





Research Article

Annual Pronghorn Survival of a Partially Migratory Population

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ABSTRACT The importance of conserving migratory populations is recognized across a variety of ungulate taxa, yet the demographic benefits of migration remain uncertain for ungulate populations that exhibit partial migration. We hypothesized that migratory pronghorn (*Antilocapra americana*) would experience greater survival compared to residents by moving longer distances to avoid severe winter weather and access higher quality forage. We used a Bayesian time-to-event approach to analyze the fates of 175 radio-collared adult female pronghorn monitored over 8 biological years (2004–2011) in the Northern Sagebrush Steppe ecosystem. Annual survivorship of migratory pronghorn was 7% higher on average compared to residents but not statistically different. Migratory pronghorn had higher survivorship in summer and winter compared to residents, and few mortalities were observed during the short autumn and spring migration periods. Mortality risk for both movement tactics intensified under more severe winter weather; winter weather severity alone best explained annual pronghorn mortality risk. The top model predicted survival rates to decline on average by 56% over the range of observed winter climatic conditions. To minimize human impacts to pronghorn during extreme climatic events, we recommend working with transportation departments and land managers to enhance pronghorn crossings of roads and railroads, and landholders to modify fences to wildlife-friendly standards. © 2020 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, LLC on behalf of The Wildlife Society.

KEY WORDS adult female survival, Alberta, *Antilocapra americana*, Bayesian, movement tactics, Montana, pronghorn, Saskatchewan, winter severity.

Concerns are growing worldwide over the loss of animal movement due to increased human activity from roads, fences, and energy development (Berger 2004, Jakes et al. 2018a, Tucker et al. 2018, Berg et al. 2019). For instance, a recent meta-analysis demonstrated that mammals inhabiting areas of relatively high human activity had movements reduced by a third to a half compared to areas of low human activity (Tucker et al. 2018). The loss of movement has cascading ecological effects on forage

biomass, nutrient cycling, predator-prey dynamics, and ecosystem function, especially for species that undertake migration (McNaughton et al. 1988, Fortin et al. 2005, Bauer and Hoye 2014, Runge et al. 2014). Given the strong potential for expanding human activity, a concerted effort is needed to maintain migratory behavior and document the demographic importance of migration for populations (Berger 2004, Harris et al. 2009, Runge et al. 2014).

Migration is defined as an individual behavioral response to variability in environmental conditions exhibited as movements between discrete seasonal ranges (Berger 2004, Dingle and Drake 2007, Gaillard 2013). Individuals undertaking migration benefit from access to higher quality resources and lower predation risk, which often translates into increased individual fitness (i.e., reproductive rates, survival) for migratory species such as ungulates (Fryxell et al. 1988, Gaidet and Lecomte 2013, Gaillard 2013). For example, Fryxell et al. (1988) demonstrated higher survival in migratory ungulates in Africa owing to lower predation rates from large carnivores. Also, Middleton et al. (2018) demonstrated that a migratory elk's (*Cervus canadensis*) ability to follow spring

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green-up of nutritional forage (i.e., surf the green wave) translated into improved adult female body condition and pregnancy rates that were large enough to influence population growth. Clearly, migration offers fitness advantages that could result in migration evolving as the only tactic in an ungulate population (Kaitala et al. 1993, Gaillard 2013). Ungulate populations, however, exhibit different levels of migration from fully migratory, to only a portion of the population being migratory, to resident.

Many ungulate populations are partially migratory because of the demographic tradeoffs of making long-distance movements between seasonal ranges (Ball et al. 2001, Hebblewhite et al. 2008, Hebblewhite and Merrill 2011, Gaillard 2013). The expectation for partially migratory populations is often that migration confers demographic advantages over the resident tactic (Fryxell et al. 1988, Berg et al. 2019). Hebblewhite et al. (2008) documented this with higher fecal nitrogen levels, pregnancy rates, and 6-month-old elk calf weights in migratory elk that surfed the green wave compared to resident animals in the same population. Migratory elk in this population were also exposed to lower wolf (*Canis lupus*) predation risk than residents (Robinson et al. 2010). More recent studies demonstrated equivalent demographic rates between the 2 tactics despite large changes in population density over time (Hebblewhite et al. 2018). These equivalent fitness payoffs for the 2 tactics resulted because predation was not dependent on density and climatic factors affected migrants and residents equally as the population declined. Conversely, residents may become more prevalent in the population over time because of anthropogenic influences (Bolger et al. 2008, Wilmers and Levi 2013) where the decision to remain a resident may be dictated by the amount of agricultural land (Henderson et al. 2018) or level of human presence (Hebblewhite et al. 2006, Robinson et al. 2010). Other studies highlight the strong influence of environmental variability in influencing partial migration (Kaitala et al. 1993, Peters et al. 2019), where a greater proportion of temperate ungulate populations are expected to exhibit migratory behavior at the northern periphery of their range because of extremes in environmental conditions (Kaitala et al. 1993).

In the northern periphery of pronghorn (*Antilocapra americana*) distribution known as the Northern Sagebrush Steppe (NSS) ecosystem in Alberta and Saskatchewan, Canada, and northern Montana, USA, populations are partially migratory with 55% of individuals making seasonal migrations on average including the longest recorded annual migration movement for the species of approximately 888 km (Jakes et al. 2018b). Pronghorn in the NSS face severe winter conditions that can translate into mass-mortality events (Martinka 1967, Wishart 1970, Hnatiuk 1972, Barrett 1982a). For example, Martinka (1967) reported a minimum loss of 500 pronghorn in 1965 near Glasgow, Montana, as a result of severe winter weather. Similarly, Barrett (1982a) reported mortality rates near 50% for a population of nearly 15,000 pronghorn in Alberta during winter 1978. He attributed the high mortality rates to poor body condition as a result of winter weather severity. Although studies have highlighted the effects of winter

weather on pronghorn survival (Taylor et al. 2016) and indices of abundance (Christie et al. 2015), few if any have addressed the extent that migration may mitigate the negative effects of winter severity on survival or documented cause-specific mortality factors in pronghorn populations.

Our broad objective was to examine differences in survival and factors influencing mortality risk for a partially migratory population of pronghorn in the NSS that is exposed to large interannual variation in winter weather conditions. First, we tested whether migratory individuals would experience greater annual survival compared to resident individuals because migration reduces the mortality risk from severe climatic conditions. We predicted that because migrants have better body condition as a result of access to higher forage quality (Hebblewhite et al. 2008, Cook et al. 2013), the greatest difference in migrant and resident survival rates would occur during years with especially severe winter weather (Fieberg et al. 2008). Alternatively, pronghorn may face similar mortality risk during severe winter weather conditions regardless of movement tactic because winter climate effects might negate differences in body condition. Second, on a seasonal basis, we predicted survivorship for both movement tactics would be lowest during winter and the following spring when body condition would be poorest (Barrett 1982a, O'Gara 2004, Reinking et al. 2018). Lastly, we determined rates of cause-specific mortality factors and predicted for migratory individuals that the primary cause of mortality would be anthropogenic (i.e., collisions on roads, railroads), whereas for resident individuals we predicted the primary cause would be from natural, non-predation causes (i.e., winter starvation). In summary, we predicted higher survivorship for migratory pronghorn, that mortality factors would depend on movement tactic, and that the effects of winter severity on annual survivorship would also depend on movement tactic.

