

DISSERTATION

REPRODUCTIVE SUCCESS, HABITAT SELECTION, AND NEONATAL MULE DEER
MORTALITY IN A NATURAL GAS DEVELOPMENT AREA

Submitted by

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ABSTRACT

REPRODDUCTIVE SUCCESS, HABITAT SELECTION, AND NEONATAL MULE DEER MORTALITY IN A NATURAL GAS DEVELOPMENT AREA

Mule deer (*Odocoileus hemionus*) populations have periodically declined throughout the western United States, with notable declines during the late 1960s, early 1970s, and 1990s (Unsworth et al. 1999) to present. Declining population levels can be attributed to low fawn survival and subsequently low population recruitment (Unsworth et al. 1999, Pojar and Bowden 2004) caused by declining habitat availability and quality (Gill 2001, Lutz et al. 2003, Watkins et al. 2007, Bergman et al. 2015). Although, general public perception is that declining deer numbers are attributed exclusively to predation (Barsness 1998, Willoughby 2012), predator control research suggests otherwise (Hurley et al. 2011, Kilgo et al. 2014) and compelling evidence exists that improving habitat quality can enhance deer populations (Bishop et al. 2009, Bergman et al. 2014). Complicating this story is the large-scale habitat alterations driven by natural gas development, which may also influence deer population dynamics.

Natural gas development and associated disturbances that can affect deer habitat and population dynamics include conversion of native plant communities to drill pads, roads, or noxious weeds and noise pollution from compressor stations, drilling rigs, increased traffic, and year round occurrence of human activities. Natural gas development alters mule deer habitat selection through direct and indirect habitat loss (Sawyer et al. 2006, Sawyer et al. 2009, Northrup et al. 2015). Direct habitat loss results from construction of well pads, access roads, compressor stations, pipelines, and transmission lines. Activity, traffic, and noise associated with

increased human presence and development may lead to indirect habitat loss. Indirect habitat loss is exacerbated because active wells produce gas for 40 years or longer (Sawyer et al. 2006, Sawyer et al. 2009). In addition, indirect habitat loss affects considerably larger areas than direct habitat loss (Sawyer et al. 2006, Sawyer et al. 2009). Recent research suggests direct and indirect losses can lead to behavioral responses to development (Sawyer et al. 2006, Dzialak et al. 2011b, Northrup et al. 2015). However, deer can behaviorally mediate these impacts by altering activity patterns or selecting habitat with topographic diversity that provides refuge from development (Northrup et al. 2015).

Obtaining a more complete understanding of the potential impacts of development is critical to comprehend population dynamics of deer and to develop viable mitigation options. Understanding how natural gas development and other factors influence reproductive success metrics (e.g., pregnancy, in utero fetal, and fetal survival rates), fetal sex ratio, habitat characteristics of birth and predation sites (i.e., habitat selection), and neonatal (i.e., 0–6 months old) mule deer mortality have been identified as knowledge gaps. Thus, my dissertation focused on addressing these knowledge gaps through individual reproductive success monitoring using vaginal implant transmitters. I conducted this research during 2012–2014 in the Piceance Basin of northwestern Colorado in study areas with relatively high (0.04–0.90 well pads/km²) or low (0.00–0.10 well pads/km²) levels of natural gas development.

In chapter 1, I examined the influence of adult female, natural gas development, and temporal factors on reproductive success metrics (i.e., pregnancy rate, in utero fetal rate, and fetal survival rate) and fetal sex ratio. Pregnancy rates were high, did not vary across years, and were essentially equal between study areas. In utero fetal rates were lower for yearling females ($n = 10$) and varied annually compared to adult females ($n = 204$) possibly from annual weather

patterns that influenced forage quality and digestibility. Fetal survival rates increased over time and were lower in the high development study areas than the low development areas in 2012 possibly caused by a compounding influence of development disturbance during extreme environmental conditions (i.e., drought). Higher road density in a female's core area (i.e., 50% minimum convex polygon) on summer range possibly contributed to better maternal body condition through increased forage quality along roads. Following the Trivers-Willard hypothesis which predicts females in good versus poor condition will produce more males, my results suggested females had a higher probability of producing more male offspring as road density increased. However, under my proposed mechanism, I would expect body condition and road density to be strongly correlated, but they were only weakly correlated ($r = 0.07$). I also note that I did not detect a biased sex ratio at the population level. Thus, I am uncertain of the exact mechanism influencing the relationship between road density and fetal sex ratio.

In chapter 2, I used global positioning system collar data in conjunction with VITs and linear mixed models to validate the use of maternal deer movement rates (m/day) to determine timing of parturition. Daily movement rate of maternal deer decreased by 39% from 1 day before parturition ($\bar{x} = 1,243.56$, $SD = 1,043.03$) to 1 day after parturition ($\bar{x} = 805.30$, $SD = 652.91$). Thus, I suggest that a mule deer female whose daily movement rate significantly decreases to ≤ 800 m/day has likely given birth. In the future, I will analyze an independent data set to validate the recommended threshold value and possibly develop a movement rate algorithm.

In chapter 3, I fit resource selection functions to examine the influence of natural gas development and environmental factors on birth site selection and habitat characteristics of predation sites. Females selected birth sites farther from producing well pads and with increased cover for concealing neonates and appeared to select habitat (e.g., north-facing slopes and further

from treed edges) that minimized neonate predation risk. Predation sites were characterized as being closer to development and in habitat (e.g., woodlands, aspen-conifer stands, and north-facing slopes) that possibly provided favorable microclimates for neonates and abundant high quality forage for lactating females. However, I note that predation sites were on average relatively far (2,057 m) from producing well pads and I have difficulty proposing a mechanism to explain how well pads that far away can influence predation site characteristics. My results suggest natural gas development and environmental factors (e.g., slope, habitat type, and aspect) can influence birth site selection with predation site characteristics possibly related to foraging habitat selection.

In chapter 4, I tested hypotheses about the influence of adult female, natural gas development, neonate, and temporal factors on neonatal mortality using a multi-state model. Predation and death by malnutrition decreased from 0–14 days old. Predation of neonates was positively correlated with rump fat thickness of adult females, but negatively correlated with the distance (0–0.4 km) from a female’s core area (i.e., 50% kernel density estimate) to a producing well pad on winter or summer range. Death by malnutrition was positively correlated with the distance from a female’s core area to a road on winter range and weakly, but negatively correlated with temperature. During my study, predation was the leading cause of neonatal mortality in both areas and mean daily predation probability was 9% higher in the high versus low development areas. However, black bear (*Ursus americanus*) predation was the leading cause of neonatal mortality in the high development areas (22% of all mortalities) compared to cougar (*Felis concolor*) predation in the low development areas (36% of all mortalities). Reduced precipitation and patchy habitat further fragmented by development possibly

contributed to less hiding cover or edge effects, potentially leading to increased predation in the high development areas.

Overall, my results suggest natural gas development may decrease fetal survival, influence birth site selection, and increase neonatal mortality, especially through predation, which may have consequences for mule deer recruitment and population dynamics depending on development intensity, habitat, and environmental conditions (e.g., drought). Consequently, developers and managers should consider strategies to mitigate impacts from development and improve forage and habitat quality and availability to minimize fitness consequences of deer. Such strategies could include development planning to avoid important habitats during critical time periods, implementing habitat treatments to rehabilitate areas, and minimizing habitat fragmentation and removal of hiding cover when constructing well pads and roads.

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I had no idea how much my life would change when I decided to pursue a PhD at Colorado State University (CSU). I interacted with numerous folks at CSU and Colorado Parks and Wildlife (CPW), which led to me enjoying my PhD journey. Thus, there are so many people who have helped me throughout my PhD journey. First, I would like to thank my advisor, Paul Doherty, Jr. Paul has always been extremely energetic, supportive, and encouraging throughout my dissertation research and I am thankful for the opportunity to have worked with him. However, my goal in life, now that I have completed my degree is to not hear Paul ask me “Are you done yet?” or “What’s cooking?”

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CHAPTER 1

REPRODUCTIVE SUCCESS OF MULE DEER AND A TEST OF THE TRIVERS-WILLARD HYPOTHESIS IN A NATURAL GAS DEVELOPMENT AREA

Synopsis. Natural gas development on public lands has caused concern about the potential impacts on wildlife populations and their habitat, particularly for ungulate species. Understanding how this development affects reproductive success metrics (e.g., pregnancy, in utero fetal, and fetal survival rates) and sex ratios that are influential for ungulate population dynamics is important to guide management of mule deer (*Odocoileus hemionus*). I examined the influence of natural gas development, temporal, and adult female factors on reproductive success metrics and fetal sex ratios of mule deer in the Piceance Basin in northwestern Colorado, USA during 2012–2014 and focused on areas with relatively high or low natural gas development. Pregnancy rates were high, did not vary across years, and were essentially equal between study areas. In utero fetal rates were lower for yearling females and varied annually compared to adult females possibly from annual weather patterns that influenced forage quality and digestibility. Fetal survival rates increased over time and rate was lower in the high development study areas than the low development areas in 2012 possibly caused by a compounding influence of development disturbance during extreme environmental conditions (i.e., drought). Following the Trivers-Willard hypothesis, my results suggested females in good condition had a higher probability of producing more male offspring as road density in a female's core area increased. However, I note that I did not detect a biased sex ratio at the population level. Thus, I am uncertain of the exact mechanism influencing road density and fetal

sex ratio. Developers and managers should collaborate on management actions to increase fetal survival. Such strategies could include implementing habitat treatments to improve forage availability and quality to minimize fitness consequences of deer in developed areas.

INTRODUCTION

Natural gas development is increasing across the West causing concern about the potential impacts on wildlife and their habitat (Walker et al. 2007, Holloran et al. 2010, Webb et al. 2011a, Kirol et al. 2014). Impacts on mule deer (*Odocoileus hemionus*) population dynamics and their habitat are of particular interest due to the deer's recreational, social, and economic importance as a game species (Sawyer et al. 2009, Lendrum et al. 2012, Northrup et al. 2015). Accurate pregnancy rates (i.e., proportion of adult females carrying ≥ 1 fetus), in utero fetal rates (i.e., the number of fetuses per pregnant female), and fetal survival rates (i.e., survival of fetuses to birth) are needed to quantify fawn recruitment and population dynamics (Bonenfant et al. 2005). Past studies have shown that using fawn:adult female ratios as an index for recruitment can be misleading and that pregnancy rates and fetal numbers should be estimated directly from marked animals (Bonenfant et al. 2005, DeCesare et al. 2012). However, the influences of natural gas development on reproductive success metrics (i.e., pregnancy, in utero fetal, and fetal survival rates) have not been studied.

Natural gas development may influence reproductive success due to direct and indirect habitat loss. Direct habitat loss results from construction of well pads, access roads, compressor stations, and pipelines, whereas, activity, traffic, and noise associated with increased human presence and development may lead to indirect habitat loss. Past studies suggest deer tend to avoid roads (Rost and Bailey 1979, Webb et al. 2011c, Lendrum et al. 2012) and well pads (Sawyer et al. 2006, Sawyer et al. 2009, Northrup et al. 2015) and development disturbances may

cause stress, alter behavior and habitat use, and decrease forage and habitat availability (Sawyer et al. 2006, Sawyer et al. 2009, Northrup et al. 2015). Thus, body condition of maternal females and reproductive success could be negatively impacted by development.

In addition to development, maternal age may also influence fetal rate. Robinette et al. (1977) found yearling females (1.5 years old) carried fewer fetuses and females reached their maximum productive potential at 2.5 years old and remained reproductively active throughout their lives. However, other studies suggest that maximum fetal productivity occurs in prime-aged females (3–7 years old), but then declines as females age (Verme and Ullrey 1984), or was similar for prime-aged and older females (DelGiudice et al. 2007).

Sex ratios can also be influenced by natural gas development and other factors. Fetal sex ratios can have varying degrees of skew towards one sex and may be based on factors including nutritional condition, habitat quality, and maternal age and mass (Robinette et al. 1957a, Verme 1965,1969, Burke and Birch 1995, Saltz 2001). Male-biased sex ratios are thought to occur to compensate for higher male mortality because males are more active than females (Jackson et al. 1972) and males in good condition are expected to pass on more genes than a female in good condition according to the Trivers-Willard hypothesis (TWH; Trivers and Willard 1973). A corollary to this hypothesis is that females in poor condition are still able to breed, but males in poor condition cannot successfully compete against healthier, stronger rivals. Results from ungulate studies examining fetal sex ratio and the TWH are inconsistent (Festa-Bianchet 1996, Hewison and Gaillard 1999, Sheldon and West 2004) and measuring maternal condition near conception when fetal sex allocation occurs might provide a better test of the TWH (Cameron 2004, Sheldon and West 2004).

