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Research Article

Annual survival in a dynamic species: pronghorn survival patterns across their northern range

Molly C. McDevitt^{1,2}, Anna K. Moeller^{1,3}, Andrew J. Lindbloom⁴, Kelly Proffitt⁵, Joshua J. Millspaugh^{1,6} and Paul M. Lukacs¹

¹Wildlife Biology Program, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA

²Blackfoot Challenge, Ovando, MT, USA

³Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, USA

⁴South Dakota Game, Fish and Parks, Rapid City, SD, USA

⁵Montana Fish, Wildlife and Parks, Bozeman, MT, USA

⁶College of Environmental Science and Forestry, State University of New York, Syracuse, NY, USA

Correspondence: Molly C. McDevitt (molly@blackfootchallenge.org)

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Quantifying variation in demographic patterns, such as survival and recruitment, is critical for understanding population dynamics and informing evidence-based and adaptive wildlife management. In this study, we leverage an extensive dataset from over 1000 GPS collared pronghorn *Antilocapra americana* to provide the first large-scale evaluation of survival patterns for an iconic North American ungulate. This research spans multiple years and regions, as well as age and sex classes, and includes more than 3000 animal-years of monitoring, representing the most spatially and temporally extensive survival dataset for the species to date. Using a hierarchical Bayesian analytical framework, we estimate the process distribution of survival, thereby capturing true biological variation in adult females, adult males, and juveniles. Our results reveal that, across pronghorn populations, mean pronghorn survival is variable yet statistically consistent across regions and through time. In contrast to other sympatric ungulates across North America (e.g. deer and elk), however, adult female pronghorn show lower and more temporally variable survival – highlighting a likely factor contributing to significant fluctuations often observed in pronghorn populations. Therefore, through this extensive survival analysis, we identify demographic mechanisms (e.g. temporally varying adult female survival rates) that contribute to dynamic population trends within the species. Our findings advance understanding of pronghorn demography and expose both species-specific vulnerability and species-specific resilience in response to stochastic events. More broadly, this work underscores the value of large-scale demographic monitoring for identifying sources of variation in population trends, critical for informing adaptive management in the context of global environmental change.

Keywords: *Antilocapra americana*, Bayesian analysis, demography, population dynamics, pronghorn, survival



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Introduction

Understanding wildlife population dynamics is crucial for effective conservation of wildlife species and the ecosystems they inhabit. For wildlife biologists, knowing how vital rates, like survival and recruitment rates, interact provides important insight into year-to-year variation observed in wildlife populations, as well as offering the ability to forecast wildlife population outcomes into the future (Wisdom et al. 2000, Johnson et al. 2010). Given its contribution to driving wildlife population dynamics, annual adult survival is often a preferred metric used by wildlife managers and conservationists to help guide wildlife management decisions. To effectively understand annual survival, biologists often use survival models (e.g. known fate, Cormack–Jolly–Seber, Cox proportional hazards) that estimate survival rates and test hypotheses connecting environmental variables to survival probabilities (Cubaynes et al. 2021). However, adequately modeling survival processes of long-lived wildlife species requires multi-year and broad-scale datasets. Without a multi-year and broad-scale dataset, it is difficult to capture the true range of conditions an individual animal experiences over its lifetime, thus limiting abilities to estimate and understand true survival processes for long-lived wildlife species.

Survival, as a demographic parameter, typically varies by sex and age, with some sex and age classes disproportionately contributing to population trends (Mills 2007). For example, for many long-lived wildlife species, annual adult female survival is high and constant across years (Gaillard et al. 2000) and, because of these characteristics, tends to drive population trajectories. Although exceptions do exist (Van Vuren and Bray 1986, Toigo et al. 1997), adult male ungulate survival is generally lower and more variable than adult female survival (Owen-Smith 1993, Loison et al. 1999, Gaillard et al. 2000), typically due to competition for breeding opportunities and hunter harvest (Clutton-Brock and Isvaran 2007). Additionally, first-year survival is generally the lowest (Delgiudice et al. 2006) and can be highly variable, which can, like adult female survival, also have significant impacts on population trajectories (Gaillard et al. 2000).

The North American pronghorn *Antilocapra americana* is a long-lived, relatively abundant, and widely distributed species that occupies much of western North America (Yoakum et al. 2014). Despite its abundance and wide distribution, however, wildlife managers have limited understanding of pronghorn's range-wide population dynamics and general insight into annual survival. Much of what is known about pronghorn ecology suggests that they have some distinct characteristics from other North American ungulates. For example, pronghorn have unique physiological qualities including smaller body sizes (Bromley 1977), different thermoregulatory capacity in the winter (i.e. pronghorn have little adipose tissue compared to other North American ungulates; Mitchell et al. 2009), flexible movement behavior (White et al. 2007, Jakes et al. 2020), seemingly distinct evolutionary history (Lindstedt et al. 1991), and uniquely variable survival and recruitment rates across years (Byers 1997,

Barnowe-Meyer et al. 2010, Taylor et al. 2016, Jones et al. 2020).

Furthermore, understanding pronghorn annual survival as it differs across sex, age, and temporal (e.g. monthly, annual, and multi-year) and spatial scales (regional and cross-regional) could offer novel insights into pronghorn ecology and drivers of population trends. Several studies have evaluated adult pronghorn survival at smaller spatial scales and suggest highly variable survival across years and the species range (Bright and Hervet 2005, Taylor et al. 2016, Woodruff et al. 2016, Jakes et al. 2020). For example, in Montana and Alberta (Jakes et al. 2020), North Dakota (Kolar et al. 2012), and Arizona (Woodruff et al. 2016), researchers found relatively high and constant adult female survival across years (i.e. 0.79–0.95). However, a 2010–2011 winter saw very low adult female survival rates in Wyoming (0.53; Taylor et al. 2016) and Montana and Alberta (0.19; Jones et al. 2020). While previous research shows signs of possible temporal variability in adult survival rates, information on survival from birth to 1 year is sparse. Two studies have found low juvenile survival: 0.42 (95% confidence interval (CI) 0.28–0.62) from 0 to 4 months (Panting et al. 2021), and 0.18 from 0 to 1 year (Byers 1997). These findings, paired with the ability of an adult female to birth twins in her first year and subsequent years (Byers 1997) suggests that recruitment may indeed be highly variable between years. Furthermore, these previously recorded adult female and juvenile survival rates suggest that distinct demographic factors could be key contributors to pronghorn's unique population dynamics. Therefore, identifying typical pronghorn demographic patterns will be critical to understanding drivers of fluctuations in pronghorn population trends, thus filling an existing knowledge gap in understanding pronghorn ecology.

In addition to understanding demographic drivers (e.g. survival and recruitment rates) of population trends, it is also important to understand the role that environmental factors (e.g. cold temperatures and snowy conditions, forage productivity, and drought severity) play in driving demographic and population trends (Owen-Smith et al. 2005, Parker et al. 2009, Bastille-Rousseau et al. 2016, Jackson et al. 2021). Pronghorn, as a species, have exhibited strong fluctuations in their population trends, resembling boom–bust population dynamics (Christie et al. 2015, South Dakota Game, Fish and Parks 2019), with multiple state wildlife management agencies tasked with monitoring and managing pronghorn observing intense fluctuations in populations across years. For example, South Dakota Department of Game, Fish and Parks found pronghorn populations more than double in 3 years from roughly 40 000 to 81 000 individuals, followed by a decline to nearly 35 000 individuals in the subsequent 3 years (South Dakota Game, Fish and Parks 2019). Similarly, Christie et al. (2015) observed large population fluctuations in their study region of western North Dakota.