STUDY AREA

Our study occurred between 2003 and 2011 and encompassed 315,876 km² of the prairie regions of Alberta, Saskatchewan, and northern Montana in the NSS (50.0757°N, -108.7526°W). Human populations were sparsely distributed with few urban population centers (Fig. 1). Cattle grazing was the dominant land use in Alberta and Montana, whereas crop production was generally more prevalent in Saskatchewan. Oil and natural gas wells occurred at high densities in Alberta and continue to be developed in Saskatchewan and Montana. The region is considered semi-arid and received an annual mean of 39.2 cm of precipitation, with approximately 70% received as rainfall (Environment Canada 2010). We defined 4 seasonal intervals as winter (11 Nov–21 Mar), spring (22 Mar–10 Apr), summer (11 Apr–30 Oct), and autumn (31 Oct–10 Nov). The winter of 2010–2011 was considered extreme for the region with cold temperatures and record snow accumulation (Fig. S1, available online in Supporting Information).

The landscape was characterized by flat, open plains and rolling hills as a result of glacial recession and deposits, with prevalent badlands and deep coulees throughout the region (Mitchell 1980). Elevation ranged from 482–910 m. The

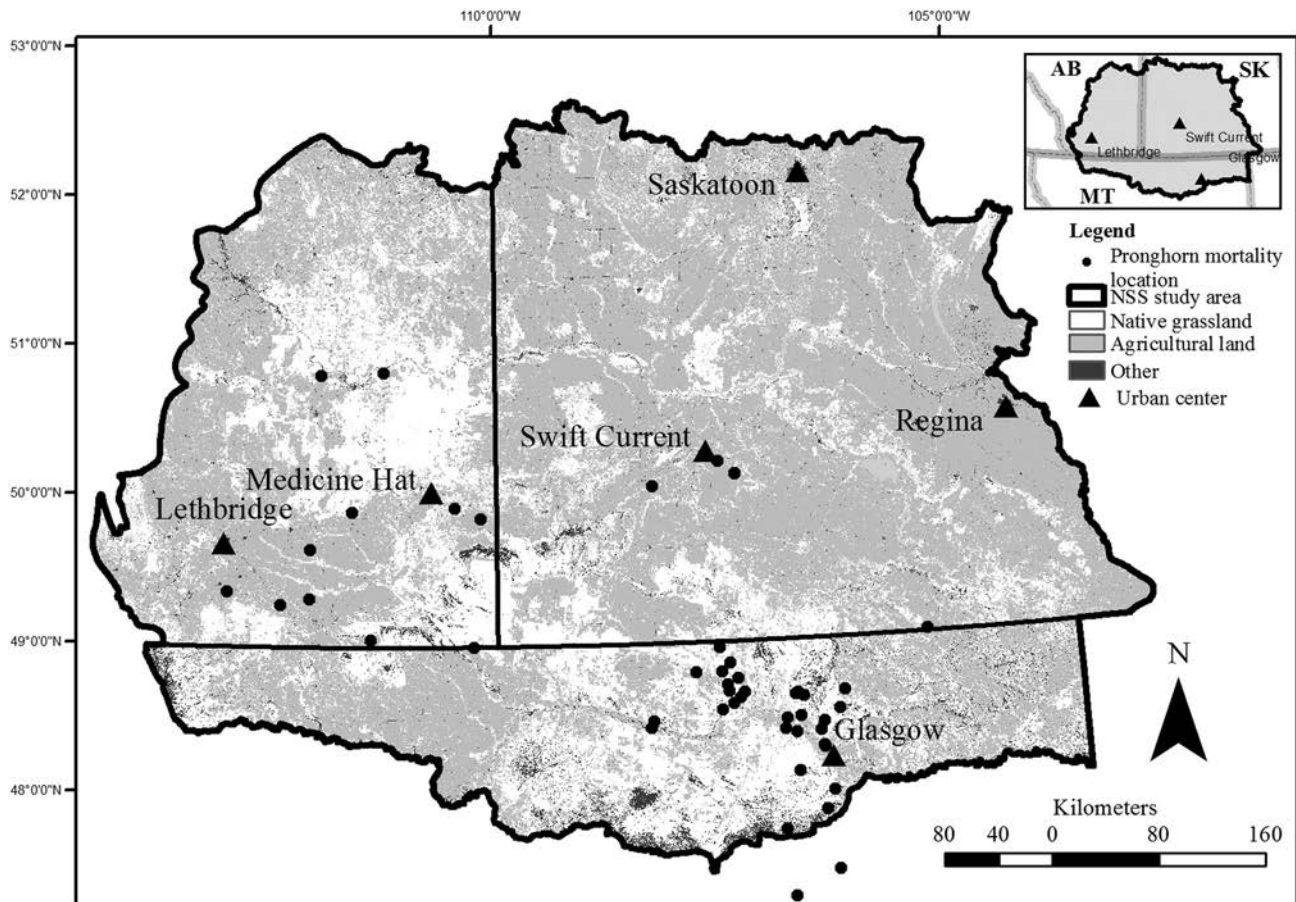


Figure 1. Mortality locations of radio-collared adult female pronghorn within the Northern Sagebrush Steppe (NSS) study area encompassing southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011). The 2 mortality locations outside of the study area were from individuals that moved south during the extreme winter of 2010–2011. Coordinate system on top and left side are latitude and longitude. We determined the boundary for the NSS study area based on a memorandum of understanding signed between the government agencies for Alberta, Saskatchewan, and Montana and it represents an area of grasslands (i.e., Northern Sagebrush Steppe) for a concerted holistic management approach for wildlife.

vegetation types included a mosaic of native prairie grasses such as blue grama (*Bouteloua gracilis*), June grass (*Koeleria macrantha*), needle and thread grass (*Hesperostipa comata*), and western wheatgrass (*Pascopyrum smithii*); tame pastures seeded to non-native forages; and irrigated and dryland agricultural fields. Dominant shrubs were big (*Artemisia tridentata*) and silver sagebrush (*A. cana*), creeping juniper (*Juniperus horizontalis*), and western snowberry (*Symphoricarpos occidentalis*). Major cultivated crops included alfalfa hay, canola, mustard, peas, and wheat (Mitchell 1980). The main predators of pronghorn in the area included coyotes (*Canis latrans*), golden eagle (*Aquila chrysaetos*), and bobcats (*Lynx rufus*; Bruns 1970, Barrett 1982b, Jones et al. 2015a).

