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RESEARCH ARTICLE

Mule deer mortality in the northern Great Plains in a landscape altered by oil and natural gas extraction

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Abstract

A worldwide increasing demand for renewable and non-renewable energy resources has been ongoing since the mid-1970s and is projected to increase for the next 2 decades. The effects of oil and natural gas development on wildlife mortality risk may play an important role in mule deer (*Odocoileus hemionus*) population dynamics. We evaluated the potential effects of oil and natural gas development on mortality risk of mule deer in western North Dakota and eastern Montana, USA. We assessed adult and juvenile female mule deer mortality risk with Poisson point process models using 265 deer fitted with global positioning system (GPS) radio-collars that were deployed from 2013–2016. Mortality covariates included proportion of area disturbed by oil and natural gas development, distance to oil and natural gas development, distance to roads, temperature, snow depth, normalized difference vegetation index (NDVI), and age of deer. During the study there was no effect of oil and natural gas development or roads on mule deer mortality, though <1% of all deer locations were within 500 m of active drilling rigs. Mule deer mortality was greatest in winter and spring, and positively related to temperature during these seasons. Estimated annual adult survival probability was 0.79 (95% CI = 0.71–0.85). Given the strong influence of season and temperature variables on mortality risk, weather had the strongest influence on mule deer mortality during this study. Although we did not detect an effect of energy development on mule deer mortality, effects on space use resulting from development could influence deer dynamics in the region through displacement and could occur over longer time scales than we evaluated. This study can be used in pre-development planning in a risk assessment framework to minimize effects of development on mule deer.

KEYWORDS
cause specific mortality, energy development, Montana, mortality, North Dakota, *Odocoileus hemionus*

An increase in worldwide demand for energy resources has been ongoing since the mid-1970s and is projected to increase for the next 2 decades (Beckmann et al. 2016, Sawyer et al. 2017, U.S. Energy Information Administration 2018). Within the United States, this increased demand for energy has fueled increases in energy resource extraction, which has further been facilitated by incentives to reduce foreign energy dependence (Copeland et al. 2009, Hebblewhite 2011, Beckmann et al. 2016) and technological advancements such as hydraulic fracturing that increase extraction efficiency (Clark 1949, Northrup and Wittemyer 2013). Increased oil and natural gas development will ultimately increase the footprint of development on the landscape.

The process of developing an oil or gas well includes well pad construction and connection to the power grid and road system, drilling the well, and installation of the pumping infrastructure. Vehicle traffic associated with well pad development is greatest during the initial drilling and fracking of the well when water, proppants (e.g., sand, ceramic material), and waste removal needs are highest (Goodman et al. 2016). In contrast, only a few vehicles visit the site each day during the production phase. Northrup et al. (2015) distinguish between 2 phases of oil and gas development: development and extraction. Development includes the road building and well drilling phases and extraction includes the production phase when the well is actively producing oil and gas. Oil and gas development broadly refers to any activity related to resource extraction, including activities in both the development and extraction phases.

Wildlife may be affected by oil and gas development. For example, habitat loss, alteration, or fragmentation may occur through the development of well pads, roads, power lines, and pipelines (Walker et al. 2007, McDonald et al. 2009, Holloran et al. 2010, Hovick et al. 2014, Jones et al. 2015). These effects may lead to avoidance, altered movement rates, and changed migration patterns (Sawyer et al. 2006, 2009, 2017; Lendrum et al. 2013; Northrup et al. 2015) Uncertainty around how oil and gas development could influence wildlife populations has raised concern for many wildlife species in landscapes that are being developed (Northrup et al. 2015).

Mule deer (*Odocoileus hemionus*) resource selection, behavior, and movement rates might be altered in the presence of oil and gas development. In landscapes with oil and gas development, mule deer avoided developed areas and associated infrastructure such as roads and pipelines (Sawyer et al. 2006, 2009, 2017; Northrup et al. 2015, 2016). Mule deer avoided roads at a greater distance when traffic levels were higher and at greater distances during the day compared to during the night (Sawyer et al. 2009, Northrup et al. 2015), which may be due to increased perception of predation risk around roads (Sawyer et al. 2009). Similarly, mule deer are sensitive to activity levels around oil and gas development. Development at oil and gas well pads is associated with increased noise and traffic, and mule deer have been documented avoiding active drilling rigs up to 1 km (Sawyer et al. 2009, 2017; Northrup et al. 2015). Once the drilling activity has ceased and well pads are actively producing, noise and traffic are reduced and mule deer are relatively more tolerant of well pads (Northrup et al. 2015). The range of avoidance from all types of well pads is influenced by the topographic relief of the area. In areas with less topographic relief, mule deer display farther avoidance distances from well pads than in areas of greater topographic relief (Northrup and Wittemyer 2013). Movement rates of migratory mule deer are also altered in landscapes with oil and gas development. Mule deer in highly developed landscapes left winter ranges later and migrated to summer ranges at a greater speed than mule deer in less developed landscapes (Lendrum et al. 2012). In contrast, migrating mule deer in northwest Colorado, USA, used areas closer to gas development than was available, perhaps because of strong fidelity to migratory routes (Lendrum et al. 2012). Alteration in migration rates could have effects on the individual's ability to acquire forage and ultimately influence demographic rates (Lendrum et al. 2013).

Alterations in space use by mule deer in the presence of oil and gas development have been clearly demonstrated in the literature, but the effects on mortality are more equivocal. For example, there was no effect of density of actively producing well pads on fawn mortality in northwestern Colorado (Peterson et al. 2018). Small changes in mortality rates, particularly for females and yearlings, can affect population dynamics (Forrester and Wittmer 2013), and there are numerous pathways by which oil and gas development can influence mule deer mortality. Habitat loss could limit resource acquisition, which could in turn (e.g., via nutritional deficiency or altered foraging behavior) influence mortality rates (Owen-Smith 2002). Further, increased road development for energy resource extraction can lead to increased access for hunting and recreational activities (Gratson and Whitman 2000, Gamo et al. 2017). Creating more roads can also increase vehicle collisions with wildlife (Litvaitis and Tash 2008, Meisingset et al. 2013). Traffic associated with energy development, recreation, and hunting can lead to greater energetic costs associated with fleeing from vehicles and increased vigilance, and decreased time spent foraging and resting, which could increase mortality rates (Ryan et al. 2014). These altered behaviors associated with oil and gas development could also increase stress (Beckmann et al. 2016). Although many of these effects may be most acute during well pad development, some effects may persist even through the extraction phase. For example, habitat loss and road effects (e.g., vehicle collisions, increased hunter access) are likely to persist when wells are in the extraction phase.

We evaluated the potential effects of oil and gas development on mortality rates of female mule deer within the Bakken oil fields and Three Forks Shale Formation, an active area of oil and gas development in North Dakota and Montana, USA. Our investigation compared mortality rates in western North Dakota, which had relatively high well pad density and had wells in the development and extraction phase, to eastern Montana, which had relatively low well pad density and had wells only in the extraction phase. We investigated the effects of the development and extraction phases on mule deer mortality, and contrast mule deer mortality in landscapes with relatively high and low densities of well pads. Given the higher density of well pads in all phases of production, we predicted that female mule deer mortality rates would be greater in North Dakota relative to Montana.

STUDY AREA

We conducted our study in western North Dakota and eastern Montana throughout the Badlands and north to the Missouri River. The study area was 8,013 km^2 in North Dakota and 933 km^2 in Montana (Figure 1). Regional predators of mule deer include coyote (*Canis latrans*) and mountain lion (*Puma concolor*), and infrequently bobcat (*Lynx rufus*) and golden eagle (*Aquila chrysaetos*). Reginal competitors of mule deer include white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and cattle. The climate in this region is characterized by long cold winters and short hot summers. The average rain precipitation is 39 cm, with the majority occurring from May to September (Godfread 1994). Precipitation from snow fall is typically 30 cm. There is a collection of perennial streams that run throughout the study site, which drain into the Little Missouri River, Yellowstone River, and the Missouri River.