Researchers hypothesize that such population variability in pronghorn populations is largely due to stochastic environmental conditions (Reinking et al. 2018). Those stochastic events are likely extreme winter conditions (e.g. deep

snow) typically found in the northern extent of their distribution, and extreme drought conditions typically found in the southern extent of their distribution (Simpson et al. 2007, Gedir et al. 2015). For example, Bright and Hervet (2005) recorded low annual pronghorn survival during disproportionately hot and dry conditions in pronghorn's southern range, whereas in pronghorn's northern range, Taylor et al. (2016), Reinking et al. (2018), and Jones et al. (2020) recorded distinctly low annual pronghorn survival during disproportionately cold and snowy winters. Therefore, as changing global climate conditions increase the likelihood of infrequent yet severe weather events, it is increasingly important that wildlife biologists work to identify both demographic and environmental factors influencing such population fluctuations.

In this paper, we advance knowledge of pronghorn survival processes by leveraging a comprehensive (multi-year, broad spatial scale, and large sample size) pronghorn GPS collar dataset across pronghorn's northern distribution – including mountain valleys, sagebrush steppe, and prairie ecosystems in Montana, USA, and mixed-grass prairie rangeland and agriculture-dominated landscapes in South Dakota, USA. We recorded survival of more than 1300 GPS-collared pronghorn from two age classes, including adult females, adult males, and juveniles, from five populations across three years. Our primary goal was to estimate annual survival and evaluate how survival varies by age, sex, space, and time, as well as how environmental conditions influence this variation. To meet this goal, we evaluated three a priori hypotheses: 1) drought severity influences survival, with the prediction that severe drought decreases survival through reduced forage and water availability (Buechner 1950, Yoakum 2004, Bright and Hervet 2005); 2) winter severity reduces survival, as persistent snow and cold temperatures limit movement and forage access (O'Gara and Janis 2004, Taylor et al. 2016, Jones et al. 2020, Aikens et al. 2025); and 3) nutrient availability increases survival, as higher productivity supports greater forage quality and body condition (Beck et al. 2006, Parker et al. 2009, Jackson et al. 2021). We also expected lower survival for juveniles and adult males compared to adult females, consistent with prior demographic studies (Gaillard et al. 2000).

Our secondary goal was to fill an existing knowledge gap in understanding overall pronghorn survival rates by estimating the process distribution of pronghorn survival for adult females, adult males, and juveniles. By calculating the process distribution, we capture the true underlying variation in survival over time and space, and distinguish between expected natural variation and biologically meaningful shifts in survival. The process distribution differs from the sampling distribution, which reflects uncertainty from a specific study's limited timeframe or spatial extent (Lukacs et al. 2009). In estimating the process distribution for various sex and age classes, we identify demographic mechanisms influencing population trends and provide information required for impactful wildlife conservation. Our findings thus advance important knowledge of pronghorn ecology and management.

Material and methods

Study region

We focused on understanding pronghorn survival across a large portion of pronghorn's northern distribution. Our study region spans from the western extent of pronghorn distribution in the mountain valleys of the northern Rocky Mountain ecosystem in western Montana, to the eastern extent of pronghorn distribution in the mixed-grass prairie and agriculture-dominated landscapes of central South Dakota. Our study region also encompasses the Northern Great Plains mixed-prairie and sagebrush steppe ecosystems in central Montana, eastern Montana and northwestern South Dakota (Fig. 1). The study region includes five study areas and makes up roughly 100 000 km² of the northern Rocky Mountains and Northern Great Plains. In the western-most study area, the topography is largely defined by valley bottoms, open meadows, and rolling hills (Mountain Valley population). In the central (central Montana and southeastern Montana populations) and eastern (northwest South Dakota and central South Dakota populations) areas of our study region, rivers and other waterways have exposed badlands, creating deep coulees and rolling hills. Elevations ranged from 294 m a.s.l. in central South Dakota to 2850 m a.s.l. in western Montana. Mean monthly temperatures across the region range from −5.6°C in January to 19.8°C in July, and mean precipitation was between 370 and 710 mm per year (Fick and Hijmans 2017).

The landscape is largely dominated by shrublands (43%) and grasslands (36%), with agriculture (11%), forest and woodlands (4%), riparian (4%), and other landcover types (3%). The mountain valley study area includes three distinct populations where the landscape is characterized by a vegetational gradient from lower elevation grasslands (i.e. bluebunch wheatgrass *Pseudoroegneria spicata*, Idaho fescue *Festuca idahoensis*, western wheatgrass *Pascopyrum smithii*) and sagebrush *Artemisia* spp. shrublands to higher elevation forests (i.e. Douglas fir *Pseudotsuga menziesii*, Ponderosa pine *Pinus ponderosa*). The central and southeast Montana study areas include five distinct populations areas, while the northwest South Dakota and central South Dakota populations are defined as single, large study areas. The central Montana, southeast Montana, northwest South Dakota, and central South Dakota study areas are dominated by Great Plains ecosystems characterized by sagebrush *Artemisia* spp. habitats, which fade into mixed-grass prairie habitats that dominate the eastern extent of our study region (i.e. thick spike wheatgrass *Elymus lanceolatus*, green needlegrass *Nassella viridula*, blue grama *Bouteloua gracilis*, needle and thread grass *Hesperostipa comata*). In addition to pronghorn, other ungulate species in the region include mule deer *Odocoileus hemionus*, white-tailed deer *Odocoileus virginianus*, elk *Cervus canadensis*, and occasionally moose *Alces alces*.

Across the study region, pronghorn move through varied landscapes and land uses. The study region includes two states (Montana and South Dakota) with some pronghorn traveling to three additional states (Idaho, Wyoming, and North