Maternal body condition may influence fetal sex allocation (Burke and Birch 1995, Kohlmann 1999, Cunningham et al. 2009) and evolutionary theory (Trivers and Willard 1973) suggests larger males possess reproductive advantages over smaller males and males are more likely to be produced when females have abundant resources for production and lactation. Thus, the TWH also predicts females lacking resources and in poor condition should maximize their reproductive fitness by bearing more female offspring (Trivers and Willard 1973) because female offspring are less expensive to produce and rear than males that require more resources contributing to higher energetic costs for adult females (Myers 1978, Williams 1979, Gomendio et al. 1990). My prediction is that development infrastructure reduces habitat availability, but potentially increases forage quality contributing to better body condition of adult females and subsequently production of more male offspring.

I examined the influence of natural gas development, temporal, and adult female factors on reproductive success metrics and fetal sex ratio of mule deer in the Piceance Basin of northwestern Colorado, USA during 2012–2014. I estimated reproductive success metrics and sex ratios in areas with relatively high (0.04–0.90 well pads/km²) or low (0.00–0.10 well pads/km²) levels of natural gas development. My objectives were to test predictions that reproductive success metrics would be lower in the high development areas than the low development areas, vary by year with increased precipitation influencing vegetation availability and quality, and that fetal rates would be lower for yearling females. I also predicted that adult females would produce more male offspring according to the TWH, where adult females are exposed to areas with potentially increased forage availability and quality (e.g., areas with increased well pad, pipeline, and road density) and higher primary productivity of vegetation (i.e., abundant resources) on their summer range. Further, I predicted that younger adult females

presumably in poorer condition would produce more female offspring than older females. My results provide the first insights into reproductive success metrics and sex ratios in a natural gas development area, which is helpful to comprehend mule deer population dynamics and address management related decisions.

METHODS

Study Area

I examined reproductive success metrics and fetal sex ratio of mule deer in the Piceance Basin in northwestern Colorado, USA, during 2012–2014 (Figure 1.1). The Piceance Basin provides crucial winter and transition range habitat for one of the largest migratory mule deer populations in North America, yet some of the largest natural gas reserves in North America reside beneath the Basin as part of the Green River Formation. My winter range study area included four study units in the Piceance Basin (Figure 1.1) and are part of a larger research project (Anderson 2015). My winter range study units were South Magnolia (83 km²; 39.898°N, -108.343°W), Ryan Gulch (141 km²; 39.894°N, -108.343°W), North Ridge (53 km²; 40.045°N, -108.153°W), and North Magnolia (79 km²; 39.966°N, -108.206°W). South Magnolia and Ryan Gulch study units had relatively high levels of natural gas development (0.6–0.9 well pads/km²; hereafter referenced as the high development study area), whereas North Magnolia and North Ridge study units had low levels of natural gas development (0.0–0.1 well pads/km²; hereafter referenced as the low development study area).

Winter range habitat was dominated by two-needle pinyon (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* Torr.) woodlands, big sagebrush (*Artemisia tridentate* Nutt.), Utah serviceberry (*Amelanchier utahensis* Koehne.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), antelope bitterbrush (*Purshia tridentate* Pursh.), rubber

rabbitbrush (*Ericameria nauseosa* Pall ex. Pursh.), and mountain snowberry (*Symphoricarpos oreophilus* A. Gray; Bartmann 1983, Bartmann et al. 1992). Shrubs, forbs, and grasses common to the area are listed in Bartmann (1983) and Bartmann et al. (1992). Drainage bottoms bisected the study units and contained stands of big sagebrush, saltbush (*Atriplex spp.*), and greasewood (*Sarcobatus vermiculatus* Hook.), with most of the primary drainage bottoms having been converted to irrigated, grass hay fields. Plant nomenclature follows the United States Department of Agriculture PLANTS Database (USDA and NRCS 2016). Winter study unit elevations ranged from 1,860 m to 2,250 m and the winter climate of the Piceance Basin is typified by cold temperatures with most of the moisture resulting from snow.

Summer range study units included parts of Garfield, Moffat, Rio Blanco, and Routt counties in northwestern Colorado (39.580°N, -107.961°W and 40.330°N, -107.028°W; Figure 1.1). Ryan Gulch and South Magnolia deer generally migrated southeast and south to the Roan Plateau (Lendrum et al. 2013) where they potentially encountered natural gas development (0.04–0.06 well pads/km²; hereafter referenced as the high development study area). North Magnolia and North Ridge deer generally migrated northeast and east across US Highway 13 towards Lake Avery and the Flat Tops Wilderness Area (Lendrum et al. 2013) where they encountered minimal natural gas development (0.00–0.01 well pads/km²; hereafter referenced as the low development study area). Not all deer ($n = 8$) migrated to summer range and instead opted to remain residents on winter range.

Summer range habitat was dominated by Gambel oak (*Quercus gambeli* Nutt.), mountain mahogany, Utah serviceberry, mountain snowberry, chokecherry (*Prunus virginiana* L.), quaking aspen (*Populus tremuloides* Michx.), big sagebrush, pinyon pine, and Utah juniper. Dominant habitat was interspersed with Douglas-fir (*Pseudotsuga menziesii* Mirb.), Engelmann

spruce (*Picea engelmannii* Parry ex. Engelm.), and subalpine fir (*Abies lasiocarpa* Hook.) forests (Garrott et al. 1987). Summer study unit elevations ranged from 1,900 m to 3,150 m and the summer climate of the Piceance Basin is typified by warm temperatures with most of the moisture resulting from spring snow melt and brief summer monsoonal rainstorms.

Adult Female Capture and Handling

During December 2011–2013, adult female mule deer (≥ 1.5 years old) were captured in each of the four winter range study units using helicopter net gunning techniques (Barrett et al. 1982, van Reenen 1982). Deer were blindfolded, hobbled, and chemically immobilized with 35 mg of Midazolam (a muscle relaxant) and 15 mg of Azapirone (an anti-anxiety drug) given intramuscularly. For each captured deer, age was estimated (Severinghaus 1949, Robinette et al. 1957b) and I performed transabdominal ultrasonography to measure rump fat thickness (Stephenson et al. 1998, Stephenson et al. 2002, Cook et al. 2010), determined a body condition score (Cook et al. 2007, Cook et al. 2010), and estimated percent ingest-free body fat (Cook et al. 2010) near conception when fetal sex allocation occurs. I fit each captured deer with a store-on-board GPS radio collar with a motion-sensitive mortality switch on an 8-hour delay and a timed released mechanism set to release 16 months after deployment (Model G2110D, Advanced Telemetry Systems, Inc., Isanti, MN, USA). Most GPS radio collars were programmed to attempt a fix every 5 hours, but some attempted a fix every 30 minutes between 1 September and 15 June and hourly between 16 June and 31 August to address different research objectives (Northrup 2015). I consolidated data to attain the same temporal scale of 5 hours for all deer.

During early March 2012–2014, radio-collared adult females were recaptured on winter ranges using helicopter net gunning techniques. I recorded morphometric and body condition metrics described above and performed transabdominal ultrasonography on each female to

determine pregnancy status and number of fetuses present using a SonoVet 2000 portable ultrasound unit (Universal Medical Systems, Inc., Bedford Hills, NY; Stephenson et al. 1995, Bishop et al. 2007). If an adult female was pregnant, I inserted a vaginal implant transmitter (VIT; Model M3930, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and followed VIT insertion procedures described in detail by Bishop et al. (2007) and Bishop et al. (2011). In 2012 and 2013, each VIT was equipped with a temperature-sensitive sensor (Bishop et al. 2011). In 2014, each VIT was equipped with a temperature- and photo-sensitive sensor, which changed the signal when the ambient temperature dropped below 32 °C or when ambient light was ≥ 0.01 lux (Cherry et al. 2013). The manufacturer programmed VITs to lock on 80 pulses per minute to minimize issues associated with hot ambient temperatures (Newbolt and Ditchkoff 2009).

Adult Female Monitoring and Neonate Capture

On winter range, field technicians monitored radio collar and VIT signals daily from the ground or a Cessna 182 or 185 (Cessna Aircraft Co., Wichita, KS, USA) fixed-wing aircraft. During the parturition period (late May–mid-July), I checked VIT signals daily by aerially locating each radio-collared female having a VIT, weather permitting. In 2014, ground crews also located adult females with VITs to aid in determining when parturition occurred because VIT photo-sensors malfunctioned. When I detected a fast (i.e., postpartum) pulse rate, ground crews used a coded telemetry receiver (Model R4520, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and 3-element Yagi antenna to simultaneously locate the VIT and radio-collared female. Ground crews searched for a birth site and neonates near (≤ 400 m) the female and expelled VIT. If a VIT was shed prior to parturition or malfunctioned (e.g., battery failure), crews located the female once per day, observed female behavior, and searched in the vicinity of the female to locate neonates and birth sites (Carstensen et al. 2003). All neonate searches lasted up to one hour.

Ground crews attempted to determine the fate of each female's fetus(es) documented in March as live or stillborn neonates. I assumed that no fetuses were resorbed based on past research (Robinette et al. 1955, Medin 1976, Carpenter et al. 1984). Unless evidence suggested a neonate was born alive at a birth site (e.g., milk in the abomasum), crews classified the neonate as stillborn. Crews collected and submitted stillborn neonates to the Colorado Parks and Wildlife's Health Laboratory (Fort Collins, CO) for necropsy to confirm that a neonate had died before birth (i.e., before breathing).

During 2012 and 2013, ground crews captured neonates and located birth sites in the high and low development study areas. In 2014, crews captured neonates and located birth sites predominantly in the high development study areas and sporadically in the low development study areas. Each captured neonate was blindfolded and sexed. All individuals who handled neonates wore nitrile latex gloves to minimize transfer of human scent. Handling time was ≤ 5 minutes per neonate and crews replaced neonates where initially found to reduce abandonment (Pojar and Bowden 2004, Powell et al. 2005, Bishop et al. 2007). All capture, handling, radio collaring, and VIT insertion procedures were approved by the Institutional Animal Care and Use Committee at Colorado Parks and Wildlife (protocol #17-2008 and #1-2012) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Statistical Methods

I modeled pregnancy rates of females as a function of study area and year using PROC LOGISTIC in SAS (SAS Institute, Cary, North Carolina, USA) and fetal rates as a function of study area, year, and age class (yearling or adult female) using PROC MIXED in SAS. I modeled fetal survival from March to birth as a function of study area and year using PROC NLMIXED in SAS and a joint-likelihood described in Bishop et al. (2008). I was unable to

determine fate of all fetuses documented in utero because neonates were challenging to detect and some VITs malfunctioned, thus I used the joint-likelihood with six nuisance parameters (relative to my interests in this paper) to estimate fetal survival probability (S_1). The six nuisance parameters are neonatal survival probability from birth to 5 days old (S_2), the probability of detecting a neonatal fawn ≤ 1 day old given that field crews conducted a search ≤ 1 day after birth (p_1), the probability of detecting a neonatal fawn > 1 day old given that crews conducted a search > 1 day after birth (p_2), the probability of detecting a stillborn fetus when a vaginal implant transmitter was not expelled at a birth site (r), the probability of locating a radio-collared adult female and searching for her neonate(s) ≤ 1 day after birth (a), and the probability a VIT was expelled at a birth site (b). I modeled S_2 as constant or as a function of study area to account for survival differences between areas. I modeled p_1 , p_2 , a , and b as constant or as a function of study area and year to account for temporal differences in detection probabilities. I constrained r to be constant because crews did not locate stillborns without the aid of a VIT during some year and study area combinations, thus I could not separately estimate r . I assumed fetal survival data were not overdispersed based on the recommendation of Bishop et al. (2008). Lastly, I fit the same model set for reproductive success metrics as Bishop et al. (2009) and that I hypothesized would influence reproductive success (Table 1.1).

I modeled sex ratio as function of summer range development, temporal, and adult female variables that I hypothesized would influence sex ratio (Table 1.1) using generalized linear models with the ‘glm’ function in the R package ‘lme4’ (Bates et al. 2015). Summer range development variables included study area, producing and drilling well pall density (pads/km²), and road density (roads/km²). We acquired the location of natural gas wells from the Colorado Oil and Gas Conservation Commission (<http://cogcc.state.co.us>). We classified each well on

summer range as either actively being drilled or actively producing natural gas with no drilling activity using a procedure described in Northrup et al. (2015). Using the classified well pad data, we calculated drilling and producing well pad density. We also created a road network map by digitizing all roads visible on NAIP imagery and calculated road density. Temporal covariates included average Normalized Vegetation Difference Index (NDVI) and year. We calculated producing and drilling well pad density, road density, and NDVI covariates in each adult female's core area (i.e., 50% minimum convex polygon) from arrival on summer range to departure from summer range during conception year using the R statistical software (R Core Team 2015). Female-specific variables included age and percent ingesta-free body fat determined during capture in December (i.e., conception year). Prior to modeling, I calculated separate correlation matrices to test for collinearity among predictor variables ($|r| \geq 0.6$). If two variables were correlated, I retained the more biologically plausible variable.