This region is characterized by highly-eroded, broken topography dominated by grassland and shrubland. Along the Little Missouri River and tributaries, silver sage (*Artemisia cana*) is the dominant shrub species and western wheatgrass (*Elymus smithii*) is the principal grass (Godfread 1994). Eastern cottonwood (*Populus deltoides*) and green

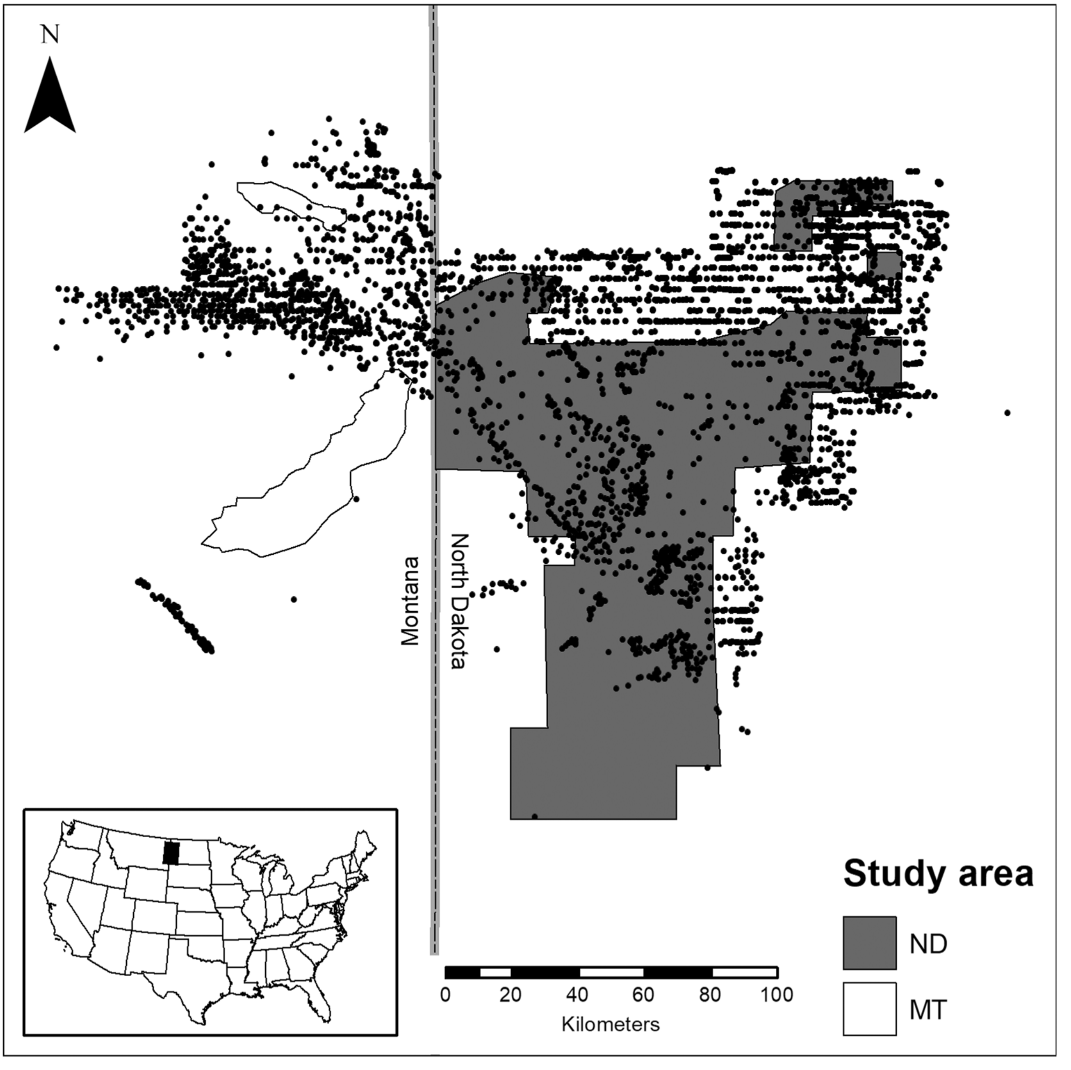

FIGURE 1 Study areas for estimating female mule deer mortality in relation to oil and gas development in western North Dakota and eastern Montana, USA, between February 2013 and May 2016. Black dots represent well pads. Polygons represent areas where we captured mule deer and fitted them with global positioning system radio-collars.

ash (*Fraxinus pensylvanica*) are the primary tree species around water resources with buckbrush (*Symphoricarpos occidentalis*) as the primary understory species. Green ash is the predominate tree species extending into upland draws with chokecherry (*Prunus virginiana*) as the primary shrub. Woody vegetation is commonly located in draws and north-facing aspects and moderately steep slopes. The dominant woody vegetation includes various juniper species (*Juniperus* spp.), woods rose (*Rosa woodsii*), and skunkbush sumac (*Rhus trilobata*). South-facing, moderate to steep slopes typically have sparse vegetation, if they are vegetated at all. These aspects are mostly dominated by rubber rabbitbrush (*Ericameria nauseosa*), longleaf sage (*Artemisia longifolia*), and greasewood (*Sarcobatus vermiculatus*; Godfread 1994). Grassland species distribution in this region is dependent on the soil type, moisture, and salinity. The dominant grasses are needle-and-thread (*Stipa comata*) and blue grama (*Bouteloua gracilis*). Little bluestem (*Schizachyrium scoparium*) is common on moderate to steep slopes with a north to east aspect. Western

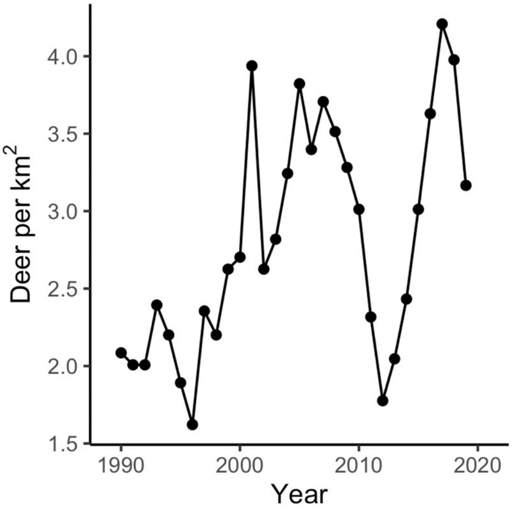

FIGURE 2 Mule deer density in western North Dakota, USA, 1990–2019, based on established blocks surveyed from fixed-wing aircraft each April (North Dakota Game and Fish Department, unpublished data).

wheatgrass, blue grama, and buffalo grass (*Buchloe dactyloides*) are on gentle slopes with finer soil types. Forbs in this area include small-flowered buckwheat (*Eriogonum pauciflorum*), gumbo lily (*Oenothera caespitosa*), butte candle (*Cryptantha celosoides*), red mallow (*Sphaeralcea coccinea*), and prickly pear (*Opuntia plycantha*).

Oil and gas developments occur in both North Dakota and Montana, but most of the recent oil and gas development has occurred in the northern portion of the North Dakota study area (Figure 1). Average active well pad density within the North Dakota study area was 0.19 active well pads/km^2, though density ranged from 0 active well pads/km^2 in the southern portion of the study area to 9 active well pads/km^2 in the central and northern portions (Figure 1). In contrast, average active well pad density within the Montana study area was 0.01 active well pads/km^2, with oil and gas development absent from most of the study area. Aside from oil and gas development, the primary human activities in this study area were ranching (e.g., cattle) and farming, including row crops, hay, and alfalfa plantings (Kolar et al. 2017).

Mule deer populations in North Dakota and Montana were rebounding during the study period following a decline caused by severe winters in 2008–2010. In North Dakota, mule deer abundance was at a 15-year low in 2012, with fewer than 1.9 deer/km^2 (15-year range = 1.7–3.9 deer/km^2; North Dakota Game and Fish, unpublished data; Figure 2). Consequently, there were no antlerless mule deer hunting seasons from 2012–2016 in the North Dakota study area. In Montana there was a moratorium on antlerless mule deer hunting in 2014. In 2013 and 2015, few antlerless hunting licenses were offered following the Adaptive Harvest Management plan (Montana Fish, Wildlife, and Parks 2001), and estimated antlerless harvest was minimal.

METHODS

Capture and handling

We captured juvenile and adult female mule deer via helicopter net-gunning (Schemnitz et al. 2012) in February and December 2013 and November 2014. To ensure a broad range of well pad density and occurrence of well pads in the development and extraction phases, we stratified captures into 3 development levels within North Dakota. We developed our 3 strata by first dividing the North Dakota study area into 4.8-km grids that approximated an adult female mule deer home range (Hamlin and Mackie 1989) and corresponded to legal description lines at properties where we had permission to capture deer. Within each grid cell, we then calculated the proportion of area affected by roads and oil and gas development. We calculated this area by first creating 100-m buffers around well pads in the extraction phase and low-grade gravel roads and 250-m buffers around well pads in the development phase, high-grade and paved roads, gas plants, and gravel pits. Because mule deer have been documented avoiding areas 100–400 m from roads (Lutz et al. 2003), and 600–3,700 m from active drilling rigs (Sawyer et al. 2009, Northrup et al. 2015), our buffers are conservative but still capture variation in development. We then combined all buffers into a single polygon and calculated the proportion of each grid cell that fell within this polygon. Finally, we classified grid cells as low development (<20% of a grid cell in the oil and gas development buffer), medium development (20–50% in the buffer), and high development (50–100% in the buffer). We divided capture effort approximately evenly across all strata and captured deer at only 1 location per grid cell. Within the Montana study site, all grid cells were low development and we only captured deer at 1 location per 4.8-km grid cell.