METHODS

Capture, Collaring, and Monitoring

We captured adult female pronghorn using a net fired from a helicopter (Jacques et al. 2009) across the NSS from 2003–2010 and fitted each female with a global positioning system (GPS) collar (Lotek GPS 3300 and ARGOS 7000SA models; Lotek Wireless, Newmarket, Ontario, Canada). We processed all captured pronghorn on-site and released them as

quickly as possible after handling to reduce risk of capture myopathy (Yoakum et al. 2014). We captured pronghorn in a mixture of native and cultivated areas in Alberta in 2003–2007 but in predominately native habitat in Saskatchewan and Montana in 2008–2011. Each GPS collar was equipped with a mortality sensor that was activated following 4 hours of no movement of the collar. All capture and handling protocols conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011). Capture protocols were approved by Alberta Fish and Wildlife (Alberta Sustainable Resource Development, Fish and Wildlife Research Permits 11861, 16707, and 20394), Montana Fish, Wildlife & Parks (Research Permit 11-2007), and the Saskatchewan Ministry of Environment (Research Permit 09FW040). Additional details on capture protocol are provided in Jones et al. (2015b) and Jakes et al. (2018b).

We used a monthly relocation schedule to monitor pronghorn with active GPS collars because the intent of the overall study was to assess migration, movement, and resource selection and a finer-scale relocation schedule was not required because all daily locations and mortality sensor data were stored in the GPS collar. If a mortality signal was detected during the relocation, we visited the site to retrieve

the collar and to assess potential cause of mortality. This approach allowed us to make inference into pronghorn survival and risk factors but limited our ability to determine mortality cause with certainty for a large proportion of cases; thus, we considered our cause-specific mortality data as ancillary in this analysis.

Bayesian Time-to-Event Analysis

We used Bayesian analysis to estimate pronghorn survival, mortality rates, and to conduct mortality risk regression from time-to-event data (Ibrahim et al. 2001). We opted for a Bayesian approach to accommodate individuals with unknown movement tactics. This allowed us to use the entire dataset rather than discard valuable data because of missing observations in explanatory variables. We used a simple approach based on the observed proportion of migratory pronghorn to model the missing data (Kéry and Schaub 2012). As a validation measure, we compared Bayesian and frequentist estimates, but we focus our inferences on the Bayesian analysis. Intuitively, we expected that parameter estimates from the 2 statistical approaches would closely agree if our Bayesian prior specifications were uninformative to posterior distributions.

Counting process formulation.—The connection between Cox proportional hazards (PH; Cox 1972) and Poisson regression is established in time-to-event analysis (Johansen 1983, Broström 2012). Specifically, the treatment of failure times as counting process data allows the Cox PH model to be generalized to include time-dependent risk factors (Andersen and Gill 1982, Therneau and Grambsch 2000) and to be estimated using Bayesian methods (Clayton 1991, Ibrahim et al. 2001).

The Bayesian PH model specifies the form of the likelihood for the data and prior distributions to estimate the baseline hazard function Λ_{0j} . For each individual, the counting data included the number of failures N_{ij} observed over the time interval $(t, t + dt)$ and an indicator of their status in the risk set at time t_j (i.e., $Y_{ij} = 1$ if at risk or $Y_{ij} = 0$ otherwise), where t_1, \dots, t_J are the unique observed failure times (note that d represents change in a variable such as time t , i.e., dt). We assumed the counting process increments (or jumps), $dN_{ij} = 1$ if pronghorn i fails at time t_j and $dN_{ij} = 0$ otherwise, were independent Poisson random variables with mean intensity $d\Lambda_{ij}$. It follows that $d\Lambda_{ij} = Y_{ij} d\Lambda_{0j} \exp(\beta X_i)$ where $d\Lambda_{0j}$ is the jump in the baseline hazard function Λ_{0j} , β are log hazard coefficients, and X_i are risk covariates for the i th individual. Thus, we can express the full posterior and joint distributions for the Bayesian PH model as:

$$\begin{aligned}
 & [d\Lambda_{0j}, \beta | dN_{ij}, Y_{ij}, X_i] \\
 & \propto \prod_{i=1}^n \prod_{j=1}^J \text{Poisson}(dN_{ij} | Y_{ij} d\Lambda_{0j} \exp(\beta X_i)) \\
 & \times \text{gamma}(d\Lambda_{0j} | c \times d\Lambda_{0j}^*, c) \times \text{Normal}(\beta | 0, 10^4)
 \end{aligned} \tag{1}$$

We specified diffuse $\text{Normal}(0, 10^4)$ priors for β and adopted the conjugate independent increments prior for $d\Lambda_{0j}$

(Kalbfleisch 1978), where $d\Lambda_{0j}^*$ is a prior guess for $d\Lambda_{0j}$ and c adjusts the prior precision with small values of c corresponding to weak prior knowledge. We used $c = 0.001$ and $r = 0.003$ to derive a prior guess as $d\Lambda_{0j}^* = r \times dt$. We derived hazard ratios (HRs) by exponentiating log hazard coefficients.

Survivorship and cause-specific mortality.—We tested whether migratory and resident adult female pronghorn experienced different survivorship in a partially migratory population that is exposed to large interannual variation in winter weather conditions. We based the survival periods on the median migration dates determined from GPS-collared pronghorn (Jakes et al. 2018b). We defined the annual (recurrent) survival origin as 11 November and seasonal intervals as winter, spring, summer, and autumn. We left-truncated individuals based on capture date (i.e., left-staggered entry), and right-censored individuals that experienced radio-collar failure, had a collar we could no longer detect, had mortality signals we could not investigate, or survived the monitoring period (DeCesare et al. 2016). We censored individuals that had collar-related failures or could no longer be detected on the day following the date they were last heard live. We removed individuals that died because of capture-related causes.

We conservatively classified mortalities and assigned mortalities as unknown if insufficient evidence remained to determine the cause of death with high certainty. Thus, we categorized cause of mortality for pronghorn as roadkill or train collision (i.e., anthropogenic), predation, winterkill (i.e., natural, non-predation), and unknown mortality following Wade and Bowns (1982) and Alt and Eckert (2017). We expected a high proportion of unknown mortalities because of the relatively long time interval between radio-signal checks, which is common for studies of adult female ungulates that typically have high and constant survival (Gaillard et al. 2000).

