the costly period of reproduction that follows (Jönsson 1997, Monteith et al. 2013). Pronghorn inhabiting northern regions fare worse in snow than many other ungulate species, largely because of their small hoof area relative to body weight (Telfer and Kelsall 1984), and they struggle with snow depths  $\geq 25$  cm (Bruns 1977, Yoakum et al. 2014). When animals experience increased variation in snow depth, and likely increased exposure to deep snow, they deplete energy reserves by incurring increased energetic costs associated with locomotion, foraging, and potentially fasting (Barrett 1982, Parker et al. 1984). These costs can be heightened when deep snow is coupled with fencing (Gates et al. 2012). Pronghorn usually elect to crawl under fences, rather than jump over them (O’Gara and Yoakum 2004), and deep snow filling the depression underneath fences can cause wildlife-friendly fencing to become an impermeable barrier (Bruns 1977, Sheldon 2005, Yoakum et al. 2014). Loss of energy reserves during winter seasons may be exacerbated by anthropogenic features like fences, and it is therefore possible for anthropogenic conditions to play a role in pronghorn mortality risk. However, we did not detect an effect of the interaction between total snow experienced and fence density during the previous winter on summer mortality risk at any spatial scale. The decreases in fat stores commonly seen in

winter make it more difficult to fuel reproduction and survival the following summer, a pattern that is intensified by the extreme reproductive effort of pronghorn relative to other ungulates (Robbins and Robbins 1979). Our results showed that body condition and exposure to increased variability in snow depth during the previous winter were important components of summer mortality risk for adult female pronghorn. Additionally, NDVI was not predictive of mortality risk, potentially suggesting that it is difficult for pronghorn to recover from the energetic losses associated with the winter season and poor body condition, even with exposure to high quality vegetation. Although pronghorn may display many characteristics consistent with ungulates using income to finance energetic expenditures (Clancey et al. 2012), they are dependent on the maintenance of stored energy reserves for survival.

## MANAGEMENT IMPLICATIONS

Our results indicate that variability in snow depth, coupled with the high energetic demand pronghorn face during gestation and lactation, may affect their ability to fuel their own survival through summer. Thus, during harsh winters with fluctuating snow conditions, it is likely that managers in Wyoming will observe higher over-winter mortality in pronghorn and increased mortality during the following summer. We did not find evidence that anthropogenic conditions within the Red Desert were influencing summer mortality of adult female pronghorn, and we did not detect an effect of the interaction between total snow depth and fence density experienced during the previous winter on summer mortality.

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