We captured and collared 96 adults and 102 juveniles in North Dakota and 29 adults and 38 juveniles in Montana (Table 1). We defined adults as individuals >1 year old at the time of capture, and juveniles as individuals <1 year old at the time of capture. The helicopter capture crew aged all deer by tooth wear and replacement or body size, as juveniles and adult deer during this time of year still exhibit a strong size difference. Crews fitted adult and juvenile mule deer with satellite global positioning system (GPS) radio-collars (G2110 Iridium and G2110L Iridium; Advanced Telemetry System, Isanti, MN, USA). The collars collected locations every 5 hours that were transmitted every 4 days via satellite. Collars were programmed to activate a mortality mode if no activity was detected for >6 hours. Once in mortality mode, the collar transmitted a real-time mortality notification and hourly coordinates until either activity was detected or the collar was retrieved. We attempted to retrieve all mortalities as soon as possible after receiving mortality notifications to investigate carcasses prior to advanced autolysis or scavenging. We retrieved 86% of the deer mortalities within 48 hours of the estimated mortality time. We examined evidence in the field (e.g., tracks, weather conditions, risks) and used the timestamp of the GPS location data to determine approximate mortality time. We transported carcasses to the North Dakota Game and Fish wildlife health laboratory where staff conducted necropsies. We assigned body condition scores ranging between 1 (emaciated) and 5 (obese) based on the visual assessment of visceral and subcutaneous fat ranging from light to heavy fat covering the organs. We examined carcasses for gross evidence of disease or trauma and collected samples for routine chronic wasting disease and bovine tuberculosis surveillance. When a cause of death was not readily apparent and postmortem autolysis was mild, we sent appropriate tissue samples to the North Dakota State University Veterinary Diagnostic Laboratory for microscopic examination and ancillary testing. We determined proximate causes of mortality, but in some instances multiple co-morbidities may have contributed (e.g., if malnutrition led to increased vulnerability to predation, the ultimate cause was likely poor forage quality). We

TABLE 1 Summary of adult and juvenile female mule deer captured in western North Dakota and eastern Montana, USA, via helicopter net-gunning from 2013–2014. North Dakota had relatively high well pad density and well pads in both the development and extraction phases during the time of the study. Montana had relatively low well pad density and well pads in only the extraction phase during the time of the study. Individuals were fitted with satellite global positioning system (GPS) collars programmed to collect a location every 5 hours.

	North Dakota			Montana		
Capture year	Adult	Juveniles	Total	Adult	Juveniles	Total
Feb 2013	59	29	88			
Dec 2013	14	29	43	19	16	35
Nov 2014	23	44	67	10	22	32
Total	96	102	198	29	38	67

considered malnutrition to be the cause of mortality when body condition was poor (body condition score ≤ 2) and there was no other evidence of disease or trauma.

Covariate estimation

At each GPS coordinate (regardless of mortality status), we recorded several covariates that potentially influence mortality of mule deer (Table 2). We recorded the state (North Dakota or Montana) of each coordinate, and the proportion of development in the 4.8-km grid cell the deer was located within. To separate the effects of active drilling rigs (development phase) and active well pads (extraction phase), we calculated the distance from these objects to each GPS coordinate. We obtained oil and gas development data from the North Dakota Industrial Commission (2017) and the Montana Department of Natural Resources (2016). We assumed all wells within 100 m of each other were from a single active well pad. We classified well pads into 2 categories: drilling rig (development phase) or active well pad (extraction phase). We classified a well pad as a drilling rig for any period when a well was being actively drilled on the well pad. The well pad then transitioned to an active well pad after the drilling infrastructure was removed from the site and there was ≥1 well on the pad producing oil or gas. We obtained

TABLE 2 Predictor variables used in evaluating female mule deer mortality using point process models. We evaluated female mule deer mortality from 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA.

Predictor variables	Covariate group	Type	Mean (range)
State	Oil and gas; Proportion developed	Categorical	ND (*n* = 473,759) MT (*n* = 124,228)
Distance to nearest drilling rig (km)	Oil and gas	Continuous	28.60 (0.16–138.86)
Distance to nearest well pad (km)	Oil and gas	Continuous	4.35 (0.00–44.67)
Proportion developed	Proportion developed	Continuous	0.36 (0.00–0.95)
Distance to nearest road (km)	Road and gravel pit	Continuous	1.23 (0.00–6.30)
Distance to nearest gravel pit (km)	Road and gravel pit	Continuous	7.75 (0.01–33.32)
Age	Environmental	Categorical	Juvenile (*n* = 74,165) Adult (*n* = 523,822)
Biological year	Environmental	Categorical	2013 (*n* = 115,385) 2014 (*n* = 186,133) 2015 (*n* = 217,126) 2016 (*n* = 79,343)
Season	Environmental	Categorical	Spring (*n* = 127,917) Summer (*n* = 161,820) Autumn (*n* = 83,222) Winter (*n* = 225, 028)
Normalized difference vegetation index (NDVI)	Environmental	Continuous	0.15 (−0.94–1.04)
Snow depth (cm)	Environmental	Continuous	1.93 (0.00–36.65)
Temperature (°C)	Environmental	Continuous	13.25 (−31.00–38.00)
Latitude (decimal degree)	Environmental	Continuous	47.34 (46.43–48.16)
Longitude (decimal degree)	Environmental	Continuous	−103.66 (−106.33 to −102.77)

drilling rig and active well pad data through 31 May 2016, and modeled mule deer mortality through this date. We calculated Euclidean distance from each deer GPS coordinate to the nearest drilling rig and active well pad using the gDistance() function within the rgeos package version 0.3-25 in R (Bivand and Rundel 2017, R Core Team 2017). To allow the effect of a 1-unit change in distance to nearest drilling rig and active well pad to diminish with distance, we log transformed both variables.

To evaluate potential mortality in the context of other variables that may influence mule deer mortality, we collected covariates associated with human development that were not necessarily a consequence of oil and gas development. We obtained road and gravel pit data from the North Dakota Department of Transportation (2016) and Montana Department of Transportation (2016). We manually digitized missing roads and manually removed inactive gravel pits based on 2015 aerial imagery at a 1:5,000 scale. We calculated log-transformed Euclidean distance from each GPS coordinate to the nearest primary or secondary road and gravel pit as described above.

We additionally measured environmental variables not associated with human development. We used the normalized difference vegetation index (NDVI) as a proxy for mule deer forage quality (Hurley et al. 2014). We calculated NDVI at each GPS coordinate using Movebank's Env-DATA interface (Dodge et al. 2013, Wikelski and Kays 2017). Band 1 (red) and band 2 (near infrared) are collected daily at a 250-m resolution (Didan 2015), from which we calculated NDVI (Jackson and Huete 1991):

$$\text{NDVI} = (\text{band } 2 - \text{band } 1)/(\text{band } 2 + \text{band } 1).$$

We obtained surface snow depth values at each GPS location using Movebanks Env-DATA interface (Dodge et al. 2013, Wikelski and Kays 2017). Snow depth was recorded at a 250-m resolution and interpolated from the National Center for Environmental Prediction (2005) North American Regional Reanalysis model. Each collar was equipped with an onboard thermometer, and ambient air temperature was recorded with each successful GPS fix. Onboard thermometers occasionally recorded extreme temperatures that were clearly incorrect, and we censored all observations with temperatures above 38°C.

Finally, we recorded information on deer age, season, and biological year. All juveniles transitioned to the adult cohort if they survived to the next biological year, which we defined as 1 June to 31 May of the following year. Thus, we only had data for juveniles from capture in December or February through 31 May each year. We categorized GPS locations into the following seasons: spring (1 Apr–31 May), summer (1 Jun–30 Sep), autumn (1 Oct–30 Nov), and winter (1 Dec–31 Mar; Kolar et al. 2017).