Montana & South Dakota Study Regions

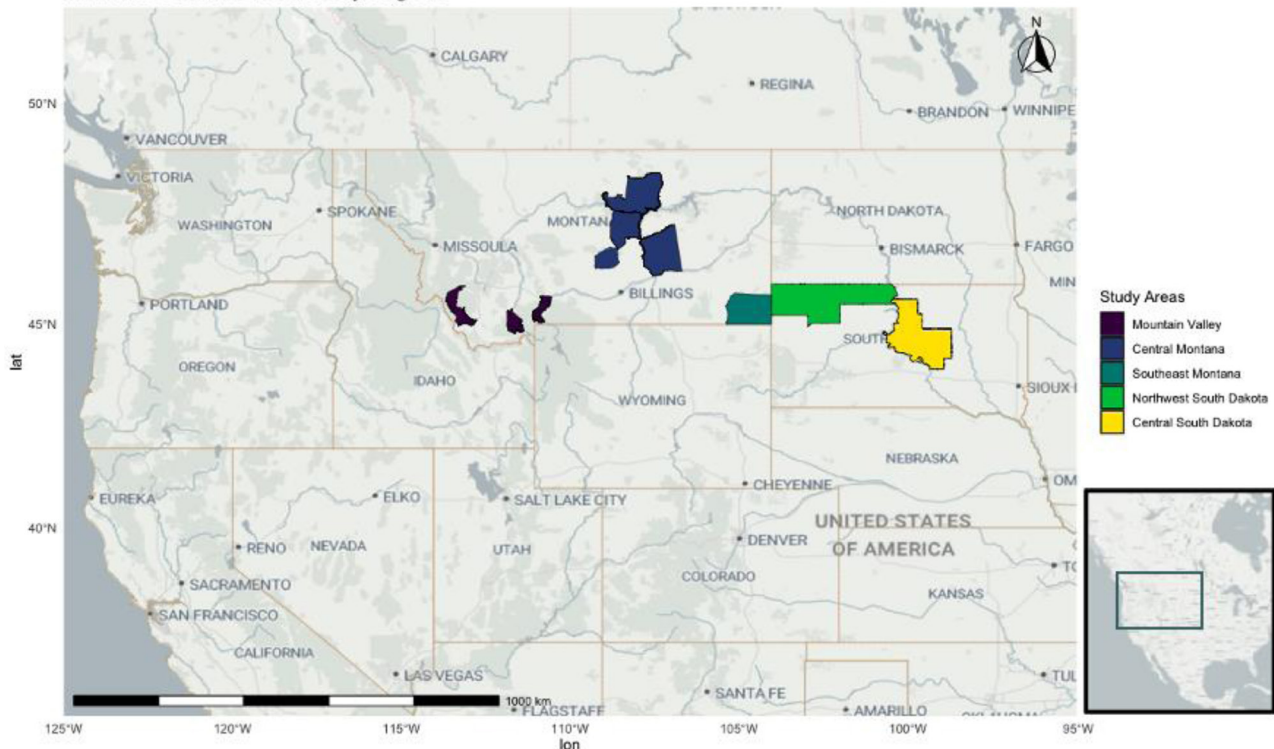


Figure 1. Five study areas where pronghorn were captured and collared. Study areas include three mountain valleys and hunting units in western Montana (Mountain Valley); four hunting units in central Montana (central Montana); two hunting units in southeastern Montana (southeast Montana); five hunting units in northwest South Dakota (northwest South Dakota); and four hunting units in central South Dakota (central South Dakota). The study region spans western, central, and eastern portions of pronghorn's northern distribution.

Dakota), a minimum of 18 harvest management units, and a mix of land ownership and management including private, tribal, state, and federal (e.g. Bureau of Land Management, National Park Service, US Fish and Wildlife Service). Cattle ranches dominate in Montana and northwest South Dakota, whereas farming is generally more prevalent in central South Dakota. Human population is relatively sparse with highest densities in Lewistown, Montana (population: 6149 and ~ 250 km from the central Montana study area center), Miles City, Montana (population: 8438 and ~ 130 km from the southeast Montana study area center), and Pierre, South Dakota (population: 12 880 and ~ 165 km from the central South Dakota study area center).

Capture and collaring

All pronghorn were captured in January and February in 2020–2022. In total, we captured and collared 1313 pronghorn across Montana and South Dakota. In Montana, we captured only adult females (632) across three study areas. In South Dakota, we captured both females (514) and males (167) and captured two age classes: adults (> 1 yr; females only=305) and juveniles (7–12 months old; males=167 and females=209) across the two study areas. We captured individuals using helicopter net gunning in accordance with animal welfare protocols approved by University of Montana IACUC no. AUP 002-20PLWB-012320. We followed the

American Society of Mammalogists' guidelines for animal capture and handling (Sikes et al. 2016).

In all three study areas in Montana, we fit individuals with GPS collars from Lotek Inc. (Lotek Wireless) that used LiteTrack Iridium 420 and were programmed to collect locations every hour. Across both study areas in South Dakota, we fit individuals with GPS collars from Telonics, Inc. that used the Recon GlobalStar satellite system and were programmed to collect locations positions every 11 hours. Adult pronghorn were fitted with non-expandable collars while juveniles were fitted with non-expandable collars that were padded with foam which would dissolve as the juveniles' necks grew.

Survival monitoring

Biologists and researchers were notified of a mortality via an email notification from the collar company. When GPS collars sent mortality messages via satellite, an observer located the collar within several days and investigated the site to confirm mortality and possible causes of mortality. Once the collar was collected, the mortality date was backdated to the date the mortality signal was first transmitted via GPS. If the collar was found with no carcass nearby, the collar was assumed to have slipped off the animal and updated in the database as mortality date unknown and classified as a collar failure. If no mortality signal was detected and the collar functioned appropriately, the animal was assumed and recorded as alive each month.

Environmental variables

To examine relationships between environmental conditions and pronghorn survival at the study area level, we collected four covariates to represent three hypotheses: drought severity's negative or positive effect on survival, winter condition's (percent snow cover and number of days below -10°C) negative effect on survival, and nutrient availability's positive effect on survival. We explored whether there was a positive or negative effect of drought on survival as a possible way to capture a delayed response to winter conditions. We intentionally limited covariate inclusion to avoid overparameterization, multicollinearity, and spurious relationships (Burnham and Anderson 2004, Dormann et al. 2013). Because we estimated annual survival from monthly survival rates across each of the five study areas (Fig. 1) within our study region, we summarized environmental conditions at the monthly temporal level and population (sub-area of each study area; see, for example, the three populations within the Mountain Valley study area) spatial level using Google Earth Engine (Gorelick et al. 2017). This accounted for pronghorn movement throughout each population within a month; therefore, calculated environmental conditions were the same for individual pronghorn within a population and month. For drought, we used the Palmer drought severity index (PDSI) from the 4 km daily Gridded Surface Meteorological (GRIDMET) dataset (Palmer 1965, Abatzoglou 2013). We calculated a median monthly PDSI value from the daily GRIDMET dataset and aggregated to the study area scale. PDSI values less than 0 indicated drier conditions and while values greater than 0 indicated wetter conditions (Palmer 1965). To capture winter condition effects, we calculated two variables: percent snow cover and the number of cold days below the lower critical thermal temperature of pronghorn (-10°C ; Pyle 1972, Yoakum 2004). To quantify the percent snow cover, we used the daily 500 m resolution MODIS dataset (Hall and Riggs 2011). We calculated a mean value per month for each study area. We calculated very cold temperatures at the study area level as the number of days per month with a nighttime low below -10°C , based on the lower critical temperature for pronghorn (Byers 1997). We calculated the maximum number of days per month with a nighttime low below -10°C across each study area. Both snow cover and cold days were equally weighted in analyses. Finally, we represented forage productivity and availability throughout each month using the normalized difference vegetation index (NDVI; Zhang et al. 2003). NDVI is a measure of the amount of photosynthetic tissue, which we use as a proxy for forage productivity and, thus, forage availability. We chose to use NDVI because pronghorn are a generalist herbivore and NDVI has been a common metric used to capture vegetation availability, phenology, and productivity (Pettoirelli et al. 2005, Hamel et al. 2009, Garrouette et al. 2016, Proffitt et al. 2025). We acquired NDVI data from the Terra MODIS vegetation index and aggregated the 16-day dataset to a month by taking the median value and then aggregated to each study area by taking the median value of 1 km pixels (MODIS data is calculated at the 250 m resolution).