For each analysis, I used Akaike's Information Criterion adjusted for small sample size (AICc), Δ AICc, and AICc weights (Burnham and Anderson 2002) for model selection. For the sex ratio analysis, I fit a global model and then fit all possible combinations of additive models and calculated the sum of AICc weights for models containing each variable of interest (Burnham and Anderson 2002, Doherty et al. 2012) using the R package 'MuMIn' (Barton 2015). Following suggestions of Barbieri and Berger (2004), I constructed a prediction model that contained all covariates with a cumulative AICc weight ≥ 0.50 . Unless otherwise noted, I used the prediction model when presenting estimates.

RESULTS

I documented pregnancy status of 358 females, of which 214 produced 397 fetuses [37, 171, or 6 females with 1, 2, or 3 fetus(es)]. Seventeen females were not pregnant and I was unable to

determine accurate fetal counts for 127 females for various reasons, which I excluded from the fetal analyses (Appendix 1.2). Ultimately, I documented sex of 195 fetuses (99 males and 96 females).

Reproductive Success Metrics

A model indicating constant pregnancy rates across years ranked highest (AICc weight = 0.569; Table 1.2), but a model with differences in pregnancy rate between the high and low development areas received some support (Δ AICc = 1.812, AICc weight = 0.230; Table 1.2). Pregnancy rate for all adult females during the study was 0.950 (SE = 0.012). Pregnancy rate for females in the high and low development areas was 0.955 (SE = 0.016) and 0.944 (SE = 0.017), respectively.

Variation in fetal rates was explained by the female age class only model (AICc weight = 0.666; Table 1.3) and slightly by the model with an interaction between age class and year (Δ AICc = 1.602, AICc weight = 0.299; Table 1.3). I found essentially no support for a study area effect (Table 1.3). In utero fetal rates were lower for yearling females and varied annually compared to adult females (Table 1.4). Fetal rates for adult females ranged from 1.82 (SE = 0.037) in 2013 to 1.86 (SE = 0.038) in 2014, whereas fetal rates for yearling females ranged from 1.36 (SE = 0.157) in 2014 to 1.56 (SE = 0.231) in 2012. However, the sample size was small ($n = 10$) for fetal rates of yearling females compared to adult females ($n = 204$; Table 1.4).

The best-fitting model for fetal survival from March until birth included an interaction between study areas and year (AICc weight = 0.248; Table 1.5). The same model for fetal survival, but without the study area variable had little support (Δ AICc = 8.005, AICc weight = 0.005). Fetal survival was higher in the low development areas than the high development areas, although survival varied annually (Figure 1.2). Fetal survival was higher in the low development

areas than the high development areas in 2012 and 2013, whereas I found no difference in 2014 (Figure 1.2). The probability of detecting a neonatal fawn ≤ 1 day old decreased each year from 0.567 (SE = 0.051) in 2012 to 0.416 (SE = 0.070) in 2014. Conversely, the probability of detecting a neonatal fawn > 1 day and ≤ 5 days old increased each year from 0.384 (SE = 0.081) in 2012 to 0.529 (SE = 0.105) in 2014. In the high and low development areas, respectively, females produced eight and zero stillborn fetuses in 2012, eight and three stillborns in 2013, and zero and zero stillborns in 2014.

Fetal Sex Ratio

I assessed relative importance of the 256 models I fit for sex ratios of mule deer. Eight models were within two $\Delta AICc$ units of the top ranked model (Table 1.6). Road density was in all the eight top models (Table 1.6) and had a cumulative AICc weight of 0.781 indicating importance. All other variables had a cumulative weight less than 0.5 and were not considered important (Barbieri and Berger 2004). The probability of producing a male increased as road density in a female's core area on summer range increased ($\hat{\beta} = 0.229$, 95% CI: 0.010 to 0.457; Figure 1.3), suggesting support for the TWH.

DISCUSSION

I found pregnancy rates were high, showed no variation across years, and were similar in the high versus low development areas. Disturbed topsoil and removal of overstory associated with well pad and pipeline construction and seeding of completed pipelines might increase forage quality (Webb et al. 2011c) and pregnancy rates. Likewise, deer have been shown to select open habitat (e.g., pipelines) and habitat closer to roads at night (Northrup et al. 2015) possibly providing abundant and higher quality forage as they arrive on winter range before the rut (Garrott et al. 1987, Monteith et al. 2011). Yet, Bishop et al. (2009) found no difference in

pregnancy rates when examining the effects of supplemental nutrition treatments versus a control group. Pregnancy rates were high in each area and in the higher range of previous estimates (0.86–1.00) across Colorado (Andelt et al. 2004, Bishop et al. 2009). Ultimately, high pregnancy rates seem to be the norm for deer despite a wide range of spatial and temporal differences across populations (Bishop et al. 2009, Hurley et al. 2011, Monteith et al. 2014) including an area with natural gas development.

In utero fetal rates were lower for yearling females and varied annually compared to adult females, but did not differ between study areas. Previous studies have also reported lower fetal rates and annual variation for yearling females (Robinette et al. 1977, Gaillard et al. 2000, Bishop et al. 2009). Nutrition is one factor that influences fetal rate, which can influence population dynamics of mule deer (McCullough 1979, Parker et al. 2009, Monteith et al. 2014). Mule deer depend more on forage quality than availability (Wallmo 1978) and annual weather patterns influence forage quality and digestibility (Marshall et al. 2005) and likely fetal rates. Yet, Bishop et al. (2009) found no difference in fetal rates between a nutritionally supplemented group of deer and a control group (Bishop et al. 2009). Bishop et al. (2009) also found fetal rates were high for each group, which equaled or exceeded past estimates (1.65–1.94) across Colorado (Andelt et al. 2004) similar to my findings. Forrester and Wittmer (2013) suggested that mule deer do not exhibit long-term population declines because of high fetal rates coupled with high and consistent survival of adult females. Of note, deer abundance is trending upward in the Piceance Basin (Anderson 2015) after a decline (White and Bartmann 1998) and could be partly explained by high fetal rates coupled with fawn recruitment, which has largely been driven by relatively high overwinter survival of fawns (Anderson 2015). Overall, pregnancy and fetal rates

did not appear to be impacted by natural gas development in the Piceance Basin during my study.

Fetal survival from March until birth was lower in the high development areas than the low development areas in 2012 and slightly lower in 2013, but equal in 2014. Fetal survival rates exceeded previous estimates (0.747–0.983) measured on the Uncompahgre Plateau, Colorado (Bishop et al. 2009). Forage quality might be higher in the low development areas and associated migration routes range due to agricultural fields along the White River and habitat treatments initiated by the Habitat Partnership Program by Colorado Parks and Wildlife. Agricultural fields and habitat treatments may provide green, succulent forbs as adult females depart winter range (Garrott et al. 1987, Stewart et al. 2010, Anderson et al. 2012). Moreover, deer from the low development areas have been shown to select habitat with increased forage while tracking emerging vegetation along spatial and elevational gradients as they migrated to summer range (Lendrum et al. 2012, Lendrum et al. 2013, Lendrum et al. 2014). Tracking emerging vegetation likely releases deer from density-dependent effects on winter range and ensures arrival on summer range prior to peak green-up (Lendrum et al. 2014) and prolonged access to high quality forage (Hebblewhite et al. 2008, Hamel et al. 2009) supporting production of neonates (Stoner et al. 2016). Access to high quality forage is necessary to meet the energetic demands of the last trimester when most fetal growth occurs (Armstrong 1950, Robbins and Robbins 1979, Pekins et al. 1998). However, deer in the high development area departed winter range later, migrated faster, and arrived on summer range before deer in the low development area possibly to reduce exposure to development disturbance (Lendrum et al. 2012, Lendrum et al. 2013). Differences in timing of migration could disrupt the tracking of emerging vegetation (Pettorelli et al. 2007, Bischof et al. 2012) and reduce net energetic gains and reproductive success of pregnant deer if

they fail to track altered plant phenology (Post and Forchhammer 2008, Post et al. 2008, Monteith et al. 2011) in developed areas. Moreover, development may displace deer to suboptimal habitat or alter habitat use (Sawyer et al. 2006, Webb et al. 2011a, Northrup et al. 2015) particularly during the energetically demanding period of late gestation (Parker et al. 2009) and could ultimately impact reproductive success (Houston et al. 2012). Thus, failure to track emerging vegetation during migration possibly exacerbated by development might have reduced fetal survival in the high development area during 2012. However, natural gas development was minimal during my study because most wells were in production, thus the influence of development could be stronger with increased development intensity.

Annual variation in fetal survival could be related to environmental conditions and development. Annual variation in precipitation may alter the onset of spring green-up (Pettorelli et al. 2005b), which can affect maternal condition (Parker et al. 2009) and possibly reduce fetal survival. Increased precipitation in arid environments is linked to forage availability (Derner et al. 2008), quality, and growth of forbs (Marshall et al. 2005), thus drought conditions may reduce forage availability and/or quality below levels needed for growth of fetuses (Parker et al. 2009). Annual precipitation was lower during 2012 (18 cm) and 2013 (31 cm) than 2014 (48 cm), suggesting reduced forage availability and growth of forbs may have contributed to lower fetal survival particularly in the high development areas during 2012. Further, dry weather likely reduced forage availability and was exacerbated by habitat loss and fragmentation associated with development possibly contributing to lower fetal survival in the high development areas during 2012. Of note, 13 more stillborn neonates were produced in the high development areas than the low development areas. Stillborn fetuses were mostly small and lightweight suggesting reduced forage availability and quality contributed to increased stillborns (Verme 1962, Verme

1969, Robinette et al. 1977) and consequently decreased fetal survival in the high development areas. Overall, development coupled with extreme environmental conditions (e.g., drought) may have contributed to lower fetal survival during 2012.

The probability of detecting a neonate ≤ 1 day old was low and decreased each year because neonates were challenging to detect and some VITs malfunctioned particularly in 2014. The probability of detecting a neonate > 1 day and ≤ 5 days old was also low, but increased each year. Most VITs failed in 2014 providing minimal assistance of detecting neonates at birth sites, thus contributing to higher detection of older neonates as mothers and presumably neonates move farther from VITs and birth sites as they age (Vore and Schmidt 2001, Long et al. 2009).

Adult females exposed to increased road density possibly exacerbated by development in the high development summer range produced more male offspring, although I did not detect a biased sex ratio at the population level. Road edges provide habitat with less canopy cover where deer forage on higher quality forage (Ager et al. 2003). Availability of high quality forage on summer range prior to conception is necessary for females to accumulate fat to combat the cost of fat loss during winter (Monteith et al. 2013). Life history theory suggests females account for the cost of reproduction when allocating fetal sex by allocating resources to current reproduction or reserving resources to enhance their own survival and future reproduction (Stearns 1992, Martin and Festa-Bianchet 2011). Females that consume high quality forage on summer range prior to parturition should be in good condition (Cook et al. 2004, Tollefson et al. 2010, Cook et al. 2013). Thus, females in good condition should maximize their reproductive fitness by investing in the production of more males according to the TWH (Trivers and Willard 1973). However, past studies suggest deer tend to avoid roads on winter range (Northrup et al. 2015) and along migration routes (Lendrum et al. 2012) in the study system. I am not sure whether deer

avoid roads during the summer. Further, under my proposed mechanism, I would expect body condition and road density to be strongly correlated, but they were only weakly correlated ($r = 0.07$). Thus, I am uncertain of the exact mechanism influencing the relationship between road density and fetal sex ratio.

My study provides the first insights into whether natural gas development influences pregnancy, in utero fetal, and fetal survival rates and fetal sex ratios of mule deer. Development did not appear to influence pregnancy rates and in years with higher precipitation, high and low development areas both had relatively high fetal survival rates. Fetal rates were lower for yearling females and varied by year compared to adult females, but development did not appear to influence fetal rates. Development coupled with environmental conditions (drought) possibly reduced forage availability and/or quality, which decreased fetal survival during 2012. Females exposed to increased road density in their core area on summer ranges produced more male offspring as road edges possibly provided favorable foraging environments for females, although the sex ratio was nearly equal during my study. However, I cannot be certain of my interpretation because I did not explicitly measure forage availability and used a coarse measure of forage quality (i.e., NDVI). I note that NDVI provides a better index of forage availability than quality because of annual variation in how precipitation influences vegetation green-up and desiccation. I also note that NDVI can perform poorly in predicting variation in productivity of forage preferred by mule deer (e.g., forbs and shrubs) when dense coniferous overstory blocks understory vegetation (Chen et al. 2004). Ultimately, future studies should quantify vegetative characteristics to fully comprehend the influence of natural gas development and environmental factors on body condition of adult females and subsequent reproductive success metrics and fetal sex ratios.