We classified all covariates into 4 groups (Table 2), which we used in model selection. One covariate group included the proportion developed (within 4.8 × 4.8-km grid cells used to stratify capture), state (ND or MT), and a state × proportion developed interaction. The proportion developed variable included effects of roads, well pad density, and whether wells were in the development or extraction phases. To separate the effects of roads from oil and gas, we created 2 additional covariate groups: oil and gas, and roads and gravel pit. Variables in the oil and gas covariate group included distance to nearest active drilling rig, distance to nearest active well pad, and state. We included state in the oil and gas covariate group because all active drilling occurred in North Dakota during the study. To account for this difference between states, we also included a state × distance to drilling rig interaction. Variables in the road and gravel pit covariate group included distance to nearest road and distance to nearest gravel pit. We included these as a separate covariate group from oil and gas because they are both anthropogenic disturbances but are not necessarily a direct consequence of oil and gas development. Our fourth covariate group included individual, temporal, and environmental variables (collectively described as environmental variables): age, biological year, season, NDVI, snow depth, temperature, and spatial coordinates (i.e., latitude, longitude, latitude × longitude). We included spatial coordinates to account for spatial variation in mortality not accounted for with other variables. Because the effects of NDVI, snow depth, and temperature may vary by season (e.g., excessively hot temperatures may be detrimental during summer, excessively cold temperatures may be detrimental in winter), we additionally included season × NDVI, season × snow depth, and season × temperature interactions.

Statistical model

We evaluated mule deer mortality using point process models (Hooten et al. 2017). The point we modeled is the time each transmitter entered mortality mode. If we index the GPS observation that each transmitter enters mortality mode as $\{t_1, t_2, ..., t_R\}$, with R indicating the number of deer that die, we can write the likelihood function f as:

$$f(d_1, d_2, ..., d_R) = \prod_{r=1}^{R} \lambda(t_r) \prod_{i=1}^{N} \exp\left(-\int_0^{T_i} \lambda(t)dt\right), \tag{1}$$

where $r = 1, 2, ..., R$ indexes all mortality events; $i = 1, 2, ..., N$ indexes all N deer; the integral is evaluated from the time the GPS unit is placed on the deer ($t = 0$) until time T_i when deer i leaves the study (either through death, GPS failure, or reaching the end of the study alive); $\lambda(t)$ is an intensity function describing the relative mortality rate at time t; and $d_1, d_2, ..., d_R$ indicate that the likelihood function $f(d_1, d_2, ..., d_R)$ depends on data associated with all R deaths. We further modeled $\lambda(t)$ as a log-linear function of covariates recorded during time t:

$$\log(\lambda(t)) = \mathbf{x}_t'\boldsymbol{\beta}, \tag{2}$$

where $\mathbf{x}_t'$ is a vector of coefficients recorded at GPS observation t and $\boldsymbol{\beta}$ is a conformable vector of slope coefficients. Finally, we approximated the integral in Equation 1 above using quadrature (Hooten et al. 2017):

$$\int_0^{T_i} \lambda(t)dt \approx \sum_{j=1}^{J_i} \lambda(j)\Delta_j, \tag{3}$$

where $j = 1, 2, ..., J_i$ indexes each GPS observation for deer i; and Δ_j is the time interval between GPS observation $j - 1$ and j. Combining Equations 1 and 3 and summing over all L telemetry observations, we can write the log-likelihood as follows:

$$l(\boldsymbol{\beta}) \approx \sum_{l=1}^{L} \Delta_l\left(y_l\mathbf{x}_l'\boldsymbol{\beta} - \exp\left(\mathbf{x}_l'\boldsymbol{\beta}\right)\right),$$

where $y_l = 0$ if a deer was alive at telemetry observation l, and $y_l = 1/\Delta_l$ if a deer was dead at telemetry observation l (Hooten et al. 2017).

To ensure the integral in Equation 3 was evaluated at a reasonably fine temporal scale, we only kept telemetry locations separated by <24 hours. This first required censoring 3 deer that died during the study because the time between locations when they were last known alive and first known dead was >24 hours. We censored an additional 1,717 locations (< 1%) that were spaced >24 hours apart. Most locations (86%) were spaced ≤5 hours apart.

We performed model selection on 10 *a priori* models that included various combinations of proportion developed, oil and gas, road and gravel pit, and environmental variables using Akaike's Information Criterion (AIC; Burnham and Anderson 2002; Table 3). If there was a clear top model (i.e., ΔAIC > 4 between the top model and all other models), we based inference on this single model. If there was model selection uncertainty (i.e., ΔAIC < 4 between the top model and any other model), we averaged across all models within the model set. We set a threshold of 4 ΔAIC units because Burnham and Anderson (2002) describe that difference as providing considerably less support for a model relative to the top model. We fit all models with custom likelihood functions in R (R Core Team 2017).

TABLE 3 Point process models used in evaluating female mule deer mortality. The model name lists the covariate groups considered for each model. Models are sorted by increasing Akaike's Information Criterion (AIC), difference in AIC between the top and current model (ΔAIC), and model weights derived from ΔAIC. The variable *K* represents the number of parameters in each model. We evaluated female mule deer mortality from 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA.

Model name	AIC	ΔAIC	Weight	*K*
Environmental	1,546.12	0.00	0.36	20
Road and gravel pit; environmental	1,546.15	0.03	0.35	22
Proportion developed; environmental	1,548.22	2.09	0.13	22
Oil and gas; environmental	1,549.00	2.88	0.08	23
Oil and gas; road and gravel pit; environmental	1,549.14	3.02	0.08	25
Road and gravel pit	1,603.98	57.86	0.00	3
Oil and gas; road and gravel pit	1,606.62	60.50	0.00	6
Intercept	1,607.73	61.61	0.00	1
Oil and gas	1,608.80	62.68	0.00	4
Proportion developed	1,609.98	63.86	0.00	3

RESULTS

We modeled female mule deer mortality risk from 597,987 GPS locations obtained between February 2013 and May 2016 from 265 female mule deer that survived >14 days post-capture. Of these 265 deer, 99 died during the study. Model selection results indicated 2 broad groups of models: those with environmental variables (ΔAIC < 4 on all models with environmental variables) and those without environmental variables (ΔAIC > 57 on all models without environmental variables; Table 3). The large difference in AIC values between models with and without environmental variables highlights the importance of these variables on mortality risk relative to all other covariates evaluated. The top 5 models were separated by <4 ΔAIC units, so we base all inference below on model-averaged estimates. Estimated adult annual survival probability was 0.79 (95% CI = 0.71–0.85) and juvenile overwinter survival probability (i.e., the 181 days from 1 Dec–31 May) conditional on a juvenile having survived to 1 December, was 0.56 (95% CI = 0.46–0.66).

There was little evidence that female mule deer mortality was affected by proximity to well pads in the development or extraction phase, proportion of area influenced by oil and gas development, or state. Models that did include proportion developed or oil and gas variables accounted for about 29% of model weights (Table 3); however, all models that excluded environmental variables had weights approximating zero. Model-averaged 95% confidence intervals of slope coefficients for proportion developed within 4.8 × 4.8-km cells, distance to rig, distance to nearest active well pad, and state all overlapped zero, suggesting no strong effect of any of these proportion developed and oil and gas variables on mule deer mortality.

Similarly, there was little evidence that distance to road or gravel pit influenced female mule deer mortality. Models that included effects of distance to road and gravel pits only accounted for about 43% of total model weights (Table 3). Model-averaged 95% confidence intervals of slope coefficients for distance to road and distance from gravel pits both overlapped zero, suggesting no strong effect of any of these variables on mule deer mortality.

In contrast, female mule deer mortality was influenced by several environmental variables. The top 5 models all included environmental variables, and models that included environmental variables accounted for >99% of model weights (Table 3). Mortality rate varied substantially by season. Mortality rate was greater in winter and spring relative to summer and autumn (Figure 3; Table 4). Weather conditions during spring and winter further influenced mule deer mortality, as mortality rate was negatively associated with spring and winter temperature (Figures 4 and 5; Table 4). Daily mortality rate was also greater for juveniles than for adults (Table 4), though it did not vary by biological year (Table 5). There was no evidence to suggest mortality rate was influenced by NDVI or geographic coordinates (i.e., 95% CI of all slope coefficients overlapped zero; Table 4).

It may be difficult to detect demographic signals from development features that are rare on the landscape because deer exposure to these features is inconsistent. (Figures 6 and 7). The average distance from all GPS locations to the nearest active drilling rig in North Dakota was 28.59 km (range = 0.16–138.86 km; there were no active drilling rigs in Montana during this study). The average distance from all GPS locations to the nearest active well pad in North Dakota and Montana was 3.73 km (range = <0.01–30.95) and 6.70 km (0.03–44.67), respectively.