Analysis

We used a ragged telemetry model (Dinsmore et al. 2002) to estimate monthly survival of pronghorn across each study area. The ragged telemetry model was developed to measure avian nest survival when the fledge date or nest failure date is unknown and thus applies well to large GPS collar datasets in which some collared individuals' fate can be observed, but the exact mortality date may not always be known (Royle and Dorazio 2009). Specifically, while GPS collars do switch to a mortality signal when a collar stops moving, predation and scavenging can lead to uncertainty in the exact mortality date. Additionally, limited field staff capacity can lead to delays in confirming the exact mortality date and location. Finally, these levels of uncertainty can add up and cause significant bias in overall analyses on large datasets if not accounted for as we do here. The ragged telemetry model also allows us to integrate different data types (e.g. different GPS collar companies, formatting, and frequency of locations being recorded, which can be challenging with such large datasets), thus producing more reliable and accurate survival estimates (Dinsmore et al. 2002). We apply the model to estimate the survival probability of individuals whose fates were not observable due to collar failures. If a collar failure occurred, we used the model to integrate over all possible alive/dead encounter histories from the last time the individual was known to be alive until the end of the study. This approach allowed us to handle individuals with unknown fates without having to right-censor them from our sample (right-censoring occurs when the exact timing of death or collar failure is unknown, but is known to occur after a certain point in time – not having to right-censor data allowed us to account for incomplete information without biasing the results). Additionally, the ragged telemetry model conditions survival probability on capture, so it allowed staggered entry without the need for left-censoring individuals (left-censoring occurs when a death or collar failure occurred before the individual enters the analysis period, but the exact timing of the event is unknown). Left-censoring can help account for phenomena like capture-related mortality or bias related to which individuals are captured – e.g. trap happy or trap shy (White et al. 1982).

We designated mortalities that occurred within 14 days of capture as capture-related and excluded these individuals from our survival analysis (Chalmers and Barrett 1982). For harvested individuals and for individuals whose collar fell off, lost battery power, or failed for any other reason, we allowed the model to integrate over all possible fates for the individual from the time of the last known alive or dead to the end of the study (Dinsmore et al. 2002).

We estimated survival probability independently for each age class (juvenile: 7–12 months old, adult: 1+ years old), sex (male and female), year (2020–2021, 2021–2022, 2022–2023), and study area (Mountain Valley, central Montana, southeast Montana, northwest South Dakota, central South Dakota). We calculated environmental covariates for each study area and month and then centered and scaled values to aid in the comparison of effect sizes. We ran the models in

JAGS ver. 4.3.1 (Plummer 2003) using R ver. 4.1.3 (www.r-project.org) and the 'R2jags' package (Su and Yajima 2021). We ran 3 chains for 30 000 iterations each and discarded the first 10 000 iterations as burn-in. We checked for chain convergence visually using trace plots and by R-hat values < 1.1 (Gelman and Rubin 1992). We also visually inspected trace plots for all parameters to confirm stationarity and good mixing. Effective sample sizes were computed for all parameters to ensure sufficient posterior precision, and posterior predictive checks were used to assess model fit (Hobbs and Hooten 2015). Posterior distribution summaries were reported as means and 95% credible intervals. We used uninformative priors for our beta coefficients $\text{Normal}(0, \tau=0.001)$. We used a $\text{Normal}(1.5, 1)$ distribution as a weakly informative prior for baseline survival probability in the absence of covariate effects.

Using estimated monthly survival, we derived annual survival for the biological year, which we defined as 1 June–31 May, as most neonates are born close to 1 June. For juvenile survival, because individuals were captured in January and became adults on 1 June, we calculated a 5-month survival rate, which estimated survival from 7 to 12 months old. We classified this as an overwinter survival rate.

Additionally, to determine significant effects of environmental covariates on pronghorn monthly and annual survival, we examined the 95% credible intervals (CRIs) of the posterior distributions for each estimated regression coefficient. We considered a covariate to have no significant effect on survival if its 95% CRI substantially overlapped zero – indicating that the posterior distribution included a high probability of both positive and negative effects. Our approach to evaluating covariate effect aligns with standard practices in Bayesian inference, where interpretation is based on the range and shape of the posterior distribution, rather than p-values or fixed thresholds (Kruschke 2018).

Finally, we estimated survival probabilities independently for each study area, month, and year to enable comparisons of pronghorn survival across spatial and temporal scales. From these data, we calculated annual survival because annual survival probability is the most relevant parameter for management decisions in the regions of our study. To provide a broader context for interpretation and address existing gaps in knowledge of pronghorn population dynamics, we also estimated an overall mean annual survival rate and its associated annual variance across all study areas and years. To do so, we estimated the process distribution for adult female,