MANAGEMENT IMPLICATIONS

Estimating reproductive success metrics from marked adult females is helpful to understand fawn recruitment and population dynamics of ungulates. My results suggest managers should not be concerned with the impacts of natural gas development on pregnancy and fetal rates respective of existing conditions during this study. However, I suggest that future research should be conducted in areas with increased development intensity to fully comprehend the influence of natural gas development on pregnancy and fetal rates. Contrarily, managers should be concerned with the impacts of development on fetal survival as my results suggest fetal survival was lower during 2012 from increased stillbirths in the high development areas when drought conditions were also present. Although, the absence of development might decrease stillbirths during extreme environmental conditions, thus increasing fetal survival if forage availability and quality is improved. Thus, I recommend that developers and managers collaborate during development planning to avoid important habitats during critical time periods and consider habitat treatments (e.g., hydro-ax, roller chopping, and seeding) to improve forage availability and quality to enhance fetal survival and fawn recruitment to maintain sustainable deer populations in natural gas development areas.

TABLES

Table 1.1. List of variables and predictions for reproductive success metrics (i.e., pregnancy, in utero fetal, and fetal survival rates) and fetal sex ratio in the Piceance Basin, northwest Colorado, USA, 2012–2014.

Reproductive success metrics		Fetal sex ratio	
Variable^a	Hypothesis	Variable^b	Hypothesis
Study area	Reproductive success will be higher in the low development areas than in the high development areas.	Study area	Adult females in the high development areas will produce more male offspring than in the low development areas.
Age class	Adult females will have higher fetal rates than yearlings.	Age	Younger adult females will produce more female offspring than older females.
Year	In utero fetal rates and fetal survival will vary annually with increased precipitation influencing vegetation quality, whereas pregnancy rates will not.	Body fat	Adult females with higher body fat will produce more male offspring than females with lower body fat.
		Drilling density	Adult females exposed to higher drilling well pad density in their core areas on summer range will produce more male offspring.
		Producing density	Adult females exposed to higher producing well pad density in their core areas on summer range will produce more male offspring.
		Pipeline density	Adult females exposed to higher pipeline density in their core areas on summer range will produce more male offspring.
		Road density	Adult females exposed to higher road density in their core areas on summer range will produce more male offspring.
		Avg NDVI	Adult females with higher average primary productivity of vegetation (i.e., NDVI) in their core areas on summer range will produce more male offspring.

Year

Sex ratios will vary annually with increased precipitation influencing vegetation quality.

^a Variable definitions: study area signifies the high and low development winter range, age class is yearling or adult females.

^b Variable definitions: study area signifies the high and low development summer range during conception year, age is adult female age in conception year, body fat is percent ingesta-free body of each female in December of conception year, drilling and producing density are the drilling and producing well pad density (well pads/km²) in each female's core area on summer range during conception year, pipeline density signifies pipeline density (pipelines/km²) in each female's core area on summer range during conception year, road density signifies road density (roads/km²) in each female's core area on summer range during conception year, avg NDVI is the average Normalized Difference Vegetation Index (NDVI) in each female's core area (50% minimum convex polygon) while on summer range during conception year.

Table 1.2. Model selection results for pregnancy rate of mule deer during early March in the Piceance Basin, northwest Colorado, USA, 2012–2014.

Model^a	ΔAICc^b	AICc weight	Model likelihood	K^c
Intercept	0.000	0.569	1.000	1
Study area	1.812	0.230	0.404	2
Year	2.895	0.134	0.235	3
Year + study area	4.732	0.053	0.094	4
Year * study area	7.467	0.014	0.024	6

^a Variables are defined as in Table 1.1.

^b AICc is Akaike Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

Table 1.3. Model selection results for in utero fetal rate of mule deer during early March in the Piceance Basin, northwest Colorado, USA, 2012–2014.

Model^a	ΔAICc^b	AICc weight	Model likelihood	K^c
Age class	0.000	0.666	1.000	2
Age class + year + age class * year	1.602	0.299	0.449	6
Age class + year	6.877	0.021	0.032	4
Age class + year + study area	8.908	0.008	0.012	5
Intercept	10.188	0.004	0.006	1
Study area	12.447	0.001	0.002	2
Year	17.219	0.000	0.000	3
Study area + year	19.417	0.000	0.000	4
Study area + year + study area * year	21.566	0.000	0.000	6

^a Variables are defined as in Table 1.1.

^b AICc is Akaike Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

Table 1.4. Model-averaged estimates and associated standard error (SE) for in utero fetal rates of adult and yearling female mule deer during early March in the Piceance Basin, northwest Colorado, USA, 2012–2014.

Year	Age class	<i>n</i>	Fetal rate	SE
2012	Adult	83	1.84	0.034
	Yearling	2	1.56	0.231
2013	Adult	75	1.82	0.037
	Yearling	5	1.37	0.143
2014	Adult	46	1.86	0.038
	Yearling	3	1.36	0.157
Average	Adult	68	1.84	0.021
	Yearling	3	1.43	0.105

Table 1.5. Model selection results for fetal survival of mule deer from March until birth in the Piceance Basin, northwest Colorado, USA, 2012–2014. Only models with an AICc weight ≥ 0.005 are shown.

Model ^a	ΔAICc^b	AICc weight	Model likelihood	K ^c
$S_1(\text{study area} * \text{year}) S_2(.) p_1(\text{year}) p_2(.) r(.) a(\text{year}) b(\text{year})$	0.000	0.248	1.000	18
$S_1(\text{study area} * \text{year}) S_2(\text{year}) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	0.196	0.225	0.906	22
$S_1(\text{study area} * \text{year}) S_2(.) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	0.600	0.184	0.741	18
$S_1(\text{study area} * \text{year}) S_2(\text{study area}) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	0.854	0.162	0.652	21
$S_1(\text{study area} * \text{year}) S_2(.) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	2.325	0.078	0.313	20
$S_1(\text{study area} * \text{year}) S_2(.) p_1(.) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	3.300	0.048	0.192	18
$S_1(\text{study area}) S_2(.) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	4.622	0.025	0.099	16
$S_1(\text{study area} * \text{year}) S_2(.) p_1(\text{year}) p_2(\text{study area} * \text{year}) r(.) a(\text{study area} * \text{year}) b(\text{study area} * \text{year})$	6.032	0.012	0.049	29
$S_1(\text{study area} * \text{year}) S_2(.) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{study area} * \text{year}) b(\text{study area} * \text{year})$	6.485	0.010	0.039	26
$S_1(\text{year}) S_2(.) p_1(\text{year}) p_2(\text{year}) r(.) a(\text{year}) b(\text{year})$	8.005	0.005	0.018	17

^a Parameter S_1 is fetal survival probability. All other model parameters are nuisance parameters: S_2 is neonatal survival probability from birth to 5 days old, p_1 is the probability of detecting a neonate ≤ 1 day old given that field crews conducted a search ≤ 1 day after birth, p_2 is the probability of detecting a neonate > 1 day old given that crews conducted a search > 1 day after birth, r is the probability of detecting a stillborn fetus when a vaginal implant transmitter (VIT) was not expelled at a birth site, a is the probability of locating a radio-collared adult female and searching for her neonate(s) ≤ 1 day after birth, and b is the probability a VIT was expelled at a birth site.

^b AICc is Akaike Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

Table 1.6. Model selection results for sex ratio of mule deer neonates in the Piceance Basin, northwest Colorado, USA, 2012–2014. Only models within two ΔAICc units of the top ranked model are shown.

Model^a	ΔAICc^b	AICc weight	K^c
Road density	0.000	0.041	2
Road density + avg NDVI	0.366	0.034	3
Road density + avg NDVI + body fat	0.843	0.027	4
Road density + body fat	0.851	0.027	3
Road density + producing density	1.604	0.018	3
Road density + pipeline density	1.632	0.018	3
Road density + producing density + avg NDVI	1.670	0.018	4
Road density + age	1.876	0.016	3
Road density + study area	1.999	0.015	3

^a Variables are defined as in Table 1.1.

^b AICc is Akaike Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

FIGURES

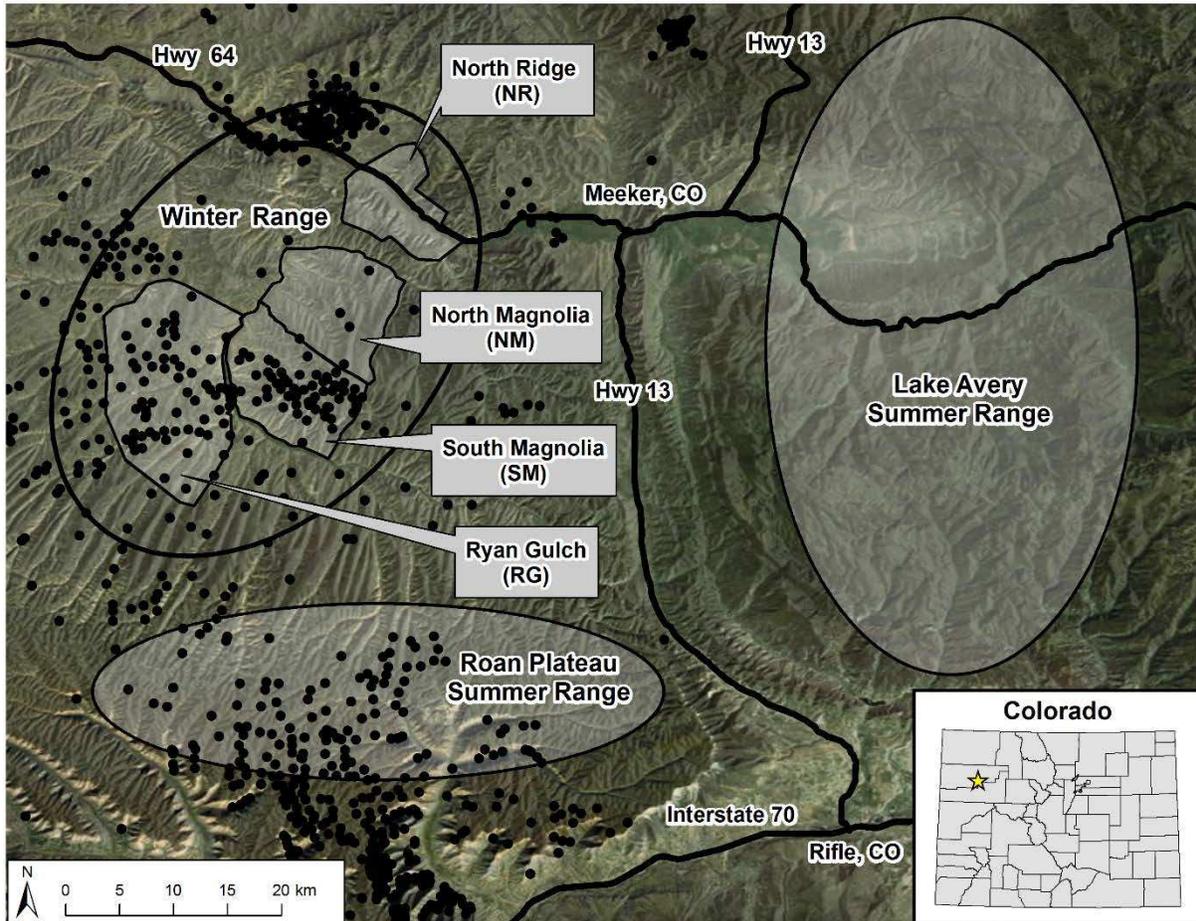


Figure 1.1. Mule deer winter and summer range study units in the Piceance Basin in northwestern Colorado, USA. Winter range study units were Ryan Gulch (RG), South Magnolia (SM), North Magnolia (NM), and North Ridge (NR). Summer range study units were Roan Plateau and Lake Avery. RG and SM deer generally migrated towards the Roan Plateau summer range, while NM and NR deer generally migrated towards the Lake Avery summer range. Overall, RG, SM, and Roan Plateau were considered the high development study areas, whereas NM, NR, and Lake Avery were considered the low development study areas. Black dots represent drilling and producing natural gas well pads.