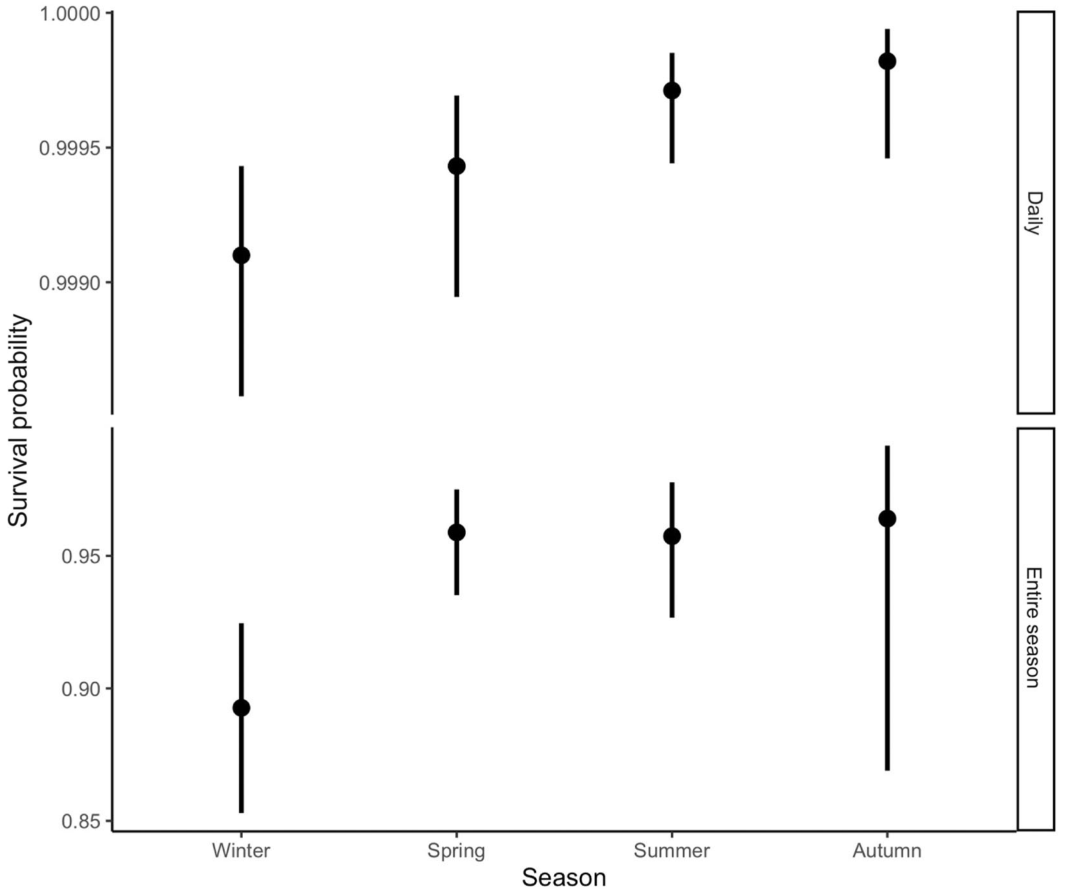

FIGURE 3 Model-averaged survival probability (±95% CI) of adult female mule deer as a function of season. The top panel reports survival probability by day and the bottom panel reports survival probability over each biological season (winter = 121 days; spring = 61 days; summer = 122 days, autumn = 61 days). Estimates were derived from Poisson point process models fitted to 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA. Daily survival probability was derived from a log-linear model assuming biological year 2015; the average latitude and longitude observed from GPS observations in North Dakota; season-specific means for normalized difference vegetation index, snow depth, and temperature; mean distance to drilling rig and mean proportion developed in North Dakota; and mean distance to well pad, road, and gravel pit. We calculated survival probability over the entire season as the geometric mean of the estimated survival probability of all adult deer over a given season.

TABLE 4 Model-averaged slope coefficients, unconditional standard error (SE), and model-averaged limits of 95% confidence intervals (CI) for variables thought to influence female mule deer mortality. Slope coefficients are obtained from Poisson point process models. We evaluated female mule deer mortality from 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA. The direction of slope coefficients corresponds to mortality risk, such that decreased mortality corresponds to increased survival.

Variable	Slope coefficient	Unconditional SE	2.5% CI	97.5% CI
State (ND)	0.17	0.37	−0.55	0.90
log(rig distance) × ND	−0.03	0.10	−0.23	0.16
log(well distance)	0.00	0.05	−0.10	0.11
Proportion developed	0.01	0.05	−0.09	0.11
log(road distance)	−0.07	0.09	−0.25	0.12
log(distance to gravel pit)	0.06	0.11	−0.15	0.28
Age (adult)	−1.29	0.23	−1.74	−0.83
Biological year 2014	0.02	0.30	−0.56	0.60
Biological year 2015	0.12	0.30	−0.47	0.71
Biological year 2016	−0.42	0.51	−1.43	0.58
Spring	1.61	0.74	0.16	3.07
Winter	1.47	0.66	0.17	2.76
Spring × NDVI[a]	−0.10	0.25	−0.58	0.39
Summer × NDVI	−0.03	0.25	−0.51	0.46
Autumn × NDVI	1.05	0.64	−0.21	2.30
Spring × snow depth	0.35	0.95	−1.51	2.20
Winter × snow depth	−0.08	0.10	−0.28	0.11
Autumn × snow depth	0.10	1.75	−3.34	3.53
Autumn × temperature	−0.55	0.68	−1.88	0.78
Spring × temperature	−0.74	0.29	−1.31	−0.16
Summer × temperature	0.64	0.50	−0.35	1.62
Winter × temperature	−0.43	0.17	−0.77	−0.09
Latitude	0.13	0.12	−0.10	0.37
Longitude	−0.01	0.19	−0.38	0.36
Latitude × longitude	0.07	0.13	−0.19	0.33

[a]Normalized difference vegetation index.

From our 473,759 GPS collar locations in North Dakota, the closest observed drilling rig was 162 m, and only 0.016% of all observations in North Dakota (74 GPS locations) were within 500 m of an active drilling rig. From our 597,987 GPS locations from the entire study, the closest observed active well pad was close to 0 m, and approximately 7% of all observations were within 500 m of an active well pad.

The leading causes of mortality in this study were malnutrition (21%), coyote predation (13%), and mountain lion predation (9%; Table 6). The main sources of adult female mortality were malnutrition (18%), mountain lion

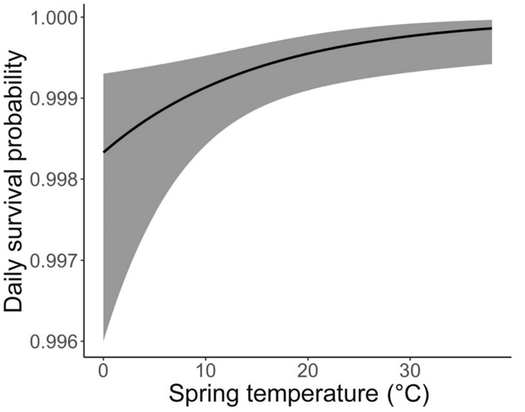

FIGURE 4 Model-averaged daily survival probability (±95% CI) of adult female mule deer as a function of spring temperature. Estimates were derived from Poisson point process models fitted to 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA. Daily survival probability was derived from a log-linear model assuming biological year 2015 and at the average latitude and longitude observed from GPS observations in North Dakota. We calculated estimates assuming season-specific means for normalized difference vegetation index, snow depth, and temperature; mean distance to drilling rig and mean proportion developed in North Dakota; and mean distance to well pad, road, and gravel pit.

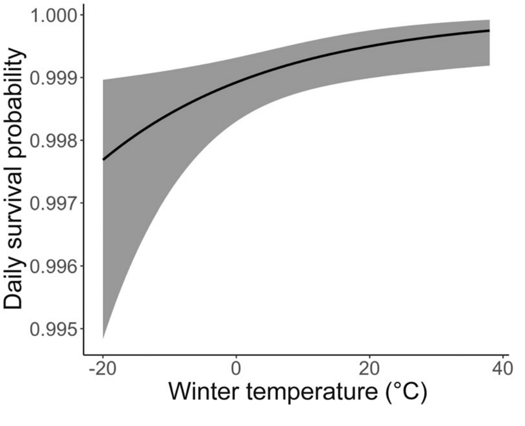

FIGURE 5 Model-averaged daily survival probability (± 95% CI) of adult female mule deer as a function of winter temperature. Estimates were derived from Poisson point process models fitted to 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA. We calculated estimates assuming biological year 2015, and at the average latitude and longitude observed from GPS observations in North Dakota. We also assumed season-specific means for normalized difference vegetation index, snow depth, and temperature; mean distance to drilling rig and mean proportion developed in North Dakota; and mean distance to well pad, road, and gravel pit.

predation (16%), coyote predation (11%), and harvest (legal and illegal, 11% total). The main sources of female fawn mortality were malnutrition (25%), coyote predation (16%), and disease or injury (9%). Mountain lion predation was restricted almost exclusively to North Dakota with only 1 event occurring in Montana. Within the North Dakota study area, all but 1 mountain lion predation events were north of Interstate 94.