We used the results of Jakes et al. (2018b) to assign migratory tactic to individual pronghorn. Briefly, we used non-linear models of net squared displacement (Bunnfeld et al. 2011) to classify migration periods and stratify individuals into migratory, mixed-migratory, or resident. We then further stratified individuals into 2 classes by combining the mixed-migratory and migratory classes, where we defined migrants as individuals that moved between 2 distinct seasonal ranges in a biological year and residents as those that remained year-round on a single range. We then estimated annual and seasonal survivorship and cause-specific mortality rates separately for each movement tactic and by pooling all observations (including those with unknown movement tactic).

In our Bayesian approach, we were able to simultaneously estimate survivorship and cause-specific mortality rates along with their uncertainty in the same model. We first used the estimated baseline hazard function Λ_{0j} to derive annual and seasonal survivorship functions as $S_{0j} = \exp(-\Lambda_{0j})$. We then estimated cause-specific mortality rates in a competing risks framework by including separate Poisson likelihoods in the model for each mortality cause. Specifically, we estimated cumulative

incidence functions (CIFs) to account for pronghorn exposure to multiple, mutually exclusive mortality risks (Heisey and Patterson 2006). We coded the observations for each k mortality cause as $dN_{ijk} = 1$ if the subject died from cause k and 0 otherwise, where the unique failure times were specific to each cause (Heisey and Patterson 2006). To describe the annual phenology of cause-specific mortality events among migrants and residents, we estimated smoothed functions of the daily cause-specific hazards using penalized B-splines in Bayesian generalized linear mixed models (Eilers and Marx 1996, Rebola et al. 2014, Lee et al. 2017).

Factors influencing annual mortality risk.—We evaluated the statistical support for our hypothesis that migration dampens the negative effects of winter severity on pronghorn mortality risk by testing for an interaction between movement tactic (Tactic) and winter severity index (WSI) in the following PH model:

$$d\Lambda_{ij} = Y_{ij} d\Lambda_{0j} \exp(\beta_1 \text{Tactic}_i + \beta_2 \text{WSI}_i + \beta_3 \text{Tactic}_i \times \text{WSI}_i), \quad (2)$$

where $d\Lambda_{ij}$ is the random intensity process for the i th individual at the j th unique failure time. We predicted that β_1 would be negative (i.e., $\text{HR} < 1$), β_2 would be positive, and the interaction term β_3 would be negative with residents set as the reference group. Along with testing our main hypothesis, we extended our Bayesian approach to a competing risks regression model to determine whether there were any important differences in the effect of winter severity on the cause-specific hazard functions. We replicated the data once for each mortality source following Lunn and McNeil (1995) and coded individuals as 1 if the subject died from cause k and 0 otherwise within each augmented dataset. We then fit a stratified Bayesian PH model to estimate cause-specific hazard ratios for annual pronghorn mortality risk (Heisey and Patterson 2006).

We calculated WSI for our regression analyses following Brinkman et al. (2005); the index accumulates 1 point for each day that the average temperature was $\leq -7^\circ\text{C}$ and 1 point for each day that the snow depth was ≥ 35 cm during winter. We retrieved snow depth (cm) and average daily temperature ($^\circ\text{C}$) from the Medicine Hat weather station (www.climate.weather.gc.ca, accessed 15 Sep 2019) for the biological years of 2004–2007 and from the Malta weather station for 2008–2011 (www.noaa.gov, accessed 15 Sep 2019). We standardized WSI for all analyses by subtracting the mean and dividing by 2 times the standard deviation (Gelman 2008) but report unstandardized effect sizes.

Model selection and posterior checks.—We used Gibbs variable selection (GVS) to determine the most-supported Bayesian PH model (Ntzoufras 2002, Tenan et al. 2014). The GVS procedure introduces a binary indicator variable (γ_j) for each j parameter under consideration in the model to compute posterior model probabilities. Because GVS tends to select simpler models as the priors become more diffuse, we evaluated posterior model probabilities using a

sensitivity analysis following Tenan et al. (2014). We considered 5 prior sets for log risk coefficients (β) that we assumed arose from a $\text{Normal}(0, \sigma^2)$ distribution for variances (σ^2) $\in \{10, 100, 10^3, 10^4, 10^5\}$. We restricted the model space to 5 nested models, which required adjusting the priors for γ_j to always include lower-order terms when selecting the interaction term (Ntzoufras 2002).

Bayesian PH models do not rely on the assumption of proportional hazards over time (Ibrahim et al. 2001), but the assumed data-generating distribution should always be tested, as is fundamental in any Bayesian analysis (Hobbs and Hooten 2015). We tested goodness of fit of the Poisson distribution for our counting process data by calculating discrepancy measures for observed and simulated mortality frequencies. We first generated new realizations of the data by sampling from the posterior distribution of the Poisson-distributed intensity rates and then calculating the expected mortality frequencies at each unique failure time j . Then, we used a Freeman-Tukey statistic to derive a discrepancy statistic (D):

$$D = \sum_{j=1}^J (\sqrt{n_j} - \sqrt{e_j})^2 \quad (3)$$

where n_j are the mortality frequencies for the observed or simulated data sets and e_j are the expected mortality frequencies. Finally, we constructed Bayesian P -values by calculating the proportion of Markov chain Monte Carlo (MCMC) iterations where $D(\text{simulated}) > D(\text{observed})$, with P -values around 0.5 indicating no evidence of lack of fit (Gelman and Shalizi 2013).

Implementation and diagnostics.—We estimated parameters by sampling from marginal posterior distributions with JAGS 4.3.0 (Plummer 2017) using the jagsUI package (Kellner 2018). Using jagsUI allowed us to run 2 MCMC chains using parallel processing with automated convergence diagnostics (i.e., Brooks-Gelman-Rubin statistic < 1.1 ; Brooks and Gelman 1998). We also visually inspected convergence in trace plots of posterior distributions. We report 95% Bayesian credibility intervals (BCI) for all parameters. We compared our Bayesian risk regression estimates with frequentist estimates using the R package survival (Therneau 2015). We performed all statistical analyses in Program R (R version 3.6.1, www.r-project.org, accessed 15 Sep 2019). We provide data, custom functions, and R code to repeat our analysis (<https://doi.org/10.5281/zenodo.3813714>).

RESULTS

The risk set included 175 individuals after removing 5 pronghorn that died of capture-related causes, which translated into 149 pronghorn risk-years. Within the risk set, we right-censored 2 individuals with collar malfunctions and 4 with completely unknown fates. Our pooled sample included 124 resident, 165 migratory, and 18 unknown observations of movement tactic, and we estimated that pronghorn had a 57% probability of being migratory

($\psi = 0.57$, BCI = 0.51, 0.62). At the individual level, we had 68 resident pronghorn, 87 migratory pronghorn, 17 pronghorn with unknown movement tactic, and 3 individuals that switched movement tactic across biological years. Because most individuals were monitored for ≤ 1 year (median = 0.96 yr, SD = 0.37), we stacked individual observations to estimate survival rather than modeling an individual frailty term (Fieberg and DelGiudice 2009).