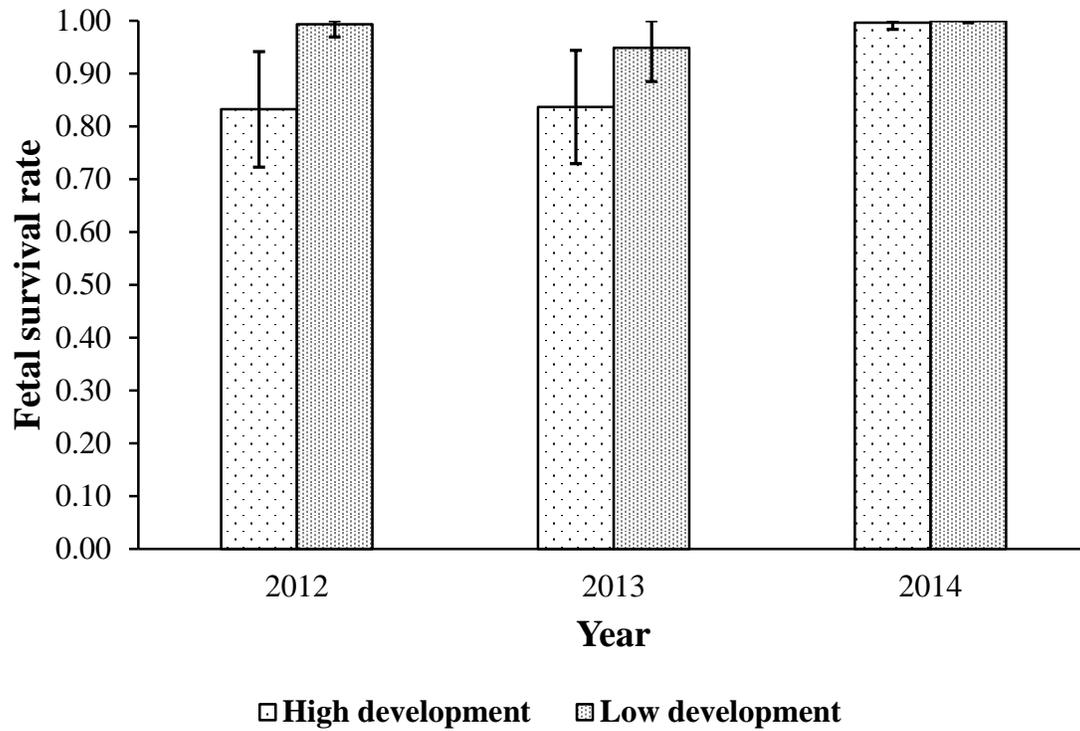


Figure 1.2. Model-averaged estimates of fetal survival (\pm 95% CI) of mule deer fetuses from March until birth in the high and low development study areas in the Piceance Basin, northwest Colorado, USA, 2012–2014.

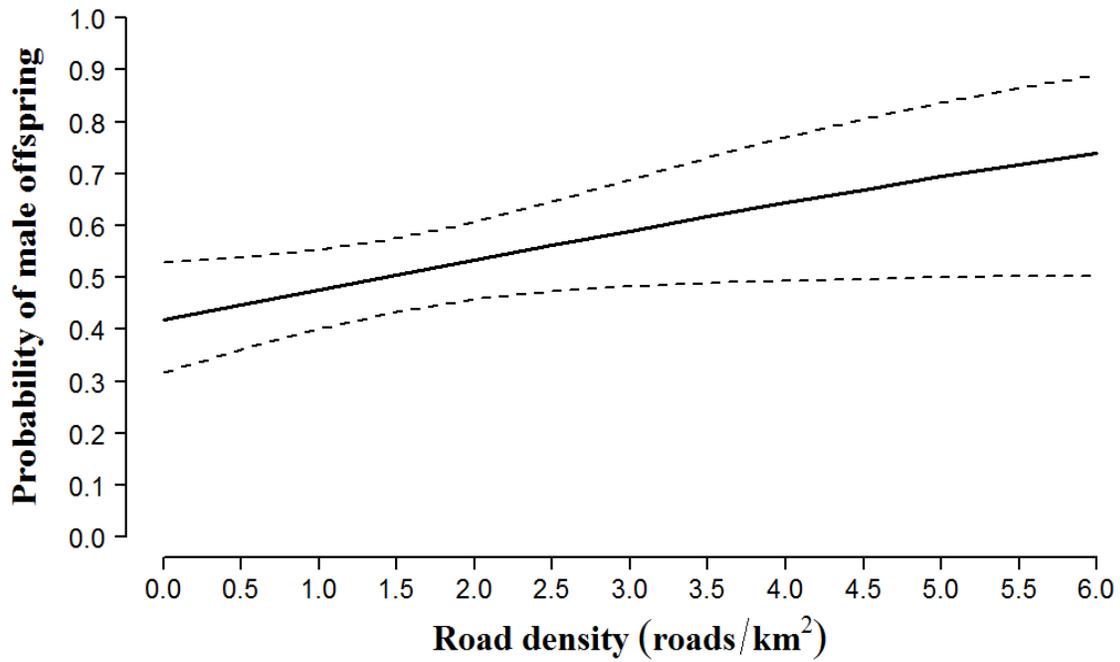


Figure 1.3. Predicted probability (\pm 95% CI) of producing a male offspring as a function of road density for adult female mule deer in the Piceance Basin, northwest Colorado, USA, 2012–2014.

CHAPTER 2:

VALIDATION OF USING MATERNAL MULE DEER MOVEMENTS TO DETERMINE TIMING AND LOCATION OF PARTURITION

Synopsis. Movement patterns of maternal ungulates have been used to determine parturition dates and locations, which are important for understanding reproductive measures, but such methods, have not been validated for mule deer (*Odocoileus hemionus*). I was able to do so using a recent technological advancement, namely vaginal implant transmitters (VITs) in conjunction with global positioning system collar data. Daily movement rate (m/day) of maternal deer decreased by 39% from 1 day before parturition ($\bar{x} = 1,243.56$, $SD = 1,043.03$) to 1 day after parturition ($\bar{x} = 805.30$, $SD = 652.91$) in the Piceance Basin in northwestern Colorado, USA, during 2012–2014. Thus, I suggest that a mule deer female whose daily movement rate decreases to ≤ 800 m/day has likely given birth. Ultimately, my results can help determine timing and location of parturition and estimate pregnancy and fetal rates as well as aid in capturing neonatal deer when the use of VITs is not feasible.

INTRODUCTION

Determining parturition dates and locations are important for estimating pregnancy, fetal, and neonate survival rates which are needed to quantify fawn recruitment (Bonenfant et al. 2005) and comprehend population dynamics of ungulates (Gaillard et al. 1998, Eberhardt 2002, Forrester and Wittmer 2013). Maternal deer movement patterns from global position system (GPS) collar data (Long et al. 2009), daily triangulation, and daily radiolocations from an aircraft have been used to approximate parturition date and aid in locating parturition sites and/or neonates (Huegel

et al. 1985, Kunkel and Mech 1994, Carstensen et al. 2003). However, problems potentially exist for effective location of parturition sites and/or neonates with these methods. First and most importantly, neonates may not always be located in a timely manner (Huegel et al. 1985, Kunkel and Mech 1994) and stillbirths and early mortalities may not be detected, which bias survival estimates (Gilbert et al. 2014). Second, when twins occur, they are not often together and often are missed when relying upon doe behavior (Carstensen et al. 2003). Third, use of triangulation and radiolocations requires daily monitoring which requires extensive time commitment, aircraft resources, and funds unless real-time monitoring is used (Wall et al. 2014). Finally, unnecessary disturbance of maternal-neonate interactions occur if neonates are not located on the first attempt and subsequent trips are needed, which may increase abandonment risk.

To better understand how maternal movement rates reflect parturition dates, knowing movement and parturition dates with minimal error is needed. A recent technological advancement, namely vaginal implant transmitters (VITs), allow for little error in determining parturition dates and locations (Bishop et al. 2009, Carstensen et al. 2009, Bishop et al. 2011), but is costly. Relying upon maternal deer movement rates to identify parturition dates is cheaper and easier, but has not been validated with VITs. Thus, I used GPS collar data and VITs in a similar way (i.e., movement patterns) that have been used for elk (*Cervus elaphus*) to determine exact parturition dates (Vore and Schmidt 2001).

Using movement patterns of maternal ungulates to determine parturition date is possible because movements change substantially after parturition (Huegel et al. 1985, Vore and Schmidt 2001, Long et al. 2009, Severud et al. 2015). Specifically, deer restricted movement rates by approximately 50% to stay within an area 1 to 7 days after parturition (Huegel et al. 1985, Long et al. 2009). Based on the relationships found by Huegel et al. (1985) and Long et al. (2009), I

predicted that mule deer movement rates would significantly decrease immediately after parturition and continue to be reduced for 7 days after parturition. Ultimately, my goal was to use VITs to validate the use of movement patterns of telemetered mule deer (*Odocoileus hemionus*) for determining parturition dates and locations.

METHODS

Study Area

During 2012–2014, I examined daily movement rates (m/day) of maternal mule deer relative to parturition date in the Piceance Basin in northwestern Colorado, USA. Deer in this area migrate from low elevation winter ranges to high elevation summer ranges (Lendrum et al. 2013) where they give birth. Summer range included parts of Garfield, Moffat, Rio Blanco, and Routt counties in northwestern Colorado (39.580°N, –107.961°W and 40.330°N, –107.028°W) and elevations ranged from 1,900 m to 3,150 m. Summer range habitat was dominated by Gambel oak (*Quercus gambeli* Nutt.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), Utah serviceberry (*Amelanchier utahensis* Koehne.), mountain snowberry (*Symphoricarpos oreophilus* A. Gray), chokecherry (*Prunus virginiana* L.), quaking aspen (*Populus tremuloides* Michx.), big sagebrush (*Artemisia tridentate* Nutt.), two-needle pinyon (*Pinus edulis* Engelm.), and Utah juniper (*Juniperus osteosperma* Torr.). Dominant habitat was interspersed with Douglas-fir (*Pseudotsuga menziesii* Mirb.), Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), and subalpine fir (*Abies lasiocarpa* hook.) forests (Garrott et al. 1987). Shrubs, forbs, and grasses common to the area are listed in Bartmann (1983) and Bartmann et al. (1992). Plant nomenclature follows the United States Department of Agriculture PLANTS Database (USDA and NRCS 2016).

Adult Female Capture and Handling

During December 2011–2013, adult female mule deer (≥ 1.5 years old) were captured using helicopter net gunning techniques (Barrett et al. 1982, van Reenen 1982). Deer were blindfolded, hobbled, and chemically immobilized with 35 mg of Midazolam (a muscle relaxant) and 15 mg of Azapirone (an anti-anxiety drug) given intramuscularly. I fit each captured deer with store-on-board GPS radio collars with a motion-sensitive mortality switch on an 8-hour delay and a timed released mechanism set to release 16 months after deployment (Model G2110D, Advanced Telemetry Systems, Inc., Isanti, MN, USA). Most GPS radio collars were programmed to attempt a fix every 5 hours, but some attempted a fix every 30 minutes between 1 September and 15 June and hourly between 16 June and 31 August to address different research objectives (Northrup 2015). I consolidated data to attain the same temporal scale of 5 hours for all deer.

In early March 2012–2014, radio-collared adult females were recaptured using helicopter net gunning techniques. I performed transabdominal ultrasonography on each captured deer to determine pregnancy status and number of fetuses present using a SonoVet 2000 portable ultrasound unit (Universal Medical Systems, Inc., Bedford Hills, NY) with a 3 MHz linear transducer (Stephenson et al. 1995, Bishop et al. 2007). If an adult female was pregnant, I inserted a VIT (Model M3930, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and followed VIT insertion procedures described in detail by Bishop et al. (2007) and Bishop et al. (2011). In 2012 and 2013, each VIT was equipped with a temperature-sensitive sensor, which changed the signal from 40 beats to 80 beats per minute (bpm) signifying VIT expulsion (Bishop et al. 2011). In 2014, each VIT was equipped with temperature- and photo-sensitive sensors, which changed the signal from 40 to 80 bpm when the ambient temperature dropped below 32 °C or when ambient light was ≥ 0.01 lux (Cherry et al. 2013). The manufacturer programmed

VITs to lock on 80 bpm to minimize issues associated with hot ambient temperatures (Newbolt and Ditchkoff 2009). All capture, handling, radio collaring, and VIT insertion procedures were approved by the Institutional Animal Care and Use Committee at Colorado Parks and Wildlife (protocol #17-2008 and #1-2012) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Adult Female Monitoring and Location of Birth Sites

During the parturition period (late May–mid-July), I checked VIT signals daily by aerially locating each radio-collared female having a VIT from a Cessna 182 or 185 (Cessna Aircraft Co., Wichita, KS, USA) fixed-wing aircraft, weather permitting. When I detected a fast (i.e., postpartum) pulse rate, ground crews used a coded telemetry receiver (Model R4520, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and 3-element Yagi antenna to simultaneously locate the VIT and radio-collared adult female. Crews retrieved VITs and recorded coordinates of birth sites using a hand-held GPS (Garmin GPSMAP 62S, Oregon 650, or Montana 650, Garmin International Inc., Olathe, KS, USA).