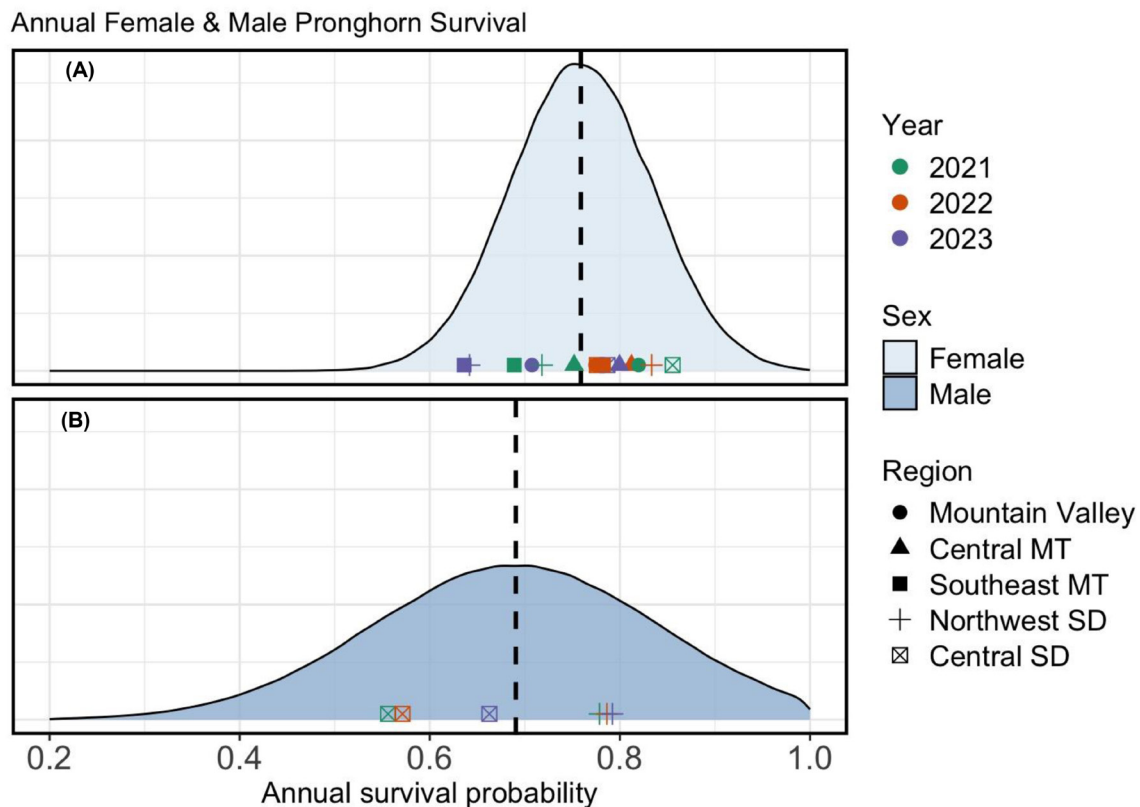


Figure 2. Pronghorn annual survival from across their northern distribution, in the absence of harvest. Mean annual survival for female pronghorn (A; $n=1089$) was 0.76 ($SD=0.074$) and male pronghorn (B; $n=150$) was 0.69 ($SD=0.152$). Mean annual survival is represented by dashed black line and variation around the mean is represented by each density plot. (A) shows annual female survival based on biological years June 2020–May 2023, totaling 3 years (color) across five study areas (shapes) spanning the western to eastern edge of pronghorn's northern distribution. (B) shows annual male survival based on biological years June 2020–May 2023, totaling 3 years (color) across two study areas (shapes) representing the eastern edge of pronghorn's northern distribution.

adult male, and juvenile (7–12 months) pronghorn survival, which captures the expected biological mean and variation in annual survival. The process distribution reflects the true underlying variation in survival over time and space, and distinguishes between expected natural variation and biologically meaningful shifts in survival. The process distribution is defined by two parameters: mean and standard deviation. To calculate the survival mean and standard deviation, we used the posterior distribution results from all years and study areas as data in a separate model in JAGS, using an uninformative prior for the parameters of interest (grand survival mean and standard deviation; Uniform[0,1]). Results from these analyses capture the spatiotemporally varying process mean and variance for pronghorn annual survival across pronghorn's northern distribution.

Results

Model convergence and fit

All Bayesian survival models converged successfully. Convergence was assessed using Gelman–Rubin diagnostics (R), trace plots, and visual inspection of posterior samples; all parameters had R -values < 1.1 and exhibited good mixing. Effective sample sizes for all estimated parameters exceeded 1000, indicating sufficient posterior sampling precision.

Posterior predictive checks showed no evidence of poor model fit. Parameter estimates and associated 95% credible intervals are presented in Figs 2–6.

Annual pronghorn survival

By estimating the process distribution of annual survival for adult female (Fig. 2A), adult male (Fig. 2B), and juvenile pronghorn (Fig. 3), we found that overall pronghorn survival was lower and more variable than previously documented for the species. Across our study region and study time period, survival did not differ significantly by sex, age class, or location (95% CRIs generally overlapped each other significantly), indicating little evidence of broad spatial or temporal variation. However, a subset of our study region exhibited notable year-to-year variation (Fig. 4–6). For example, adult female survival in rangeland-dominated mixed-grass prairie ecosystems (northwest South Dakota study area) was significantly lower in 2023 than in 2022, and the 95% CRI for that difference did *not* overlap, indicating a statistically supported decline in survival for that region and year.

Monthly survival probabilities for pronghorn across all study areas ranged from 0.76 (95% CRI 0.60–0.89) to 0.97 (95% CRI 0.92–0.99), with the lowest occurring in November 2021 in both the northwest South Dakota and central South Dakota areas, and the highest, and more common monthly survival rates, occurring in many months and

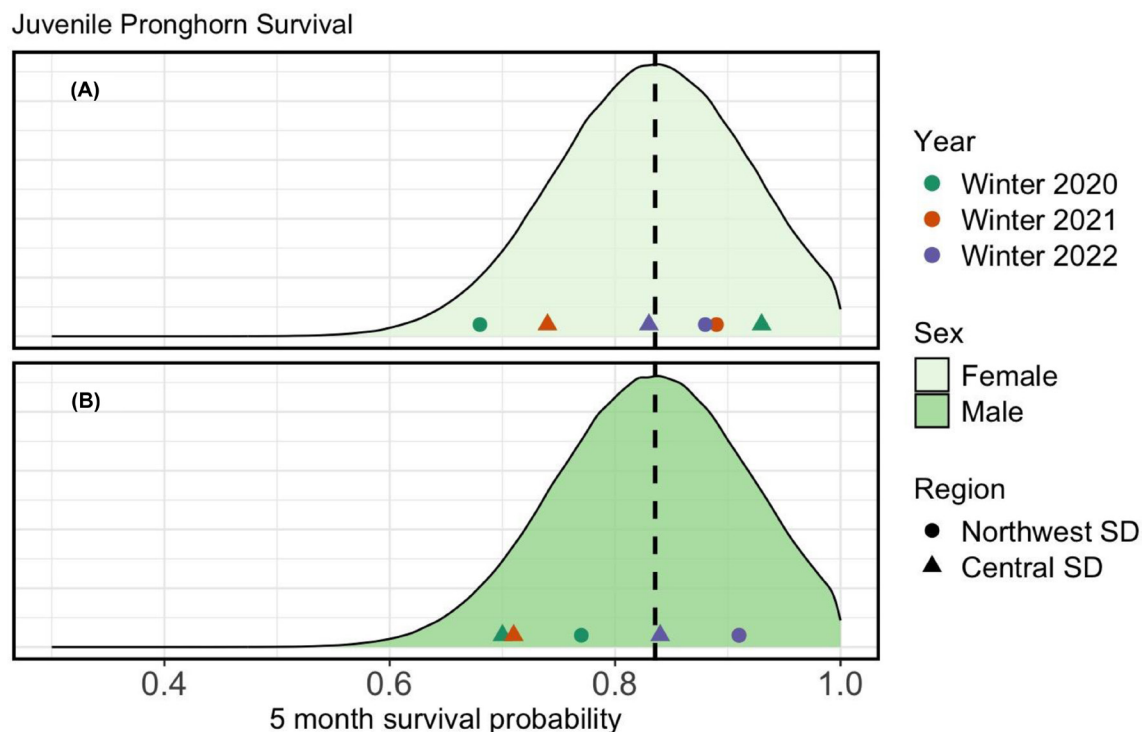


Figure 3. Juvenile pronghorn 5-month, overwinter survival from across the eastern edge of their northern distribution. We estimated juvenile overwinter survival for females (A) and males (B) from January to May for 3 years: 2020, 2021, and 2022 (color) and two study areas (shapes). Mean overwinter survival for juvenile pronghorn ($n = 404$) was 0.84 ($SD = 0.089$). Mean overwinter survival is represented by dashed black line and variation around the mean is represented by density plots. Results demonstrate juvenile overwinter survival is variable across space and time.