TABLE 5 Model-averaged adult annual (365 days) and juvenile overwinter (181 days) survival probability and model-averaged limits of 95% confidence intervals (CI) for female mule deer based on 597,987 global positioning system (GPS) locations obtained from 265 mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA.

Age	Year	State	Estimate (CI)
Adult	2013	ND	0.80 (0.70, 0.88)
Adult	2014	ND	0.77 (0.55, 0.85)
Adult	2015	ND	0.79 (0.71, 0.86)
Adult	2016	ND	0.84 (0.70, 0.93)
Juvenile	2013	ND	0.52 (0.31, 0.68)
Juvenile	2014	ND	0.55 (0.40, 0.68)
Juvenile	2015	ND	0.57 (0.44, 0.69)
Adult	2014	MT	0.82 (0.62, 0.91)
Adult	2015	MT	0.82 (0.68, 0.90)
Adult	2016	MT	0.85 (0.70, 0.94)
Juvenile	2014	MT	0.62 (0.45, 0.76)
Juvenile	2015	MT	0.61 (0.44, 0.74)

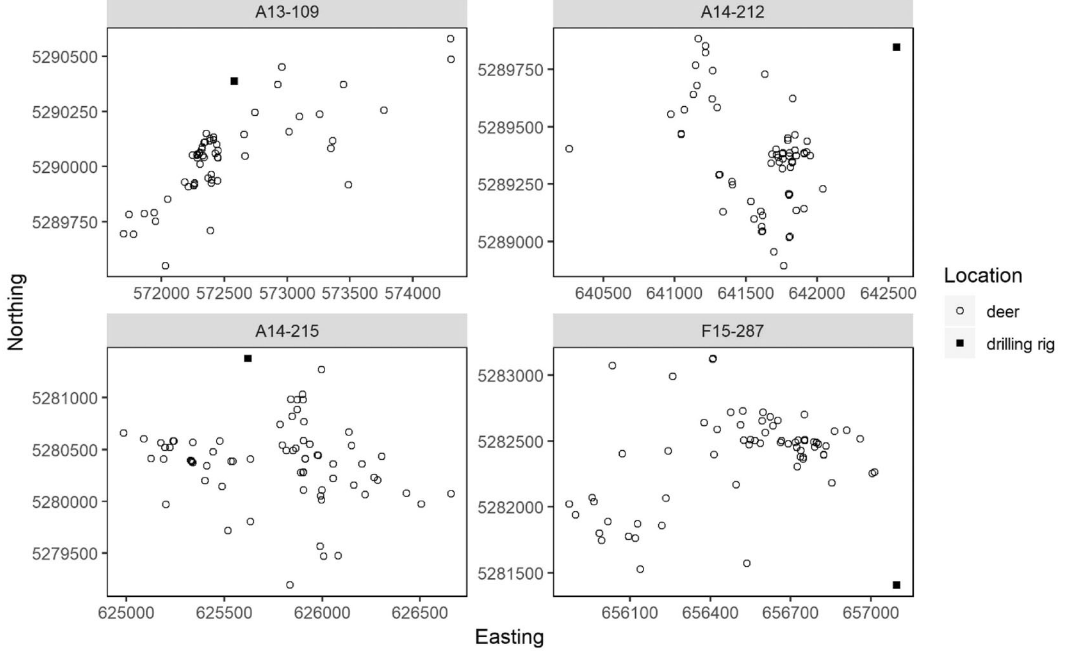

FIGURE 6 Mule deer locations in North Dakota, USA, collected between February 2013 and May 2016. Open circles represent mule deer locations over the 2-week interval that the deer was at its closest to an active drilling rig (black square). These plots represent the 4 individual deer (gray headers represent individual deer IDs) with the closest locations to an active drilling rig we observed over the study duration.

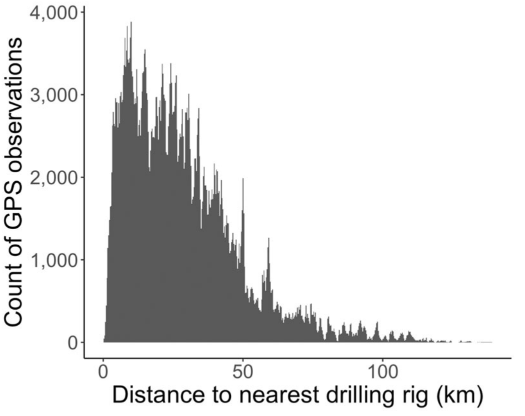

FIGURE 7 Histogram of observed distance of female mule deer to active drilling rigs in North Dakota, USA, obtained from 473,759 global positioning system (GPS) observations from 198 female mule deer between February 2013 and May 2016.

TABLE 6 Cause-specific mortality sources for adult and fawn mule deer between February 2013 and May 2016 in western North Dakota and eastern Montana, USA. There were 265 deer at risk of death during the study period.

Cause of mortality	Adult	Fawn	Total
Malnutrition	10	11	21
Mountain lion	9	0	9
Coyote	7	7	14
Legal harvest	1	0	1
Illegal harvest	5	0	5
Disease or injury	5	5	10
Vehicle collision	2	2	4
Parturition	3	0	3
Unknown	12	20	32
Total	54	45	99

DISCUSSION

Contrary to expectations, there was no correlation between oil and gas variables and mortality probability of female mule deer in western North Dakota or eastern Montana. Although few investigations have examined the effect of energy development on juvenile and adult mule deer mortality, these results are consistent with research showing no effect of distance to oil and gas wells on pronghorn summer mortality risk (Reinking et al. 2018) or mule deer fawn mortality (Peterson et al. 2018). A possible reason we failed to detect a relationship between distance to oil and gas development and mortality risk is because mule deer locations were rarely in proximity to these areas (Kolar et al. 2017, Skelly 2018; Figure 6). Mule deer avoidance of all types of oil and gas development (i.e., active drilling rigs and well pads) has been previously documented in Wyoming and Colorado, USA (Northrup et al. 2015, Sawyer et al. 2006, 2009, 2017). Use of areas farther from high-traffic oil and gas features such as drilling rigs might have mitigated effects to mortality risk. Thus, although oil and gas development can influence ungulate space use (Northrup et al. 2015), movements (Lendrum et al. 2012), and fetal development (Peterson et al. 2017), we detected no effect on female mortality. Shifts in space use could lead to effects on survival through habitat loss (Sawyer et al. 2017). Although we did not see effects on mortality probability in this study, consequences of habitat loss from development could be delayed or cumulative, and long-term demographic effects may take longer to manifest at the population level than our 4-year study period.

Given the different intensity of oil and gas development between North Dakota and Montana, we predicted that mortality would be greater in North Dakota relative to Montana. Although model-averaged estimates suggest a slightly greater mortality rate in North Dakota relative to Montana, model-averaged 95% confidence intervals overlap zero, indicating no strong evidence for a difference in mortality between states. The oil and gas landscape differed between the states during this study. In the North Dakota study area, average active well pad density was $0.19/km^2$, with some areas having up to 9 active well pads/km^2 (Kolar et al. 2017). In contrast, average active well pad density in Montana was $0.01/km^2$, and there was no new well pad construction in those areas during the study (i.e., active well pads in those areas were limited to the extraction phase). Failure to detect differences in mortality probability between these different landscapes further suggests there is no effect of oil and gas development on mortality risk of mule deer. We recognize, however, that this comparison is imperfect, as other confounding factors between these regions (e.g., differences in agriculture) could mask potential differences in mortality. During our study, antlerless mule deer hunting was closed in North Dakota, and antlerless harvest estimates in Montana were minimal, so the short-term differences in management strategies should not have confounded the state effect. This result highlights the importance of study designs contrasting areas with and without development, such as before-after control-impact studies, when evaluating the potential effects of displacement due to oil and gas infrastructure on mule deer mortality. To account for potential avoidance of development features, managers who wish to conduct studies on the effects of oil and gas energy development on ungulates should also aim to bolster samples in highly developed areas. Further, because highly intensive portions of oil and gas energy development (e.g., drilling rigs) are short-term and sparse across the landscape, much higher sample sizes of collared deer may be required for detecting potential effects on mortality.