Daily Movements of Maternal Females, Parturition Date, and Statistical Methods

Radio collars deployed on adult females were programmed to release 16 months post-capture. Crews retrieved collars then, or from mortality sites, and downloaded GPS data. I imported data into ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA) to determine locations for each female. I analyzed daily movement rate of maternal females relative to the parturition date. Ground crews determined exact parturition dates primarily based on VIT expulsion date and secondarily based on hoof characteristics, condition of the umbilical cord, pelage, and behavior of neonates (Haugen and Speake 1958, Sams et al. 1996). We fixed the parturition date of each female equal to zero and dates before and after were calculated as

negative and positive, respectively. We then calculated daily movement rate from 7 days before to 7 days after parturition.

I fit linear mixed models using daily movement rate as the response variable, day relative to parturition as a fixed effect, and maternal female identity as a random effect using PROC MIXED in SAS (SAS Institute, Cary, North Carolina, USA). I also fit intercept-only models to account for no difference in movement rates. To determine a covariance model structure for repeated measures, I fit models with autoregressive, heterogeneous autoregressive, compound symmetry, heterogeneous compound symmetry, and Toeplitz covariance structures (Littell et al. 2006). The autoregressive model assumes that the covariance between two time periods decreases exponentially, depending on the time between periods and equal variance for each period. The heterogeneous autoregressive model is the same as the autoregressive model, except each time period has its own variance. The compound symmetry model assumes that the covariance between time periods is equal and equal variance for each period. The heterogeneous compound symmetry model is the same as the compound symmetry model, except each time period has its own variance. The Toeplitz model is similar to the autoregressive model, except the covariance between two time periods do not have to decrease exponentially. I used Akaike's Information Criterion adjusted for small sample size (AICc), Δ AICc, and AICc weights to determine the best-fitting covariance structure model (Burnham and Anderson 2002). I then used the best-fitting model to determine differences in movement rate among days and a Tukey's post-hoc comparison.

RESULTS

Daily Movements of Maternal Females

My sample size was 129 maternal females. A model indicating a heterogeneous autoregressive covariance structure ranked highest (AICc weight = 1.000; Table 2.1). Tukey's post-hoc testing indicated females moved significantly ($p < 0.001$) more 1 day before parturition ($\bar{x} = 1,243.56$, SD = 1,043.03) than the day of parturition ($\bar{x} = 805.30$, SD = 652.91), a 35% reduction in mean daily movement rate (Figure 2.1). Tukey's post-hoc testing also indicated females moved significantly ($p < 0.001$) more 1 day before than 1 day after parturition ($\bar{x} = 756.67$, SD = 629.24), a 39% reduction in mean daily movement rate (Figure 2.1). Overall, maternal deer moved ≤ 820 m/day from 1 to 7 days after parturition (Figure 2.1).

DISCUSSION

As predicted, maternal mule deer exhibited distinct daily movement patterns before versus after parturition. I suggest that a mule deer female whose daily movement rate significantly decreases to ≤ 800 m/day has likely given birth. Restricted movement of females after parturition may be attributable to neonates that are entirely dependent on a hiding strategy for survival (Lent 1974, Geist 1981) because of vulnerability to predation (Bishop et al. 2009, Monteith et al. 2014).

My results can be beneficial for other studies that do not have VIT data or few resources and need to rely upon deer movements to determine parturition. I suggest that GPS collar data surrounding a parturition period be plotted to detect a sudden and sustained reduction in daily movement rate, suggesting parturition date. The recent advent of Iridium (i.e., 2-way satellite communication) and remotely downloadable collars paired with my method could reduce aerial and field monitoring and allow for verification of parturition and capture of neonates without VITs. Other studies have successfully used real-time movement patterns of radio-collared

ungulates without using VITs to document parturition (DeMars et al. 2013, McGraw 2014) and aid in neonate captures (Severud et al. 2015).

If fetal and neonatal survival rates are desired in addition to parturition date, then a combination of my method with real-time GPS data could be used to send field capture crews in at the correct time. Specifically, a suspected parturition event could be investigated by locating the radio-collared female and observing her behavior to determine if parturition occurred and aid in capturing neonates (Huegel et al. 1985, Carstensen et al. 2003). However, a finer temporal scale than what I used (5 hours) may be needed to capture neonates before they become too mobile.

Technologically advanced radio collars and VITs are increasingly being used to study and understand population dynamics (Hebblewhite and Haydon 2010). Knowledge of parturition dates and locations and pregnancy and survival rates are needed to comprehend population dynamics of ungulates (Gaillard et al. 1998, Bonenfant et al. 2005, Forrester and Wittmer 2013). Ultimately, my proposed method could help validate such estimates when the use of VITs is not cost-effective or logistical feasible.

TABLE**Table 2.1.** Model selection results for covariance structures of daily movement rates of maternal mule deer from 7 days before to 7 days after parturition in the Piceance Basin, Colorado, USA, 2012–2014.

Covariance structure^a	ΔAICc^b	AICc weight	K^c
Heterogeneous autoregressive	0.00	1.00	16
Heterogeneous compound symmetry	41.10	0.00	16
Toeplitz	228.70	0.00	15
Autoregressive	257.70	0.00	3
Heterogeneous autoregressive (.)	264.30	0.00	16
Compound symmetry	319.30	0.00	2
Heterogeneous compound symmetry (.)	393.10	0.00	16
Toeplitz (.)	474.80	0.00	15
Autoregressive (.)	532.20	0.00	3
Compound symmetry (.)	657.20	0.00	2

^a (.) represents intercept only model.

^b AICc is Akaike Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

FIGURE

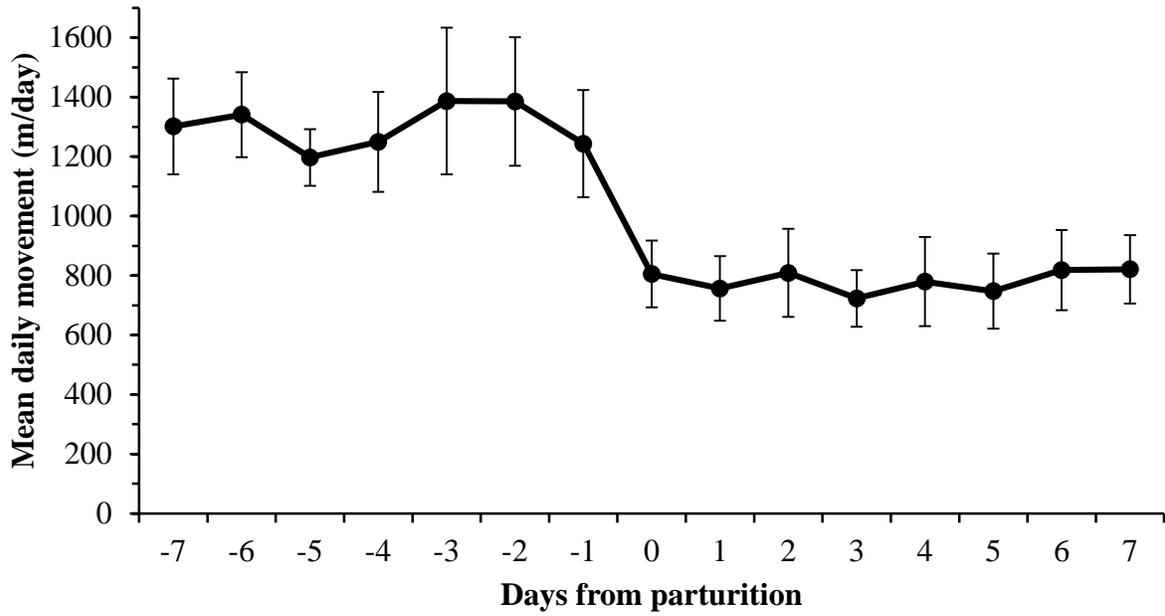


Figure 2.1. Mean daily movement rate (\pm 95% CI) of maternal mule deer from 7 days before to 7 days after parturition in the Piceance Basin, Colorado, USA, 2012–2014.

CHAPTER 3:

BIRTH SITE SELECTION BY MULE DEER AND PREDATION SITE CHARACTERISTICS IN A NATURAL GAS DEVELOPMENT AREA

Synopsis. Natural gas development potentially impacts wildlife populations and their habitat, especially for ungulate species. Of special importance are impacts on reproductive success (e.g., birth site selection and neonatal survival) that are influential for ungulate population dynamics. Birth site selection by mule deer (*Odocoileus hemionus*) is the result of deer trading off nutritional demands and minimizing predation risk of neonates. To investigate this trade-off, I fit resource selection functions (RSFs) to examine the influence of natural gas development and environmental factors on birth site selection and habitat characteristics of predation sites in the Piceance Basin in northwestern Colorado, USA during 2012–2014. Females selected birth sites farther from producing well pads and with increased cover for concealing neonates and appeared to select habitat (e.g., north-facing slopes and further from treed edges) that minimized neonate predation risk. Predation sites were characterized as being closer to development and in habitat (e.g., woodlands, aspen-conifer stands, and north-facing slopes) that possibly provided favorable microclimates for neonates and abundant high quality forage for lactating females. However, I note that predation sites were on average relatively far (2,057 m) from producing well pads and I have difficulty proposing a mechanism to explain how well pads that far away can influence predation site characteristics. My results suggest natural gas development and environmental factors (e.g., slope, habitat type, and aspect) can influence birth site selection with predation site characteristics possibly related to foraging habitat selection. Consequently, developers and managers should consider strategies to mitigate impacts from development to maintain cover for

concealing neonates, potentially enhancing survival. Such strategies could include development planning to avoid important habitats during critical time periods and minimizing habitat fragmentation and removal of hiding cover when constructing well pads and roads.

INTRODUCTION

Selection of birth sites by ungulates is a fundamental behavioral process with fitness consequences. Parturient ungulates need to select birth sites and surrounding habitat that maximizes both their own and their neonate's survival. Habitat characteristics of birth sites are important for neonate (i.e., newborn fawn) survival (i.e., 0–6 months old) because neonates depend on cryptic coloration (Lent 1974), hiding (Walther 1965, Lent 1974, Geist 1981), and concealment cover (Van Moorter et al. 2009, Barbknecht et al. 2011, Freeman 2014) to minimize predation risk. Additionally, females need to account for favorable microclimates (Picton 1984, Bowyer et al. 1998, Barbknecht et al. 2011, Freeman 2014) and steepness of slope when selecting birth sites to promote neonate survival by minimizing predation risk and energy expenditure associated with locomotion after parturition (Parker et al. 1984, Riley and Dood 1984, Fox and Krausman 1994, Long et al. 2009).

In addition to selecting birth sites with appropriate cover and slope to avoid predation, parturient ungulates also need to select sites near abundant high quality forage to support high energetic demands of parturition and lactation (Sadleir 1982, Carl and Robbins 1988, Cook et al. 2004). Time spent at birth sites likely influences the strength of this energy need on birth site selection (Barbknecht et al. 2011). For instance, moose (*Alces alces*) remain at birth sites for 3–4 weeks (Bowyer et al. 1999) in contrast to elk (*Cervus elaphus*) which remain at birth sites from several hours to one day (Harper et al. 1967, Rearden 2005) and mule deer (*Odocoileus hemionus*) which can leave birth sites within six hours of birth (Johnstone-Yellin et al. 2006).

Thus, birth site selection might be more strongly related to microclimate and predation risk of neonates instead of nutritional demands of lactating females for mule deer (Freeman 2014) and elk (Barbknecht et al. 2011) than moose (Bowyer et al. 1999).

Minimizing predation risk by choosing concealed birth sites is inversely related to availability of forage because high quality forage occurs in open habitat (Bowyer et al. 1999, Poole et al. 2007, Panzacchi et al. 2010). One change occurring across the West that results in more open habitat is the rise in natural gas development and associated features (e.g., well pads, pipelines, and roads). Increased open habitat could be beneficial for deer in terms of potential foraging areas (Bergman et al. 2014), or could be detrimental to deer if increased predation results (Pierce et al. 2004). The actual influence of natural gas development on mule deer birth site selection is unknown and complex.