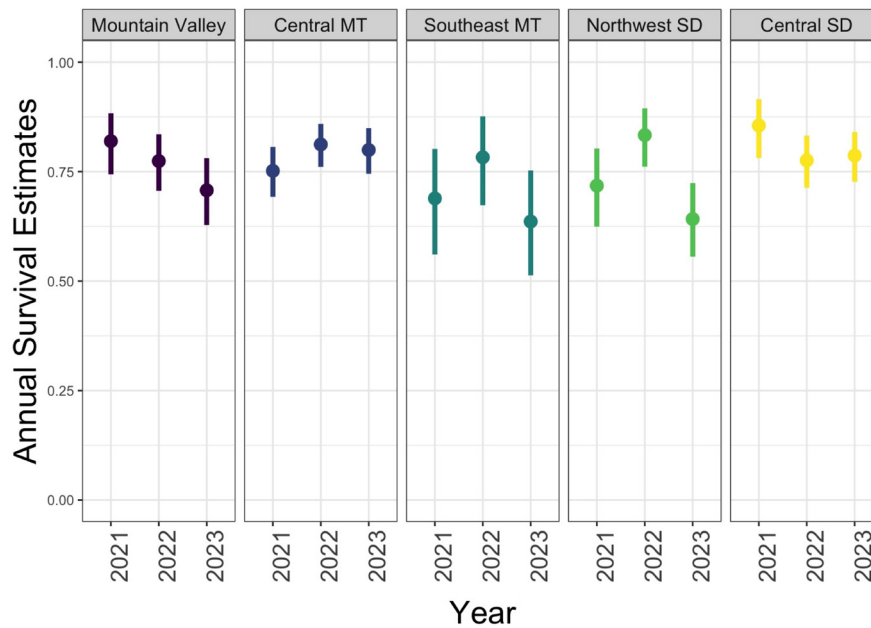


Figure 4. Estimated survival and 95% CRI for 1089 adult female pronghorn from June 2020 to May 2023, totaling 3 years of survival monitoring across five study areas (2373 animal-years).

study areas, respectively. Finally, in accounting for harvest, we recorded 92 harvested individual pronghorn across the study region. Half of these (41 of 92) were harvested in the northwest South Dakota study area.

Adult female survival

Adult female survival was statistically consistent based on overlapping 95% CRI from 2021 (biological year June 2020–May 2021) to 2023 (biological year June 2022–May 2023), with three of the five study areas showing slight increases in survival from 2021 to 2022, followed by slight decreases from 2022 to 2023 (Fig. 4). When calculating the process distribution for annual pronghorn survival, we estimated that adult female pronghorn mean survival was 0.734 (variance 0.06) in the presence of harvest and 0.759 (variance 0.074) in the absence of harvest (Fig. 2A). When comparing adult female survival across the all study areas, we found that annual survival probability for adult females in the absence of harvest (Fig. 2A) ranged from 0.624 (95% CRI 0.501–0.739) in 2023 in the southeastern Montana study area, to 0.855 (95% CRI 0.781–0.916) in 2021 in the central South Dakota study area. The Mountain Valley area was an exception and showed a consistent decline in mean survival from 2021 to 2023. The central South Dakota population survival also declined from 2021 to 2022, but then increased from 2022 to 2023. The most distinct difference in survival occurred in northwest South Dakota, where mean survival dropped from 0.833 in 2022 to 0.642 in 2023. In general, however, mean survival estimates and variability among study areas were more similar across all years and study areas for females in Mountain Valley, central Montana, and central South Dakota compared to southeast Montana and northwest South Dakota.

Adult male survival

Annual male survival was statistically consistent across both space and time based on overlapping 95% CRI. When calculating the process distribution for annual pronghorn survival, we found that annual survival probability for adult male pronghorn was 0.574 (variance 0.166) in the presence of harvest and 0.690 (variance 0.152) in the absence of harvest (Fig. 2B). Annual rates for adult male survival in the absence of harvest (Fig. 2B) ranged from 0.415 (95% CRI 0.229–0.617) in 2021 within the central South Dakota study area to 0.792 (95% CRI 0.697–0.872) in 2023 within the northwest South Dakota study area (Fig. 5). Overall, while mean annual male survival estimates were slightly lower in central South Dakota compared to northwestern South Dakota, we found the mean annual survival decreased slightly from 2021 to 2022 and increased slightly from 2022 to 2023 (Fig. 5). However, again, the differences in annual survival across space and time were not statistically significant.

Juvenile survival

Mean 5-month juvenile survival varied across space and time, though variation was not statistically significant based on overlapping 95% CRIs (Fig. 3, 6). We estimated that juvenile 5-month survival for both sexes was 0.836 (variance 0.089; Fig. 3). These values ranged from 0.68 (95% CRI 0.54–0.80) in 2020 within the northwest South Dakota study area to 0.93 (95% CRI 0.84–0.98) in 2022 within the central South Dakota study area.

Environmental covariates

After a thorough evaluation of environmental covariates' effect on survival, we did not find a relationship between survival and drought severity, cold temperatures, percent snow

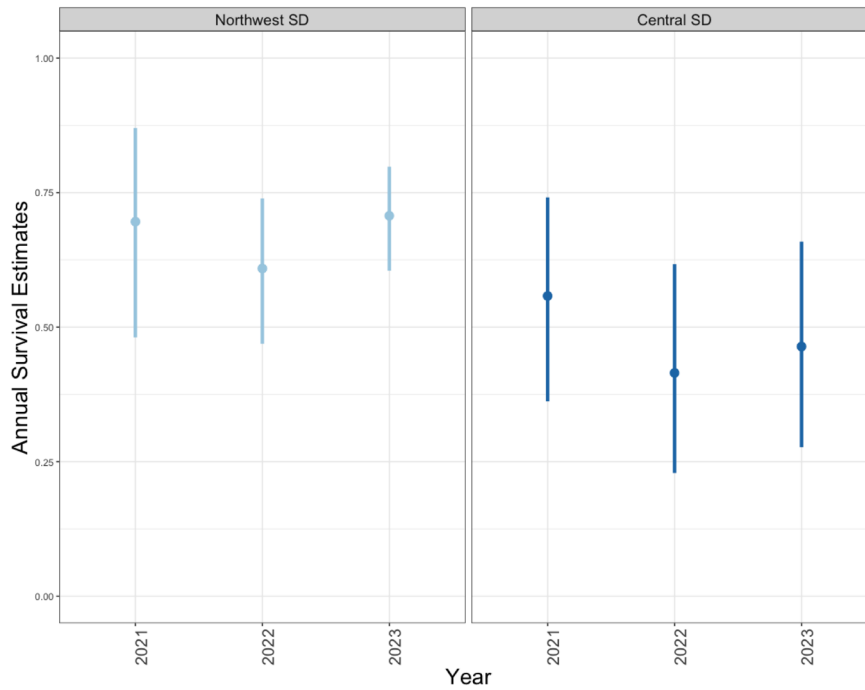


Figure 5. Estimated annual adult male pronghorn survival from across their northeastern distribution and 95% CRI for June 2020–May 2023, totaling 3 years of survival monitoring across two study areas (211 animal-years).

cover, or NDVI. As stated previously, we considered a covariate to have no significant effect on survival if its 95% CRI substantially overlapped zero, indicating that the posterior distribution included a high probability of both positive and negative effects. In our analysis, a significant proportion of

each covariate's 95% CRIs did overlap zero (> 75% of CRIs), and in no case did the 95% CRI entirely exclude zero. Based on this, we concluded that none of the environmental covariates that we evaluated had a statistically significant or directionally consistent effect on survival.