Although the relative contribution of weather, predation, and forage availability on mule deer population dynamics remains unresolved (Forrester and Wittmer 2013), weather is consistently a strong influence on mule deer vital rates (Hurley et al. 2017, Schuyler et al. 2019) and appeared to be the strongest factor influencing variation in mule deer mortality during our study. Spring and winter weather was a particularly strong determinant of mule deer mortality risk. Lower temperatures in winter and spring were associated with increased risk of mortality. Mule deer survival is typically lowest in winter (White et al. 1987, Lomas and Bender 2007, Hurley et al. 2011, Brodie et al. 2013, Ciuti et al. 2015), and low winter survival can be a result of poor nutrition, competition for resources (density dependence), increased predator efficiency, or restricted movements (Nelson and Mech 1986, Ciuti et al. 2015, Beckmann et al. 2016). The mule deer population in the study area is non-migratory and mule deer densities were rebounding during our study, so it is unlikely that high winter mortality was due to restricted movements or competition for resources. Mule deer tend to be in a negative energy balance during winter and spring, and low temperatures and high snow depths could result in increased energy expenditures (Short 1981, Nelson and Mech 1986). In addition, predation rates are reported to be higher when nutrition is poorer (Bishop et al. 2005). Increased winter mortality may therefore be caused by a combination of poor nutritional condition coupled with increased predation rates. Finally, even though we failed to detect an effect of oil and gas on mule deer mortality, lag effects may manifest themselves as increased mortality in response to other external stressors. For example, if chronic exposure to oil and gas infrastructure reduced mule deer body condition (Kolar et al. 2017), increased winter mortality may happen months or years after initial exposure.

Malnutrition was the leading cause of mortality, despite the population likely being below carrying capacity. Combined with winter and spring seasons being the time of highest mortality, this lends support to winter weather being a more important influence on mule deer populations than predators. Many of our predation events were likely linked to poor body condition during winter and spring. For example, we observed poor to fair body condition in 5 of 9 necropsies of coyote-predated deer where we could assess body condition. Furthermore, we only detected coyote predation in winter ($n = 13$) and spring ($n = 1$) seasons, when poor body conditions might be expected (Shallow et al. 2005). In contrast, only 2 of 17 summer or autumn mortalities attributed to unknown causes had evidence suggesting a possible coyote predation. Alternatively, malnutrition could occur if oil and gas development is displacing mule deer into areas with reduced food resources. In these circumstances, we would expect mule deer mortality to be related to the proportion of oil and gas development on the landscape, or to vary between states with relatively high and low well pad density. We did not detect effects of these covariates on mule deer mortality; however, if even relatively low amounts of oil and gas development leads to habitat displacement, mule deer in both study areas may experience increased mortality risk that our study design was unable to detect.

The lowest mortality rates occurred during summer and autumn, when resources were least limiting. Most mortalities during the summer season were attributed to mountain lion predation ($n = 4$), which accounted for 40% of adult deer mortalities in this season. Similarly, we detected only 5 mortalities during the autumn season, 3 of which were attributed to human causes (1 illegal harvest, 1 legal harvest, and 1 vehicle collision). Unlike coyote predation, predation by mountain lions and humans is not as strongly linked to poor body condition, as both predators can kill healthy adults. But predation by mountain lions and hunter harvest are not likely limiting this population of mule deer. Malnutrition during winter was the leading cause of mortality, suggesting that predation by mountain lions and hunters during summer and fall may have been compensatory mortality.

Our point estimates of annual adult female survival probabilities (0.79) were lower than previously reported in Colorado, Idaho, and Montana (0.85; Unsworth et al. 1999) and the range-wide mean (0.84; Forrester and Wittmer 2013), though it is within the range of survival estimates reported in other studies (0.72–0.91; Forrester and Wittmer 2013). Similarly, our estimate of overwinter juvenile survival (0.56) was lower than the range-wide estimate of winter fawn survival (0.61; Forrester and Wittmer 2013) but still well within the range of reported estimates (0.25–0.85; Forrester and Wittmer 2013). Survival rates we observed may have been lower than expected because of an aging adult population. Regional mule deer abundance decreased substantially following severe winters in 2009–2010 and 2010–2011 (Figure 2) and it is likely that the mule deer population we studied was skewed toward older age-classes. Despite observing lower than average survival, the mule deer population we studied continued to grow because of relatively high recruitment. Gill (2001) reported 50–60 fawns/100 females is necessary for a sustainable population, and Unsworth et al. (1999) reported 70–80 fawns/100 females is necessary for a stable or growing population, given the survival estimates we report. Fawn-to-female ratios were 89 and 74–93 fawns/100 females in North Dakota and Montana, respectively, during our study, which is above the recruitment threshold for maintaining stable populations.

There was no support for our original prediction of greater mortality risk in proximity to primary and secondary roads. Although mule deer have been demonstrated to avoid areas close to roads (Sawyer et al. 2009, Northrup et al. 2015, Skelly 2018), the effects of proximity to roads on mortality risk is unknown. Hunting can be the main source of mortality in adult mule deer (83% [Wood et al. 1989], 22.6% [Carnes 2009]), and hunter success increases with increased road density (Dorning et al. 2016). We may have failed to detect an effect of distance to roads on mortality because antlerless hunting opportunities were limited during this study, and it is possible that during years with higher antlerless quotas and harvest a positive relationship between mortality and road density would be evident (Fox 1989). Although roads may heighten mortality risk because of increased likelihood of vehicle collisions and hunter access (Diefenbach et al. 2005), studies with other species including white-tailed deer (Haus et al. 2019) have failed to find such a relationship. Perhaps heightened mortality risk close to roads could be offset if other sources of mortality are reduced (e.g., if predators also avoid roads; Chetkiewicz and Boyce 2009), leading to no clear effect of proximity to roads on mortality risk. We did not detect high rates of vehicle collisions or illegal harvest, but even small increases in female adult mortality could have significant effects on mule deer populations because positive population growth rates depend on high, stable female adult survival (Forrester and Wittmer 2013). Vehicle collision rates in our study may have been low because we avoided high-traffic roads while capturing. Nonetheless, road density did not appear informative when evaluating mortality rates of mule deer in our study.

MANAGEMENT IMPLICATIONS

We did not detect an effect of energy development on mule deer mortality, but mule deer in our study were almost never detected near areas of active development. Mule deer densities were low (Figure 2) and mule deer may have been able to mitigate mortality risks by shifting their home ranges on the landscape. Managers should therefore consider whether resources proximal to oil and gas developments exist prior to construction. Our results could inform a pre-development risk assessment to minimize potential effects on mule deer. For example, a risk assessment map that integrates demography and habitat use could be used to evaluate relative impacts of proposed development and to ensure there are resources within the surrounding area for potentially displaced deer.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All field protocols were approved by the University of Missouri Institutional Animal Care and Use Committee (protocol number 8548).

DATA AVAILABILITY STATEMENT

Code is published at Zenodo, https://zenodo.org/doi/10.5281/zenodo.11224519.

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REFERENCES

Beckmann, J. P., S. H. Olson, R. G. Seidler, and J. Berger. 2016. Sub-lethal effects of energy development on a migratory mammal—the enigma of North American pronghorn. Global Ecology and Conservation 6:36–47.

Bishop, C. J., J. W. Unsworth, and E. O. Garton. 2005. Mule deer survival among adjacent populations in southwest Idaho. Journal of Wildlife Management 69:311–321.

Bivand, R., and C. Rundel. 2017. rgeos: interface to Geometry Engine—open source ('GEOS'). R package version 0.3-25. <https://CRAN.R-project.org/package=rgeos>

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, et al. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York, New York, USA.

Carnes, J. C. 2009. Mule deer population ecology and chronic wasting disease study. Montana Fish Wildlife & Parks, Miles City, USA.

Chetkiewicz, C. L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036–1047.

Ciuti, S., W. F. Jensen, S. E. Nielsen, and M. S. Boyce. 2015. Predicting mule deer recruitment from climate oscillations for harvest management on the Northern Great Plains. Journal of Wildlife Management 79:1226–1238.

Clark, J. B. 1949. A hydraulic process for increasing the productivity of wells. Journal of Petroleum 2510:1–8.

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009. Mapping oil and gas development potential in the US Intermountain West and estimating impacts to species. PLoS ONE 4:e7400.

Didan, K. 2015. MYD13Q1 MODIS/Aqua vegetation indices 16-day L3 global 250m SIN grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. <https://doi.org/10.5067/MODIS/MYD13Q1.006>. Accessed 2 Jan 2020.

Diefenbach, D. R., J. C. Finley, A. E. Luloff, R. Stedman, C. B. Swope, H. C. Zinn, and G. J. San Julian. 2005. Bear and deer hunter density and distribution on public land in Pennsylvania. Human Dimensions of Wildlife 10:201–212.

Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski. 2013. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Movement Ecology 3:1–14.