Survivorship and Cause-Specific Mortality

The pooled annual survivorship including individuals with unknown movement tactic was 0.73 (BCI = 0.66, 0.80). Annual survivorship of migratory pronghorn was approximately 7% higher on average ($\hat{S}_{\text{annual}} = 0.82$, BCI = 0.73, 0.89) compared to residents ($\hat{S}_{\text{annual}} = 0.75$, BCI = 0.65, 0.84), but the credibility interval of the difference overlapped zero (-0.06, 0.20). Survivorship was especially low at 0.22 and 0.18 (pooled = 0.19) for migratory and resident pronghorn, respectively, in 2011, when an anomalous winter occurred that had a WSI 3 times greater than the median over the study period (Table 1; Fig. S1). Pronghorn survivorship averaged 0.82 (BCI = 0.76, 0.88) in winter and was lower compared to the summer period ($\hat{S}_{\text{summer}} = 0.91$, BCI = 0.87, 0.95; Fig. 2). Although not statistically significant, migratory pronghorn had 2% and 4% higher survivorship in winter ($\hat{S}_{\text{winter}} = 0.87$, BCI = 0.79, 0.94) and summer ($\hat{S}_{\text{summer}} = 0.94$, BCI = 0.88, 0.98), respectively, compared to residents ($\hat{S}_{\text{winter}} = 0.85$, BCI = 0.75, 0.92; $\hat{S}_{\text{summer}} = 0.90$, BCI = 0.82, 0.96). Pronghorn survivorship during the mean 20-day spring migration period was 0.97 (BCI = 0.94, 0.99), and no mortalities occurred during the short mean 10-day autumn migration period.

We documented 47 mortalities including 16 migratory pronghorn, 18 residents, and 13 individuals with unknown movement tactic during 10 December 2003–27 February 2011. As expected, the majority (34%) of our pooled

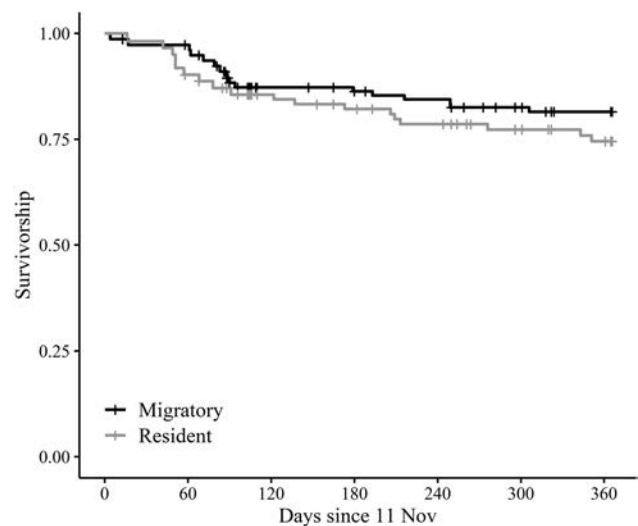


Figure 2. Median estimates of annual survivorship with 95% Bayesian credibility intervals for migratory and resident adult female pronghorn in southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011).

(migrant, resident, and unknown movement tactic) mortalities were classified as unknown. Despite this uncertainty, the pooled annual mortality from known causes was greatest from winterkill (CIF = 0.07, BCI = 0.036, 0.118), followed closely by predation (CIF = 0.05, BCI = 0.03, 0.10) and anthropogenic causes (CIF = 0.05, BCI = 0.02, 0.09; Table 2). This CIF for anthropogenic causes suggested that annually, an average of 5 of every 100 pronghorn in the population had succumbed to death directly from roadkill or train collisions such that 500 mortalities would be expected per year in a population of 10,000 pronghorn. Pooled annual rates of unknown mortality had the highest overall CIF (0.09, BCI = 0.05, 0.14), and were especially high for residents (CIF = 0.12, BCI = 0.06, 0.23). Residents had rates of unknown mortality over 6 times higher than migratory

Table 1. Bayesian estimates of annual survivorship (\hat{S}) with 95% Bayesian credibility intervals (BCI [2.5–97.5%]) and maximum number of individuals at risk (n) for pronghorn monitored in southeastern Alberta, Canada, during the biological years of 2004–2007, and those monitored in northcentral Montana, USA, and southwestern Saskatchewan, Canada, during 2008–2011. Annual survivorship estimates are stratified for migratory and resident pronghorn and pooled across individuals.

Area	Year	n	Migratory		Resident		Pooled ^a	
			\hat{S}	BCI	\hat{S}	BCI	\hat{S}	BCI
Alberta	2004	23	1.00	1.00–1.00	1.00	1.00–1.00	0.84	0.66–0.95
	2005	26	1.00	1.00–1.00	0.88	0.66–0.98	0.93	0.79–0.99
	2006	23	1.00	1.00–1.00	0.71	0.43–0.90	0.83	0.63–0.95
	2007	21	1.00	1.00–1.00	0.95	0.75–1.00	0.97	0.84–1.00
Montana and Saskatchewan	2008	20	1.00	1.00–1.00	0.87	0.64–0.98	0.87	0.68–0.97
	2009	46	0.90	0.77–0.97	0.77	0.42–0.96	0.81	0.68–0.91
	2010	47	0.87	0.72–0.96	0.89	0.67–0.98	0.77	0.63–0.87
	2011 ^b	33	0.22	0.06–0.50	0.18	0.02–0.56	0.19	0.06–0.41

^a Pooled annual survivorship estimates include individuals with unknown movement tactics.

^b We corrected the survival estimates for an annual survival period because the study ended during the late winter (day 109) in 2011; thus, by assuming an exponential (constant) hazard rate over the year, we calculated a comparable annual survival rate for 2011 using the hazard rate (λ) as: $S_{365} = S_{109} \times S_{256} = S_{109} \times \exp(-\lambda \times (365 - 109)) = S_{109} \times \exp(-\frac{-\log(S_{109})}{109} \times (256)) = 0.19$. For example, our pooled 2011 survivorship estimate to 109 days was $S_{109} = 0.61$. Therefore, we solved the following equation to get our pooled annual survivorship estimate (S_{365}) for 2011 of 0.19: $S_{365} = 0.61 \times \exp(-\frac{-\log(0.61)}{109} \times (256)) = 0.19$.