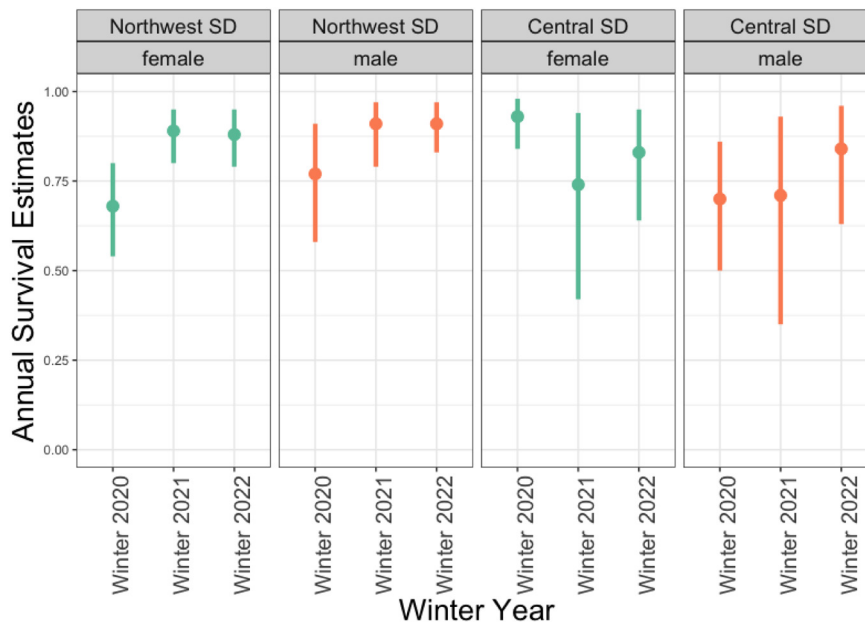


Figure 6. Estimated overwinter survival and 95% CRI for female (green) and male (orange) (total of 404) juvenile pronghorn in the two South Dakota study areas from January 2020 to May 2020, January 2021 to May 2021, and January 2022 to May 2022, totaling three winter seasons of survival monitoring.

Discussion

Our results provide important insights into the demographic variables driving pronghorn population dynamics, thus deepening our understanding of the life history of an understudied ungulate species. We shed light on these likely demographic drivers of pronghorn's distinct population fluctuations by estimating the survival process distributions for adult females – a key demographic rate influencing population dynamics in ungulates – as well as adult males and juveniles (Byers 1997). Specifically, we find that, although mean survival estimates varied across years and regions, overlapping credible intervals indicate that these differences were not statistically distinct or directional through time or space (e.g. Fig. 4). Pronghorn survival, therefore, appears variable but not systematically increasing or decreasing across spatiotemporal conditions.

However, while we did not detect a consistent spatiotemporal trend in pronghorn survival estimates, adult female pronghorn exhibited markedly lower and more variable survival compared to adult females of other similarly managed ungulates across North America (Fig. 7). These findings could help explain pronghorn's unique life history strategy, characterized by potentially high reproductive rates and sensitivity to environmental variability (Byers 1997). Specifically, the low and variable female survival rates we estimate are consistent with expectations that pronghorn experience periodic 'die-off' years, during which adult female survival may fall below 50% approximately once every two decades (Aikens et al. 2025). Our results therefore, highlight the importance of anticipating and planning for such events – for instance, by adjusting harvest rates to facilitate population recovery. Overall, these findings address a critical gap in pronghorn demographic data and demonstrate the value of adopting dynamic management strategies for species that deviate from the typical pattern of high and stable adult female survival seen in most long-lived ungulates (Gaillard et al. 2000).

In leveraging our large sample size of GPS-collared pronghorn and broad spatial extent of our study region, we offer the first opportunity to calculate the process distribution of pronghorn survival for disparate sex and age classes. This concept – central to wildlife demography – reflects the true underlying variation in survival over time and space, after accounting for sampling error (Lukacs et al. 2009). The process distribution distinguishes between expected natural variation and biologically meaningful shifts in survival. In contrast, the sampling distribution of survival reflects uncertainty of a specific study's limited timeframe or spatial extent and cannot reveal true survival variability for a species under normal conditions. As a result, by calculating the process distribution, we offer an important reference range to assess whether observed changes in survival in a given year are unusual and warrant a management response or not.

Adult female survival

Across North American ungulates, adult female survival typically exhibits low variability and high elasticity, exerting a strong influence on population growth compared to juvenile

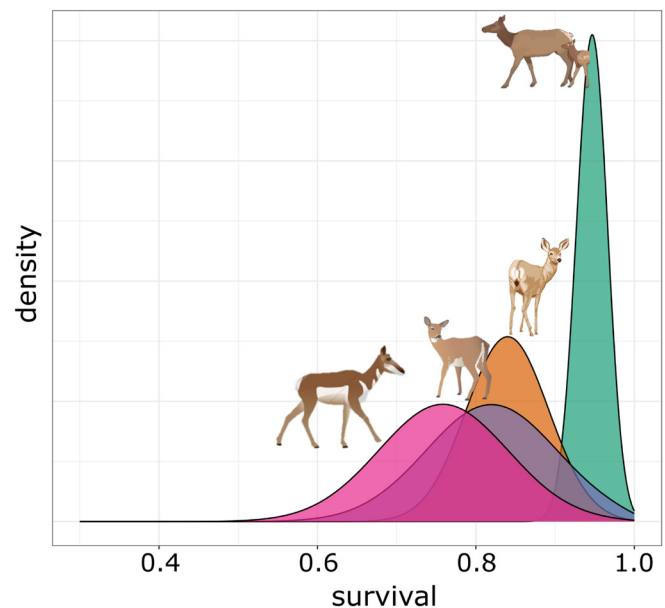


Figure 7. Density plots showing annual adult female survival probabilities and their variation for common North American ungulate species, including elk (mean 0.95), mule deer (mean 0.84), white-tailed deer (mean 0.82), and pronghorn (mean 0.76). Results show that adult female pronghorn survival is lower and slightly more variable than other similarly managed ungulate species in North America. All annual survival estimates are in the absence of harvest.

or male survival (Gaillard et al. 2000, Heppell et al. 2000). Although most previous pronghorn studies have reported relatively high adult female pronghorn survival (0.80 and 0.90; Sawyer and Lindzey 2000, Bryant and Canon 2006, Jacques et al. 2007, Keller et al. 2013, Jones et al. 2020), extreme climatic events such as the severe winter of 2010–2011 in pronghorn's northern range and intense droughts at the southern edge of pronghorn's range have produced dramatically lower estimates (0.17–0.53; Bright and Hervert 2005, Bender et al. 2013, Taylor et al. 2016, Jones et al. 2020). Our results offer valuable context for both high and low survival estimates reported in previous studies and suggest that, across time and space, adult female pronghorn survival is lower and more variable than previously recognized for the species, as well as compared to other similarly managed North American species (e.g. mule deer, white-tailed deer, and elk). To understand and offer context for our findings on low pronghorn adult female survival, we compared our process distribution results to other common North American ungulates' survival process distributions (Unsworth et al. 1993, Lubow et al. 2002, Pac and White 2007, DeYoung 2011, Brodie et al. 2013, Forrester and Wittmer 2013).