Development can influence birth site selection due to direct and indirect habitat loss. Direct habitat loss results from construction of well pads, access roads, compressor stations, and pipelines. Whereas, traffic and noise associated with increased human presence and development may lead to indirect habitat loss. Past studies suggest deer tend to avoid roads (Rost and Bailey 1979, Webb et al. 2011c, Lendrum et al. 2012) and well pads (Sawyer et al. 2006, Sawyer et al. 2009, Northrup et al. 2015). However, mule deer have been shown to use areas closer to well pads and during spring migration because disturbed topsoil near well pads possibly provided the first nutritious herbaceous vegetation of the growing season (Webb et al. 2011c, Lendrum et al. 2012). Further, increased human presence associated with development might provide a refuge from predators (Berger 2007, Dussault et al. 2012), although gas-developed areas are correlated with higher perceived risk of predation and exposure to noise (Frid and Dill 2002, Barber et al. 2010, Dzialak et al. 2011b, Lynch et al. 2014). Consequently, selection of birth sites could be

positively or negatively related to distance from development (Webb et al. 2011b) and could affect neonate survival.

Ungulate juvenile survival (i.e., 0–1 year old) is typically low and variable compared to adult survival, and variation in juvenile survival can influence population dynamics (Gaillard et al. 1998, Gaillard et al. 2000, Forrester and Wittmer 2013). A birth pulse of neonates provides predators with an influx of vulnerable prey (Petroelje et al. 2014), consequently predation is often the leading cause of neonate mortality, especially during the first 8 weeks after parturition (Bishop et al. 2009, Monteith et al. 2014, Marescot et al. 2015, Shallow et al. 2015). Predatory behavior likely influences habitat characteristics of predation sites (Hornocker 1970, Riley and Dood 1984, Lingle 2000). Neonates 2–8 weeks old are bold enough to leave cover (Lent 1974), but not agile enough to evade predators (Nelson and Woolf 1987, Lingle and Pellis 2002). As neonates age, female ungulates likely need to select habitat with abundant high quality forage, but that also provides neonates with cover to minimize predation risk and a favorable microclimate for thermoregulation (Gustine et al. 2006, Van Moorter et al. 2009, Grovenburg et al. 2010, Pitman et al. 2014). Therefore, not only testing hypotheses concerning birth site selection, but also examining habitat characteristics of predation sites in high or low development areas will provide useful information on the influences of natural gas development.

I examined the influence of environmental and natural gas development factors on birth site selection and habitat characteristics of predation sites in the Piceance Basin of northwestern Colorado, USA from 2012–2014. I fit resource selection functions (RSFs) using a matched-case design (Manly et al. 2002, Boyce 2006) to determine selection of birth sites and habitat characteristics of predation sites within an adult female's home range (3rd order selection; Johnson 1980) in two areas, with relatively high (0.04–0.90 well pads/km²) or low (0.00–0.10

well pads/km²) natural gas development. My objective was to test predictions that birth sites would be on moderately steep and rugged (e.g., with fewer predators), north-facing slopes (e.g., more cover), primarily in woodlands (e.g., more cover) and secondarily in aspen-conifer stands (e.g., more cover and forage), farther from producing and drilling well pads, roads, and treed edges (e.g., more cover), and in areas with higher primary productivity of vegetation (e.g., more cover). I predicted predation sites would be on gentle or flat, south-facing slopes at lower elevations (e.g., with more predators and less cover), primarily in aspen-conifer stands and secondarily in woodlands (e.g., more cover and forage), and closer to producing and drilling well pads, roads, and treed edges (e.g., less cover). My results provide the first insights into mule deer birth site selection and habitat characteristics of predation sites in a natural gas development area, which is helpful to address conservation and management related decisions.

METHODS

Study Area

I examined parturient mule deer birth site selection and habitat characteristics of predation sites in the Piceance Basin in northwestern Colorado, USA, during 2012–2014 (Figure 3.1). The Piceance Basin provides crucial winter and transition range habitat for one of the largest migratory mule deer populations in North America (White and Lubow 2002), yet some of the largest natural gas reserves in North America reside beneath the Basin as part of the Green River Formation. My winter range study area included four study units in the Piceance Basin (Figure 3.1) and are part of a larger research project (Anderson 2015). My winter range study units were South Magnolia (83 km²; 39.898°N, –108.343°W), Ryan Gulch (141 km²; 39.894°N, –108.343°W), North Ridge (53 km²; 40.045°N, –108.153°W), and North Magnolia (79 km²; 39.966°N, –108.206°W). South Magnolia and Ryan Gulch study units had relatively high levels

of natural gas development (0.6–0.9 well pads/km²; hereafter referenced as the high development study area), whereas North Magnolia and North Ridge study units had low levels of natural gas development (0.0–0.1 well pads/km²; hereafter referenced as the low development study area).

Winter range habitat was dominated by two-needle pinyon (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* Torr.) woodlands, big sagebrush (*Artemisia tridentate* Nutt.), Utah serviceberry (*Amelanchier utahensis* Koehne.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), antelope bitterbrush (*Purshia tridentate* Pursh.), rubber rabbitbrush (*Ericameria nauseosa* Pall ex. Pursh.), and mountain snowberry (*Symphoricarpos oreophilus* A. Gray; Bartmann 1983, Bartmann et al. 1992). Shrubs, forbs, and grasses common to the area are listed in Bartmann (1983) and Bartmann et al. (1992). Drainage bottoms bisected the study units and contained stands of big sagebrush, saltbush (*Atriplex spp.*), and greasewood (*Sarcobatus vermiculatus* Hook.), with most of the primary drainage bottoms having been converted to irrigated, grass hay fields. Plant nomenclature follows the United States Department of Agriculture PLANTS Database (USDA and NRCS 2016). Winter study unit elevations ranged from 1,860 m to 2,250 m and the winter climate of the Piceance Basin is typified by cold temperatures with most of the moisture resulting from snow. During my study, winter (October–April) precipitation averaged 22.4 cm and mean winter temperatures ranged from –14 °C to 14 °C at the Rifle 23 NW weather station located at 2,301 m elevation (National Climatic Data Center 2015).

Summer range study units included parts of Garfield, Moffat, Rio Blanco, and Routt counties in northwestern Colorado (39.580°N, –107.961°W and 40.330°N, –107.028°W; Figure 3.1). Ryan Gulch and South Magnolia deer generally migrated southeast and south to the Roan Plateau (Lendrum et al. 2013) where they potentially encountered natural gas development

(0.04–0.06 well pads/km²; hereafter referenced as the high development study area). North Magnolia and North Ridge deer generally migrated northeast and east across US Highway 13 towards Lake Avery and the Flat Tops Wilderness Area (Lendrum et al. 2013) where they encountered minimal natural gas development (0.00–0.01 well pads/km²; hereafter referenced as the low development study area). Not all deer ($n = 8$) migrated to summer range and instead opted to remain residents on winter range.

Summer range habitat was dominated by Gambel oak (*Quercus gambeli* Nutt.), alderleaf mountain mahogany, Utah serviceberry, mountain snowberry, chokecherry (*Prunus virginiana* L.), quaking aspen (*Populus tremuloides* Michx.), big sagebrush, pinyon pine, and Utah juniper. Dominant habitat was interspersed with Douglas-fir (*Pseudotsuga menziesii* Mirb.), Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), and subalpine fir (*Abies lasiocarpa* Hook.) forests (Garrott et al. 1987). Summer range elevations ranged from 1,900 m to 3,150 m and the summer climate of the Piceance Basin is typified by warm temperatures with most of the moisture resulting from spring snow melt and brief summer monsoonal rainstorms. During my study, summer (May–September) precipitation averaged 20.3 cm and mean summer temperatures ranged from 2 °C to 31 °C (Rifle 23 NW weather station; National Climatic Data Center 2015).

Adult Female Capture and Handling

During December 2011–2013, adult female mule deer (≥ 1.5 years old) were captured in each of the four winter range study units using helicopter net gunning techniques (Barrett et al. 1982, van Reenen 1982). Deer were blindfolded, hobbled, and chemically immobilized with 35 mg of Midazolam (a muscle relaxant) and 15 mg of Azapirone (an anti-anxiety drug) given intramuscularly. For each captured deer, age was estimated (Severinghaus 1949, Robinette et al. 1957b) and I fit each captured deer with store-on-board GPS radio collars with a motion-

sensitive mortality switch on an 8-hour delay and a timed released mechanism set to release 16 months after deployment (Model G2110D, Advanced Telemetry Systems, Inc., Isanti, MN, USA). Most GPS radio collars were programmed to attempt a fix every 5 hours, but some attempted a fix every 30 minutes between 1 September and 15 June and hourly between 16 June and 31 August to address different research objectives (Northrup 2015). I consolidated data to attain the same temporal scale of 5 hours for all deer.

During early March 2012–2014, radio-collared adult females were recaptured on winter ranges using helicopter net gunning techniques. I performed transabdominal ultrasonography on each captured deer to determine pregnancy status and number of fetuses present using a SonoVet 2000 portable ultrasound unit (Universal Medical Systems, Inc., Bedford Hills, NY) with a 3 MHz linear transducer (Stephenson et al. 1995, Bishop et al. 2007). If an adult female was pregnant, I inserted a vaginal implant transmitter (VIT; Model M3930, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and followed VIT insertion procedures described in detail by Bishop et al. (2007) and Bishop et al. (2011). In 2012 and 2013, each VIT was equipped with a temperature-sensitive sensor, which changed the signal from 40 beats to 80 beats per minute (bpm) signifying VIT expulsion (Bishop et al. 2011). In 2014, each VIT was equipped with temperature- and photo-sensitive sensors, which changed the signal from 40 to 80 bpm when the ambient temperature dropped below 32 °C or when ambient light was ≥ 0.01 lux (Cherry et al. 2013). The manufacturer programmed VITs to lock on 80 bpm to minimize issues associated with hot ambient temperatures (Newbolt and Ditchkoff 2009).

Adult Female Monitoring, Neonate Capture, and Location of Birth Sites

On winter range, field technicians monitored radio collar and VIT signals daily from the ground or a Cessna 182 or 185 (Cessna Aircraft Co., Wichita, KS, USA) fixed-wing aircraft. During the

parturition period (late May–mid-July), I checked VIT signals daily by aerially locating each radio-collared female having a VIT, weather permitting. In 2014, ground crews also located adult females with VITs to aid in determining when parturition occurred because VIT photo-sensors malfunctioned. When I detected a fast (i.e., postpartum) pulse rate, ground crews used a coded telemetry receiver (Model R4520, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and 3-element Yagi antenna to simultaneously locate the VIT and radio-collared adult female. Ground crews searched for neonates and a birth site near (≤ 400 m) the female and expelled VIT. All neonate searches lasted up to 1 hour. Crews retrieved VITs and recorded coordinates of birth sites using a hand-held GPS (Garmin GPSMAP 62S, Oregon 650, or Montana 650, Garmin International Inc., Olathe, KS, USA). Crews identified birth sites based on detection of neonates and VIT or by birth site characteristics, including placental remnants, a large deer bed with flattened vegetation radiating outward, browsed or grazed vegetation, moist soil, fresh fecal pellets, tracks, hair, and characteristic odor (Barbknecht et al. 2011, Bishop et al. 2011, Rearden et al. 2011).

During 2012 and 2013, ground crews captured neonates and located birth sites on the high and low development study areas. In 2014, crews captured neonates and located birth sites predominantly in the high development study areas and sporadically in the low development study areas because VIT photo sensors malfunctioned. Crews blindfolded and handled each captured neonate with nitrile latex gloves to minimize transfer of human scent. Crews fit each neonate with a radio collar (Model M4210, Advanced Telemetry Systems, Inc., Isanti MN, USA) equipped with an 8-hour mortality sensor. Crews modified radio collars for temporary attachment by cutting the collar in half and splicing the ends with two lengths of rubber surgical tubing (5.7 cm each). Handling time was ≤ 5 minutes per neonate and crews replaced neonates

where initially found to reduce marking-induced abandonment. Past neonatal deer studies have reported minimal or no marking-induced abandonment (Pojar and Bowden 2004, Powell et al. 2005, Bishop et al. 2007). All capture, handling, radio collaring, and VIT insertion procedures were approved by the Institutional Animal Care and Use Committee at Colorado Parks and Wildlife (protocol #17-2008 and #1-2012) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Neonate Monitoring, Cause-specific Mortality, and Location of Mortality Sites

From the air, field technicians or I monitored radio-collared neonates daily during the parturition period, weekly until deer migrated from summer range, and daily from the ground when deer arrived on winter range. Technicians or I monitored radio-collared neonates from birth until death, collars were shed, or the end of the neonate survival period (i.e., 0–28 weeks) on 15 December 2012, 2013, or 2014. Daily monitoring during the parturition period when a majority of mortalities occurred, allowed crews or I to investigate mortalities typically within 24 hours, thus I am confident in our determination of cause-specific mortality. When I detected a mortality signal, ground crews located the neonate and/or radio collar and conducted a mortality site investigation and field necropsy, if possible, to determine cause-specific mortality. During the mortality site investigation, crews documented GPS coordinates of the site, predator tracks, predator scat, drag trails, blood at the site or on the radio collar, hair, and any other signs (e.g., matted vegetation or broken shrub branches) that could help determine cause-specific mortality or scavenging. Crews used predation site characteristics and predatory feeding behavior reported in the literature to help differentiate between predation and other causes of mortality or scavenging (White 1973, Wade and Bowns 1982, Acorn and Dorrance 1990, Stonehouse et al. *In prep*).