Table 2. Median posterior estimates of cumulative incidence functions (CIFs) with 95% Bayesian credibility intervals (BCI [2.5–97.5%]) for adult female pronghorn mortality ($n = 47$) over winter (11 Nov–Mar 21), spring (22 Mar–10 Apr) and summer (11 Apr–30 Oct) periods in southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011). The CIFs are stratified for migratory and resident pronghorn and pooled across individuals for 3 mortality causes in spring and summer and 4 mortality causes in winter; we also provide raw mortality counts (n). We did not observe any mortalities in the autumn period.

Period (cause)	Migratory			Resident			Pooled ^a		
	n	CIF	BCI	n	CIF	BCI	n	CIF	BCI
Winter									
Anthropogenic ^b	3	0.032	0.008–0.087	0	0.000	0.000–0.000	4	0.024	0.007–0.056
Predation	3	0.036	0.008–0.097	1	0.011	0.000–0.059	7	0.040	0.016–0.081
Unknown	0	0.000	0.000–0.000	4	0.059	0.018–0.142	6	0.039	0.015–0.079
Winterkill	4	0.046	0.014–0.111	5	0.071	0.025–0.154	11	0.065	0.034–0.114
Spring									
Predation	0	0.000	0.000–0.000	0	0.000	0.000–0.000	2	0.010	0.001–0.032
Unknown	0	0.000	0.000–0.000	0	0.000	0.000–0.000	2	0.010	0.001–0.031
Winterkill	0	0.000	0.000–0.000	1	0.009	0.000–0.048	1	0.004	0.000–0.020
Summer									
Anthropogenic ^b	3	0.029	0.007–0.080	2	0.026	0.004–0.082	5	0.029	0.011–0.066
Predation	1	0.007	0.000–0.040	0	0.000	0.000–0.000	1	0.004	0.000–0.024
Unknown	2	0.018	0.003–0.062	5	0.069	0.024–0.148	8	0.049	0.021–0.092

^a Pooled CIF estimates include individuals with unknown movement tactics, which accounted for 8 mortalities in winter, 4 mortalities in spring, and 1 mortality in summer.

^b Anthropogenic refers to mortality caused by human factors such as vehicles or trains.

pronghorn (CIF = 0.02, BCI = 0.00, 0.05). Overall, migratory pronghorn had higher annual rates of anthropogenic and predation-caused mortality compared to resident pronghorn (Table 2; Fig. 3), whereas resident winterkill had

the highest cumulative rate of all known causes. Differences in cause of death among movement tactics were not statistically significant; credibility intervals overlapped among CIFs (Table 2).

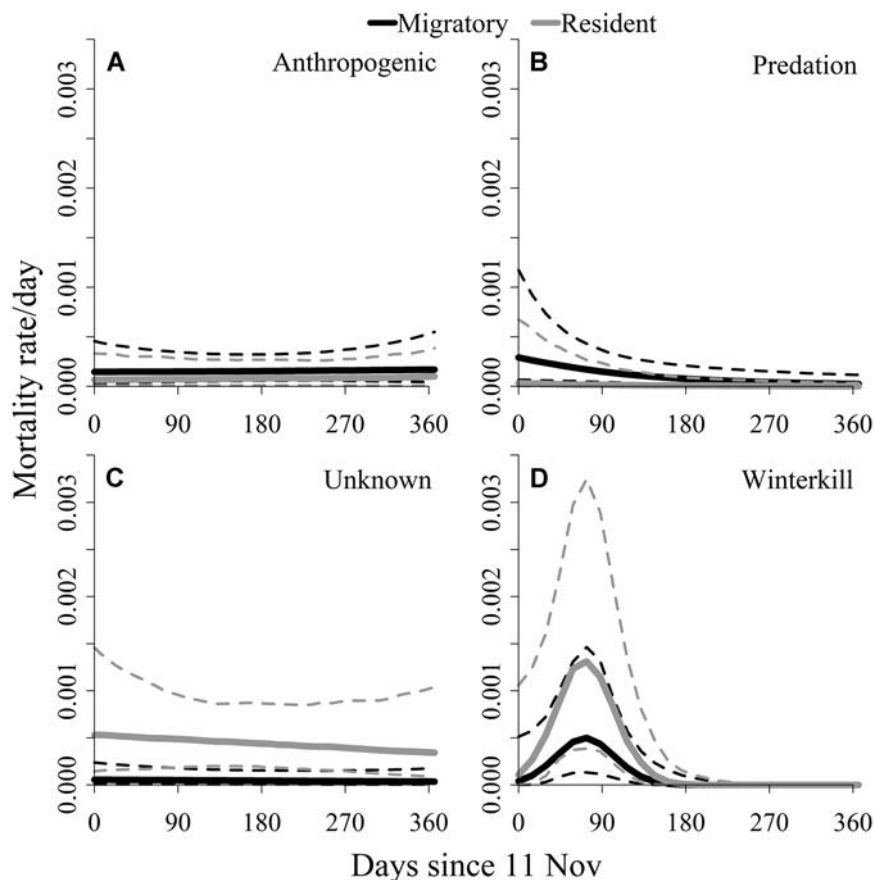


Figure 3. Smoothed posterior estimates of the daily cause-specific mortality rate with 95% Bayesian credibility intervals for anthropogenic (A), predation (B), unknown (C), and winterkill (D) mortalities pooled over study years for migratory and resident adult female pronghorn in southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011).

Factors Influencing Annual Mortality Risk

Our model selection for annual pronghorn mortality risk heavily favored a simple Bayesian PH model (i.e., $\hat{p}[M_3|y] = 0.65\text{--}0.93$) that included only the effects of WSI (Table 3). We found weak evidence of lack of fit (Bayesian P -value = 0.91) because few mortalities occurred in the sample at observed mortality times (i.e., underdispersion; Fig. S2, available online in Supporting Information), and Bayesian posterior estimates closely agreed with frequentist estimates as expected under uninformative priors (Table S1, available online in Supporting Information). The support for more complex models increased under the most-informative priors, yet the inclusion of movement tactic ($\hat{p}[M_4|y]$) had only a 29.8% posterior model probability at most, and the interaction of movement tactic and WSI ($\hat{p}[M_5|y]$) had only a 5.3% probability (Table 3). Thus, the final model estimated a 1.7% (BCI = 0.01%, 2.5%) increase in mortality risk with every unit increase in WSI, which predicted annual survival rates would decline by 56% from 0.82 (BCI = 0.76, 0.88) to 0.26 (BCI = 0.05, 0.53) over the range of observed winter severity conditions (Fig. 4). Despite the lack of statistical support for an interaction, the coefficient estimate was in the opposite direction of what we predicted, where mortality risk slightly intensified for migratory pronghorn under more extreme winter weather relative to residents (HR = 1.004, BCI = 0.99, 1.02; Fig. 4).