Dorning, M. A., S. L. Garman, J. E. Diffendorfer, D. J. Semmens, T. J. Hawbaker, and K. J. Bagstad. 2016. Oil and gas development influences big game hunting in Wyoming. Journal of Wildlife Management 81:379–392.

Forrester, T. D., and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer (*Odocoileus hemionus*) in North America. Mammal Review 43:292–308.

Fox, R. A. 1989. Mule deer (*Odocoileus hemionus*) home range and habitat use in an energy-impacted area of the North Dakota badlands. Thesis, University of North Dakota, Grand Forks, USA.

Gamo, S. R., K. T. Smith, and J. L. Beck. 2017. Energy development and hunter success for mule deer and pronghorn in Wyoming. Wildlife Society Bulletin 41:62–69.

Gill, R. B. 2001. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife Special Report 77, Fort Collins, USA.

Godfread, C. 1994. The vegetation of the Little Missouri Badlands of North Dakota. Pages 14–24 *in* Proceedings: Leafy Spurge Strategic Planning Workshop. Theodore Roosevelt National Park, 29–30 March 1994, Dickinson, North Dakota, USA.

Goodman, P. S., F. Galatioto, N. Thorpe, A. K. Namdeo, R. J. Davies, and R. N. Bird. 2016. Investigating the traffic-related environmental impacts of hydraulic-fracturing (fracking) operations. Environmental International 89-90:248–260.

Gratson, M. W., and C. L. Whitman. 2000. Road closure and density and success of elk hunters in Idaho. Wildlife Society Bulletin 28:302–310.

Hamlin, K. L., and R. J. Mackie. 1989. Mule deer in the Missouri River Breaks, Montana: a study of population dynamics in a fluctuating environment. Montana Department of Fish, Wildlife and Parks, Helena, USA.

Haus, J. M., S. L. Webb, B. K. Strickland, J. E. Rogerson, and J. L. Bowman. 2019. Land use and dispersal influence mortality in white-tailed deer. Journal of Wildlife Management 83:1185–1196.

Hebblewhite, M. 2011. Effects of energy development on ungulates. Pages 71-95 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Hooten, M. B., D. S. Johnson, B. T. McClintock, and J. M. Morales. 2017. Animal movement: statistical models for telemetry data. CRC Press, Boca Raton, Florida, USA.

Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behavior. Journal of Applied Ecology 51: 1680–1689.

Hurley, M. A., M. Hebblewhite, J. M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society B 369:20130196.

Hurley, M. A., M. Hebblewhite, P. M. Lukacs, J. J. Nowak, J. M. Gaillard, and C. Bonenfant. 2017. Regional-scale models for predicting overwinter survival of juvenile ungulates. Journal of Wildlife Management 81:364–378.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in Southeastern Idaho. Wildlife Monographs 178:1–33.

Jackson, R. D., and A. R. Huete. 1991. Interpreting vegetation indices. Preventive Veterinary Medicine 11:185–200.

Jones, N. F., L. Pejchar, and J. M. Kiesecker. 2015. The energy footprint: how oil, natural gas, and wind energy affect land for biodiversity and the flow of ecosystem services. BioScience 65:290–301.

Kolar, J. L., J. J. Millspaugh, B. A. Stillings, C. P. Hansen, C. Chitwood, C. T. Rota, and B. P. Skelly. 2017. Potential effects of oil and gas energy development on mule deer in western North Dakota. North Dakota Game and Fish State Report, Bismarck, USA.

Lendrum, P. E., C. R. Anderson, Jr., R. A. Long, J. G. Kie, and T. R. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3:1–19.

Lendrum, P. E., C. R. Anderson, Jr., K. L. Monteith, J. A. Jenks, and T. R. Bowyer. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. PLoS ONE 8:e64548.

Litvaitis, J. A., and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. Environmental Management 42:688–697.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884–894.

Lutz, D. W., B. F. Wakeling, L. H. Carpenter, D. Stroud, M. Cox, D. McWhirter, S. Rosenstock, L. C. Bender, and A. F. Reeve. 2003. Impacts and changes to mule deer habitat. Pages 13-61 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

McDonald, R. I., J. Fargione, J. Kiesecker, W. M. Miller, and J. Powell. 2009. Energy sprawl or energy efficiency: climate policy impacts on natural habitat for the United States of America. PLoS ONE 4:e6802.

Meisingset, E. L., L. E. Loe, O. Brekkum, B. Van Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181–191.

Montana Department of Natural Resources. 2016. Board of Oil and Gas Conservation <http://www.bogc.dnrc.mt.gov/gisdata/> Accessed 2 Feb 2017.

Montana Department of Transportation. 2016. Montana spatial data infrastructure <https://msl.mt.gov/geoinfo/msdi/transportation/> Accessed 2 May 2016.

Montana Fish, Wildlife, and Parks. 2001. Adaptive harvest management. Montana Fish, Wildlife, and Parks, Helena, USA.

National Centers for Environmental Prediction. 2005. NCEP North American Regional Reanalysis (NARR). Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory. <http://rda.ucar.edu/datasets/ds608.0/> Accessed 20 Nov 2017.

Nelson, M. E., and D. L. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

North Dakota Department of Transportation. 2016. North Dakota GIS hub data portal. <https://gishubdata-ndgov.hub.arcgis.com> Accessed 17 Feb 2016.

North Dakota Industrial Commission. 2017. Oil and Gas: ArcIMS Viewer. <https://www.dmr.nd.gov/OaGIMS/viewer.htm> Accessed 2 Jan 2020.

Northrup, J. M., C. R. Anderson, Jr., and G. Wittemyer. 2015. Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. Global Change Biology 21:3961–3970.

Northrup, J. M., C. R. Anderson, Jr., and G. Wittemyer. 2016. Environmental dynamics and anthropogenic development alter philopatry and space-use in a North American cervid. Diversity and Distribution 22:547–557.

Northrup, J. M., and G. Wittemyer. 2013. Characterizing the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecological Letters 16:112–125.

Owen-Smith, R. N. 2002. Resource-dependent mortality: nutrition, predation and demography. Pages 205–231 *in* Adaptive herbivore ecology: from resources to populations in variable environments. Cambridge University Press, Cambridge, United Kingdom.

Peterson, M. E., C. R. Anderson Jr., J. M. Northrup, and P. F. Doherty. 2017. Reproductive success of mule deer in a natural gas development area. Wildlife Biology 2017:wlb.00341.

Peterson, M. E., C. R. Anderson Jr., J. M. Northrup, and P. F. Doherty. 2018. Mortality of mule deer fawns in a natural gas development area. Journal of Wildlife Management 82:1135–1148.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reinking, A. K., K. T. Smith, K. L. Monteith, T. W. Mong, M. J. Read, and J. L. Beck. 2018. Intrinsic, environmental, and anthropogenic factors related to pronghorn summer mortality. Journal of Wildlife Management 82:608–617.

Ryan, R. W., D. D. Gustine, and K. Joly. 2014. Evaluating potential effects of an industrial road on winter habitat of caribou in North-Central Alaska. Artic Institute of North America 67:472–482.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Sawyer, H., N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer and energy development – long-term trends of habituation and abundance. Global Change Biology 23:4521–4529.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Schemnitz, S. D., G. R. Batcheller, M. J. Lovallo, H. B. White, and M. W. Fall. 2012. Capturing and handling wild animals. Pages 64–117 *in* N. J. Silvy, editor. The wildlife techniques manual, 7th edition, volume 1: research. Johns Hopkins Press, Baltimore, Maryland, USA.

Schuyler, E. M., K. M. Dugger, and D. H. Jackson. 2019. Effects of distribution, behavior, and climate on mule deer survival. Journal of Wildlife Management 83:89–99.

Short, H. L. 1981. Nutrition and metabolism. Pages 99–127 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

Skelly. B. P. 2018. Potential effects of oil and natural gas development on mule deer (*Odocoileus hemionus*) survival and fawn rearing resource selection. Thesis, West Virginia University, Morgantown, USA.

Unsworth, D. F., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management. 63:315–326.

U.S. Energy Information Administration. 2018. Annual energy outlook 2018. <www.eia.gov/outlooks/aeo/data/browser/>. Accessed 25 Jun 2018.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

White, G. C., R. A. Garrott, R. M. Bartmann, L. H. Carpenter, and W. A. Alldredge. 1987. Survival of mule deer in Northwest Colorado. Journal of Wildlife Management 51:852–859.

Wikelski, M., and R. Kays. 2017. Movebank: archive, analysis and sharing of animal movement data. Hosted by the Max Planck Institute for Animal Behavior. <www.movebank.org>. Accessed 2 June 2017.

Wood, A. K., R. J. Mackie, and K. L. Hamlin. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Montana Fish Wildlife and Parks, Helena, USA.

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