Our review comparing adult female survival for elk, mule deer, white-tailed deer, and pronghorn found a clear distinction between species, with pronghorn demonstrating the lowest and most variable survival rate (Fig. 7; DeYoung 2011, Brodie et al. 2013, Forrester and Wittmer 2013). The

paired importance of adult female survival in influencing population dynamics of long-lived species and our results provide evidence for pronghorn's distinct population dynamics. These findings highlight the importance of accounting for high levels of annual adult female survival variability in advancing pronghorn ecological knowledge and effective pronghorn management.

Adult male survival

We estimated that mean annual survival for adult male pronghorn, in the absence of harvest, was 0.690 (variance 0.152). While we offer a robust sample size and further advance understanding of overall pronghorn population dynamics, our results for adult males are limited to South Dakota (pronghorn's northeastern distribution). This is particularly relevant considering the difference we observed in survival across space, given that central South Dakota includes the easternmost edge of pronghorn's distribution as a species. Given the geographic context of our data for male pronghorn, we caution against extrapolation of our results to other geographic regions. Nonetheless, we feel confident that our robust sample of over 150 adult male pronghorn offers insight into pronghorn ecology, and thus improves information guiding pronghorn conservation and management. Additionally, in contrast to adult female survival, in ecology, it is largely accepted that, for long-lived species like North American ungulates, adult male survival rates tend to be lower and more variable (Gaillard et al. 2000). Our results align with these findings and generally align with estimates of annual survival of other North American ungulates (Unsworth et al. 1993, Lubow et al. 2002, Pac and White 2007, DeYoung 2011).

Juvenile survival

Our findings suggest that juvenile overwinter survival is variable across sex, space, and time (Fig. 3) and is lower and more variable compared to adult female survival rates. We estimated that the mean 5-month survival rate for juvenile pronghorn, 7–12 months old, is 0.836 (variance 0.089). From our results, we offer the largest sample of juvenile pronghorn survival rates to date (404 individuals), thus contributing to a broader and deeper understanding of factors influencing pronghorn population dynamics and recruitment rates. Our results generally align with estimates of overwinter to spring survival of other North American ungulates (Hurley et al. 2014). However, understanding pronghorn juvenile recruitment to 1 year old is particularly important for furthering insight into pronghorn population dynamics, given the potential for high twinning rates in adult females (Byers 1997) and/or extremely low fawn survival (Panting et al. 2021). Adding to our research, we recommend prioritizing understanding pronghorn fawn summer and fall survival to expand knowledge of pronghorn recruitment rates and their contributions to overall population trends. Finally, similar to the limitations of our adult male pronghorn data, while we offer a robust sample size in our results, it will be important to consider the geographic context of our data on juvenile pronghorn.

Survival and environmental conditions

Bright and Hervet (2005), Taylor et al. (2016), and Aikens et al. (2025) present examples of how pronghorn populations can be disproportionately sensitive to stochastic climatic events. However, given the complexity and dynamic component of environmental conditions, the structure of current mathematical models, and the way that survival data are recorded and analyzed, it can be difficult to draw direct analytical links between survival probability and environmental covariates with confidence. Our analyses, despite our robust data and variable environmental conditions across our geographies and three years of research, did not find an explicit or significant link between environmental covariates and survival. These findings are likely due to the limited capability of standard survival models to capture the cumulative experience of environmental conditions that individual animals (or populations) encounter throughout their lifetime. Further research focused on the development of spatially explicit survival models that capture the cumulative experience of environmental conditions throughout an individual animal's life will be key to further connecting survival to environmental conditions. As a result, we recommend exploring novel models like the survival habitat quality model (Moeller et al. 2025) that leverage autoregressive algorithms to directly estimate the cumulative effect of habitat on an individual's unobservable survival probability. Finally, effectively linking wildlife survival rates to environmental and landscape conditions that allow us to extrapolate to population levels will further benefit managers tasked with understanding not only drivers of survival variation, but also fluctuations in population sizes as they relate to management.

There is no doubt that fluctuations in survival, as observed by Taylor et al. (2016) and Jones et al. (2020), and population trends, as noted by Christie et al. (2015) and South Dakota Game, Fish and Parks (2019) are influenced by changes in environmental conditions (Hurley et al. 2014). However, we also know that factors like carnivore species richness (Berger et al. 2008, Griffin et al. 2011), hunting pressure (Kolar et al. 2012), and habitat characteristics and land use strategies (Melis et al. 2009, Reinking et al. 2018, Eacker et al. 2023), in addition to climatic events (Bright and Hervet 2005, Taylor et al. 2016, Jones et al. 2020), contribute to lower pronghorn survival. Furthermore, as infrequent but severe weather events become more common with climate change, the potential for negative environmental impacts on survival is likely to increase. Therefore, to better quantify factors affecting pronghorn adult female survival and, consequently, population trends, it is essential to further test hypotheses and analytical tools that more directly connect the cumulative effects of landscape and weather impacts to survival (Gibson et al. 2023, Moeller et al. 2025).

Conclusion

Wildlife management often assumes, and aims to manage for, relatively stable population trends, yet pronghorn exhibit

complex dynamics characterized by variable survival that can complicate management decisions. Quantifying expected variation in annual survival allows managers to distinguish between natural interannual fluctuations and sustained declines – an essential distinction for adaptive harvest management. Recognizing that episodic mortality is frequently driven by severe winters and drought underscores the need for flexible harvest and habitat management strategies that mitigate the effects of climatic extremes. Our findings identify demographic mechanisms underlying pronghorn boom-and-bust cycles and emphasize the importance of quantifying the environmental drivers of these dynamics. Given the comparatively lower and more variable survival of adult female pronghorn relative to similarly managed species, we recommend that management agencies adapt monitoring and harvest strategies that account for this demographic variability. Consistent population monitoring – guided by the process distributions presented here – can help managers interpret year-to-year fluctuations, anticipate population responses to extreme events, and make more informed, responsive decisions. Integrating this demographic understanding into wildlife management frameworks (e.g. anticipated fluctuation in adult female survival as it interacts with annual harvest management) will be increasingly critical as climate variability intensifies and interacts with the inherently dynamic population patterns of species like pronghorn.

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Author contributions

Molly C. McDevitt: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Anna K. Moeller:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (equal); Writing – review and editing (supporting). **Andrew J. Lindbloom:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Resources (equal); Supervision (supporting). **Kelly Proffitt:** Conceptualization (equal); Data curation (equal); Supervision (supporting). **Joshua J. Millspaugh:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Project administration (lead); Resources (lead); Supervision (lead). **Paul M.**

Lukacs: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Project administration (lead); Resources (lead); Supervision (lead).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dv41ns2cd> (McDevitt et al. 2026).

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