Given the support for WSI in explaining the overall risk of mortality, we stratified the overall mortality hazard into cause-specific hazards to assess whether the effects of WSI were due to a specific mortality source. Of known causes of mortality, the effects of winter severity on annual mortality risk were mainly correlated with anthropogenic and winterkill causes, with respective magnitudes of increase in mortality risk of 1.03 (BCI = 1.01, 1.05) and 1.07 (BCI = 1.03, 1.14) times with every unit increase in WSI. Predation-caused mortality risk was also predicted to positively correlate with WSI but had a weaker relationship compared to other causes (HR = 1.02, BCI = 1.00, 1.04). The risk of unknown-caused mortality declined for pronghorn with increasing WSI (HR = 0.95, BCI = 0.89, 0.99), which is expected given that residents experienced higher levels of unknown mortality than migrants and tended to be more prevalent in the sample during the first (i.e., 59%, 2004–2007) compared to the latter half of the study (i.e., 33%, 2008–2011) when winter weather was more severe on average (Fig. S1).

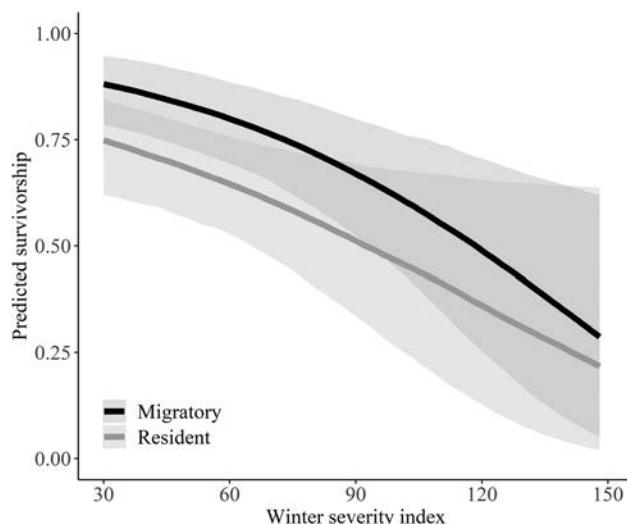


Figure 4. Median estimates of annual survivorship with 95% Bayesian credibility intervals predicted from a Bayesian proportional hazards model over the observed range of winter severity index values for migratory and resident adult female pronghorn in southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011).

DISCUSSION

We assessed if a fitness advantage in terms of increased survival was gained by migratory pronghorn compared to residents for a population at the northern periphery of their range. Few studies of partially migratory pronghorn populations, if any, have monitored a relatively large sample of individuals over 8 years to test for differences in survival and the extent that migration reduces the effects of severe winter climatic conditions on pronghorn mortality risk. As predicted, migrating pronghorn had higher annual survival rates compared to individuals that remained resident, though these differences were not statistically supported. But migrants had 7% higher survival on average, which we think is biologically important and demonstrates a large effect size for adult female survival in large herbivores (Gaillard et al. 2000).

In most ungulate populations, adult female survival rates tend to be high and constant, and are considered more resistant to variation in stochastic environments compared to juvenile survival because of their large potential (i.e., high elasticity) to influence population growth (Gaillard et al. 2000, Heppell et al. 2000). For instance, in most years of our

Table 3. Posterior model probabilities derived by Gibbs variable selection under 5 different prior sets for regression coefficients in Bayesian proportional hazards models of annual mortality risk for adult female pronghorn in southeastern Alberta, Canada (2004–2007), and northcentral Montana, USA, and southwestern Saskatchewan, Canada (2008–2011). The 5 models (M_i) considered included a null model (without an intercept), the additive effects of movement tactic (migratory or resident) and winter severity index (WSI), and the interaction between movement tactic and winter severity index.

Model		Priors				
		N(0, 10)	N(0, 100)	N(0, 10 ³)	N(0, 10 ⁴)	N(0, 10 ⁵)
M_1	Null	0.002	0.005	0.030	0.090	0.209
M_2	Tactic	0.000	0.001	0.000	0.000	0.000
M_3	WSI	0.647	0.855	0.926	0.899	0.786
M_4	Tactic + WSI	0.298	0.132	0.043	0.011	0.004
M_5	Tactic + WSI + Tactic × WSI	0.053	0.007	0.000	0.000	0.000

study, pooled adult female survival rates were consistently high and ranged from 0.77–0.97. These survival estimates are similar to other adult female pronghorn studies that occurred south of our study system in northwestern Wyoming, South Dakota, and the Trans-Pecos region of Texas, USA, which ranged from 0.80–0.91 (Sawyer and Lindzey 2000, Canon and Bryant 2006, Jacques et al. 2007, Keller et al. 2013). But pooled adult female survival declined greatly during our study because of severe climatic conditions in winter 2010–2011 to an estimated survival rate of 0.19. This survival rate was based on extrapolation (for days 110–365) to estimate an annual adult female survival rate because our study ended on day 109 (28 Feb 2011) of that biological year. We estimated a comparable annual adult female survival rate of 0.26 based on the average mortality rate from Taylor et al. (2016) during the same winter in south-central Wyoming. Also, despite our study ending in winter 2010–2011, our 0.19 annual survival rate seems reasonable because continued severe winter weather and profound spring flooding occurred in March through July that year, which would have resulted in additional pronghorn mortalities. We are aware of mortalities that occurred during spring and summer 2011 of pronghorn perishing while trying to swim across Fort Peck Reservoir in Montana as they attempted to return to summer ranges to the north (A. F. Jakes, National Wildlife Federation, personal communication). This is corroborated by aerial trend surveys during summer 2011 that reported overall pronghorn numbers decreased by 71% (range = 38–89% per hunting district) in northern Montana (Johnson 2012). Similarly, in Arizona, USA, at the southern periphery of pronghorn range, adult female survival of Sonoran pronghorn (*A. a. sonoriensis*) had a low annual survival rate of 0.17 during an extreme drought event (Bright and Hervert 2005). Thus, the variability and importance of adult female survival for pronghorn population dynamics may be underappreciated in stochastic environments such as those at the periphery of their range, where infrequent but severe climatic conditions occur. For pronghorn the stochastic events are winter conditions (i.e., snow depth) at the northern periphery of their range, whereas summer conditions (i.e., lack of precipitation) are the stochastic events at the southern periphery (Simpson et al. 2007, Gedir et al. 2015).

Although we estimated that migrants maintained a biologically significant advantage over residents during the study, we found little support for our hypothesis that migratory pronghorn would gain an increasing survival advantage over residents as winter severity intensified. Our stratified annual survival estimates, although generally higher for migratory pronghorn, were also similar between migrants and residents during the most extreme winters observed. The result of similarly low survival regardless of movement tactic suggests that summer forage quality, and thus body condition, may have been similar between the 2 tactics or that the effects of winter (i.e., increased mortality risk [direct and in-direct] associated with anthropogenic features) negated any differences in body condition. We did not directly test these underlying mechanisms (e.g., body condition, forage quality, anthropogenic features) that potentially influence differences

or lack thereof in survival between movement tactics (Hebblewhite et al. 2008, White et al. 2014, Reinking et al. 2019). Also, the strong signal of winter severity was mainly influenced by the extreme outlying winter of 2010–2011, which resulted in substantial uncertainty in our predicted survivorship under the most severe winter observed. Despite this uncertainty, our prediction that annual survivorship would decline by 56% under the range of observed winter conditions is comparable to the 50% mortality rate reported by Barrett (1982a) during the severe winter of 1978 in Alberta. Although they did not account for movement tactic, Christie et al. (2015) documented a declining index of pronghorn abundance in North Dakota due to severe winter weather conditions of heavy snowfall and low temperatures, and Reinking et al. (2018) reported that pronghorn in Wyoming had a greater chance of mortality when exposed to greater daily snow depth during the previous winter. Given that the effect of winter severity on adult female survival was large enough to detect in our study, it is likely that pronghorn making long-distance migrations interact more with linear features (i.e., fences, roads, railroads), which intensifies cause-specific mortality risk from anthropogenic features. This may have eliminated the survival advantage of migrants over residents during this extreme winter but requires further investigation.

We demonstrated the flexibility and advantages of conducting time-to-event analysis in a Bayesian framework, which allowed us to easily accommodate pronghorn with unknown movement tactics, estimate all desired quantities, and conduct rigorous model selection and goodness-of-fit tests. For our analysis, including the entire dataset by estimating migration probability in the model was especially important because, like many studies of adult female ungulates (Gaillard et al. 2000), we had relatively small sample sizes. This was especially true for our estimates that were stratified by movement tactic and biological years. Our 8-year pooled sample sizes ($n = 175$ collared individuals and 47 mortalities) were comparable to the 47 collared adult female pronghorn and 13 mortalities reported in Taylor et al. (2016) over their 3-year study. Another caveat of our study was that we likely underestimated the amount of mortality due to the extreme winter because of the timing of collaring, which could have affected our regression results if mortality rates significantly diverged between migratory and resident pronghorn after the end of winter 2010–2011. Finally, although we provide cause-specific mortality and competing risk regression estimates, we caution the reader to not over-interpret these results because our study was not specifically designed to make strong inference into these various mortality sources but simply to document them whenever possible. Given the potential importance of these and other risk factors for pronghorn survival, we recommend that future studies include age and body condition as covariates, and whenever possible, increase sample sizes of collared pronghorn.

We acknowledge the high level of uncertainty in our cause-specific mortality data, but all 3 known causes of mortality (anthropogenic, winterkill, predation) could potentially be exacerbated from extreme winter weather and

the highly disturbed landscape in the NSS that is fragmented by anthropogenic linear features. We found evidence that pronghorn mortality risk from the 3 known mortality sources increased under increasing winter severity conditions, with the strongest signals from winterkill and anthropogenic-caused mortality. These anthropogenic disturbances are known to cause direct mortality events to pronghorn and other ungulates (Harrington and Conover 2006, Jones 2014) and become ecological traps for migratory and resident animals during winter as individuals congregate on or near railroad tracks and roads to avoid deep snow pack (Fletcher et al. 2012, Hale and Swearer 2016). For example, during our study, state agency personnel in Montana estimated that >800 pronghorn and deer died directly or were put down as a result of injuries sustained from collisions with trains during the extreme winter 2010–2011, including 1 incident where 270 pronghorn were killed (Associated Press 2011). Taylor et al. (2016) also reported that pronghorn mortality risk in winter decreased by 20% with every 1-km increase in average distance from major roads.

Anthropogenic linear features also have indirect mortality consequences for pronghorn, which are often overlooked. These linear features create barriers to movement (fragment habitat), which increases energetic demands while navigating features and decreases access to forage (Gates et al. 2012, Taylor et al. 2016, Jakes et al. 2018a). Railroads, although occurring at lower densities in our study area, have been documented to fragment habitat and become complete barriers to movement (Ito et al. 2013, Hamr et al. 2019). In addition, Jones et al. (2019) reported that the probability of resource selection during the winter decreased with increasing road density, fence density, and the number of fence crossings made between consecutive locations for pronghorn in our study area. They also determined a 16–38% increase in selection of high-quality habitat with the removal of fences in the NSS (Jones et al. 2019). This increase in selection of high-quality habitat would likely translate into increased survival and population numbers, especially during years with severe winter weather. Given the potential importance of anthropogenic factors on pronghorn, we recommend that future studies include linear spatial covariates when modeling survival and cause-specific mortality. Though we did not include anthropogenic factors in our annual mortality risk models, it is reasonable to suspect that the survival advantages for pronghorn making long-distance migrations have declined over time because of an increasingly fragmented landscape and human development, which has been noted for an array of land mammals worldwide (Berger 2004, Tucker et al. 2018). Thus, efforts are greatly needed to mitigate the effects of these anthropogenic features on the landscape, especially at the periphery of a species' range, to maintain connectivity and movement (Seidler et al. 2015, 2018; Jones et al. 2018).

MANAGEMENT IMPLICATIONS

At the periphery of pronghorn range, stochastic events influence range expansion and contraction and anthropogenic

features at the edges may magnify the intensity of severe conditions on survival. At the northern periphery, pronghorn populations will naturally fluctuate in response to stochastic events associated with winter severity. To dampen fluctuations in population numbers, managers need to maintain the ability of pronghorn to freely move or migrate across the landscape. Managers need to consider the effect of barriers such as fences, highways, and railroads on daily movements, which may act as ecological traps that can reduce survival for migratory and resident pronghorn by increasing energetic demands and causing direct mortality. Strategies such as working with transportation departments to enhance crossings will provide opportunities for pronghorn movement. Fencing of roads and railroads to keep pronghorn away from linear features during the winter is an option, but only if crossing structures are installed to allow free movements over roadways and railroad tracks, particularly during migratory periods. An important factor of these mitigation efforts should be an assessment of traffic volume and landscape view (i.e., how much visibility is afforded pronghorn as they approach the anthropogenic feature). In areas with low traffic volume and high landscape view, an acceptable alternative may be the use of wildlife-friendly fencing. In addition, working with landholders to make fence lines more permeable (i.e., smooth bottom wire at a minimum of 45 cm from the ground) and leaving gates open when livestock are not present will assist pronghorn daily and seasonal movements. A concerted effort by all will ensure continued population persistence for partially migratory pronghorn populations in the NSS.

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