Habitat Use and Availability

Crews retrieved adult female radio collars after they released 16 months post-capture, or from mortality sites, and downloaded GPS data. I imported data into ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA) to determine summer and winter range locations for each adult female. Using helicopter net gunning techniques to capture deer can potential impact mule deer behavior (Northrup et al. 2014), thus I censored location data for 4 days following capture. Deer in this area are migratory, thus I classified winter range locations as being from capture to departure from winter range and summer range locations as being from arrival to departure or date of death for neonates that died. I determined migration patterns for each deer by examining GPS locations in ArcMap 10.2. I created 100% minimum convex polygons (MCPs) around summer or winter range locations for each deer using the Geospatial Modeling Environment (Beyer 2012). I considered MCPs as representing habitat available to each deer for birth sites and to predators for predation sites, whereas actual birth and predation site locations represented used sites. We conducted a sensitivity analysis to determine an optimal random availability sample size (Northrup et al. 2013) using the R statistical software (R Core Team 2015). Results of the sensitivity analysis indicated that a sample size of 10,000 random available locations for each deer would provide accurate $\hat{\beta}$ coefficients for my RSF analysis (below).

Environmental and Anthropogenic Predictor Variables

I included environmental and anthropogenic predictor variables in RSF models that I hypothesized would influence birth site selection and predation sites based on previous deer (Bowyer et al. 1998, Long et al. 2009, Freeman 2014) and elk (Barbknecht et al. 2011, Rearden et al. 2011) studies. I calculated or measured distance from the variables for each available and

used birth or predation site using the R statistical software (R Core Team 2015). I hypothesized the following environmental variables would influence birth site selection and habitat characteristics of predation sites (Table 3.1): elevation, slope, aspect, terrain ruggedness, Normalized Difference Vegetation Index (NDVI), habitat type, and distance from treed edge. I calculated elevation (m) using a 30-m resolution digital-elevation model (DEM; <http://nationalmap.gov/viewer.html>). From the DEM, I calculated slope (%) and aspect using ArcMap 10 Spatial Analyst Tools. I transformed aspect into four categories representing north (315° – 45°), east (45° – 135°), south (135° – 225°), and west (225° – 315°) directions (Barbknecht et al. 2011, Lendrum et al. 2012, Smith et al. 2015). I calculated terrain ruggedness with the vector ruggedness measure (VRM) using a 3×3 m pixel window and the DEM (Sappington et al. 2007). I acquired 7-day composites of NDVI from NASA’s Moderate Resolution Imaging Spectroradiometer (MODIS) satellites at a 250-m² resolution (<http://earthexplorer.usgs.gov/>). I calculated NDVI on the parturition date to reflect primary productivity of vegetation (Pettorelli et al. 2005a, Pettorelli et al. 2007). I acquired a 25-m resolution map of vegetation from the Colorado Vegetation Classification Project (<http://gis.colostate.edu/data.aspx>) containing 87 vegetation classes, which I reclassified into four categorical habitat types: woodlands, shrubland-steppe, aspen-conifer stands, and forbs-grasslands (Appendix 3.1). Using the reclassified habitat types, I determined a habitat type for each available and used birth and predation site. Lastly, I calculated distance from nearest treed edge (i.e., into cover) to each available and used birth and predation site.

I hypothesized the following anthropogenic variables would influence birth site selection and habitat characteristics of predation sites (Table 3.1): distance from nearest drilling well pad, producing well pad, pipeline, and road. Well pads and pipelines were absent or at very low

densities in the low development study areas, thus I did not include distance from these variables for these study areas. We acquired the location of natural gas wells and facilities (e.g., compressor stations) from the Colorado Oil and Gas Conservation Commission (<http://cogcc.state.co.us>). We classified each well on the high development summer range as either actively being drilled or actively producing natural gas with no drilling activity using a procedure described in Northrup et al. (2015). Using the classified well pad data, we calculated distance (m) from nearest drilling and producing well pad on the parturition date for each available and birth site. We also calculated the distance (m) from nearest drilling and producing well pad on the estimated date of a predation event for each available and predation site. We acquired a pipeline map from the Bureau of Land Management and updated the map by digitizing pipelines visually present on NAIP imagery and calculated distance (m) from nearest pipeline to each available, birth, and predation site. We created a road network map by digitizing all roads visible on NAIP imagery and calculated distance (m) from nearest road to each available, birth, and predation site.

Statistical Methods

After consideration of scale (Bowyer and Kie 2006, Boyce 2006), I examined birth site selection (Table 3.2) and habitat characteristics of predation sites (Table 3.2) within an adult female's home range (3rd order selection; Johnson 1980) by fitting RSFs. I estimated RSFs using a matched-case design separately for each deer by comparing each of 10,000 random available locations to each birth or predation site using conditional logistic regression (Hosmer and Lemeshow 2000, Manly et al. 2002, Boyce 2006) with the 'survival' package in the R statistical software (Therneau 2015). Using this method was advantageous because it controlled for differing availability by using available sites only within each deer's home range (Manly et al.

2002). Prior to modeling, I calculated separate correlation matrices to test for collinearity among predictor variables ($|r| \geq 0.6$). If two variables were correlated, I retained the more biologically plausible variable. Also prior to modeling, I standardized all continuous predictor variables $\left(\frac{x-\bar{x}}{\sigma}\right)$ to allow direct comparisons of $\hat{\beta}$ coefficients.

I conducted four separate analyses: on the high development or the low development study areas, I focused on comparing habitat characteristics of birth or predation sites with random available sites. For each analysis, I used Akaike's Information Criterion adjusted for small sample size (AICc), Δ AICc, and AICc weights (Burnham and Anderson 2002) for model selection. I fit a global model for each analysis and then fit all possible combinations of additive models and used model averaging to obtain model-averaged parameter estimates (Burnham and Anderson 2002, Doherty et al. 2012) using the R package 'MuMIn' (Barton 2015). I calculated the sum of AICc weights for models containing each variable of interest (Burnham and Anderson 2002). I considered variables with a cumulative AICc weight ≥ 0.5 as important (Barbieri and Berger 2004) and examined overlap of 95% confidence intervals around their $\hat{\beta}$ coefficients. For each continuous variable, a positive $\hat{\beta}$ coefficient indicated selection for a variable, whereas a negative $\hat{\beta}$ coefficient indicated avoidance.

RESULTS

Respectively in the high and low development study areas, I radio-collared 128 and 56 neonates and detected 5 and 4 neonates killed before collaring and located 90 and 41 birth and 56 and 24 predation sites. Of the 193 radio-collared and detected neonates, 171 (87%) were ≤ 2 days old and 188 (97%) were ≤ 3 days old when captured. Of the 89 neonates killed by predators, 56 (63%) were ≤ 2 weeks old and 26 (33%) were 2–8 weeks old. Respectively in the high and low development study areas, predation was attributed to black bears (*Ursus americanus*; $n = 18$ and

6), coyotes (*Canis latrans*; $n = 9$ and 1), cougars (*Puma concolor*; $n = 8$ and 5), felids ($n = 3$ and 1), bobcats (*Felis rufus*; $n = 2$ and 2), domestic dogs (*Canis familiaris*; $n = 0$ and 2), raptor ($n = 1$ and 0), and unknown predation ($n = 15$ and 6).

Birth Site Selection

I assessed relative importance of the 512 birth site selection models I fit to the data from the high development study areas. Ten models were within two Δ AICc units of the top ranked model (Table 3.3). Distance to producing well pad was in all the top 10 models and had a cumulative AICc weight of 0.854 (Table 3.4) indicating importance in birth site selection by mule deer. Slope was in six of the top 10 models including the top model and had a cumulative AICc weight of 0.559 (Table 3.4) indicating some importance. Deer selected birth sites farther from producing well pads relative to available sites (Figure 3.2A). Birth sites were on average 132 m farther from producing well pads compared to available sites, but were on average 2,429 m from a producing well pad (Table 3.2). Deer selected birth sites on moderately steep slopes, although the 95% confidence interval (CI) slightly overlapped zero (Figures 3.2A).

Fourteen of the 128 birth site selection models I fit to the data from the low development study areas were within two Δ AICc units of the top ranked model (Table 3.3). Slope (cumulative AICc weight = 0.572; Table 3.4) was in 10 of the top 14 models and was the top model and distance to nearest treed edge (cumulative AICc weight = 0.535; Table 3.4) was in eight of the top 14 models, signifying their importance in birth site selection by mule deer (Table 3.3). Aspect (cumulative AICc weight = 0.360; Table 3.4) was in four of the top 14 models suggesting marginal importance (Table 3.3). Mule deer selected birth sites on moderately steep slopes, farther from treed edges, and on north-facing slopes relative to south-facing slopes and available sites (Table 3.2), although the 95% CIs slightly overlapped zero (Figure 3.2B).

Habitat Characteristics of Predation Sites

Of the 512 models I fit for habitat characteristics of predation sites on the high development study areas, 21 models were within two ΔAICc units of the top ranked model (Table 3.5). Habitat type (cumulative AICc weight of 0.970; Table 3.4) was in all the top 21 models and aspect (cumulative AICc weight 0.532; Table 3.4) was in 15 of the top 21 models including the top model, indicating they were important in differentiating between predation and available sites (Table 3.5). Slope (cumulative AICc weight of 0.500; Table 3.4) was in eight of the top 21 models and distance to producing well pad (cumulative AICc weight of 0.486; Table 3.4) was in nine of the top 21 models suggesting marginal importance (Table 3.5). Compared to available sites, predation sites were in woodlands and on north-facing slopes with more cover compared to shrubland-steppe and south-facing slopes, respectively (Figure 3.3A). Compared to available sites, predation sites were in woodlands with more cover than forbs-grasslands, closer to producing well pads, and on steeper slopes ($\bar{x} = 33.84\%$, $SD = 15.46$), although 95% CIs overlapped zero (Figure 3.3A). Predation sites were on average 99 m closer to producing well pads compared to available sites, but were on average 2,057 m from a producing well pad (Table 3.2).

Fifteen of the 128 models I fit for habitat characteristics of predation sites on the low development study areas were within two ΔAICc units of the top ranked model (Table 3.5). Elevation (cumulative AICc weight of 0.429; Table 3.4) and distance to nearest road (cumulative AICc weight = 0.417; Table 3.4) were each in six of the top 15 models, indicating slight support (Table 3.5). Habitat type (cumulative AICc weight of 0.317; Table 3.4) was in three of the top 15 models suggesting little support (Table 3.5). Compared to available sites, predation sites were at

lower elevations and farther from roads (Table 3.2), although 95% CIs overlapped zero, and in aspen-conifer stands with more forage and cover than woodlands (Figure 3.3B).

DISCUSSION

As predicted, parturient mule deer selected birth sites farther from producing well pads possibly to avoid disturbances. Producing well pads elicit behavioral responses to development (Sawyer et al. 2006, Sawyer et al. 2009), particularly up to 600 m away during the day (Northrup et al. 2015) and possibly impacts habitat selection, rearing of young, and foraging (Frid and Dill 2002). Selection of birth sites farther from development may result in sites with lower forage availability and/or quality in exchange for lessened predation risk (Festa-Bianchet 1988, Kauffman et al. 2007, Hebblewhite and Merrill 2009). Additionally, wildlife may perceive development areas similarly to the risk of predation and respond by avoiding these areas if suitable habitat devoid of development is available nearby (Gill et al. 1996, Frid and Dill 2002). Moreover, Sawyer et al. (2006) reported large-scale displacement of deer on a relatively flat, sagebrush dominated winter range with natural gas development in the Pinedale area of Wyoming, whereas Northrup et al. (2015) found smaller-scale displacement of deer on developed winter range with increased topographic and vegetation diversity in the Piceance Basin. Deer are constricted to smaller winter range areas compared to expansive summer range areas in the Piceance Basin. Expansive summer range might permit selection of birth sites farther from development in suitable habitat. Although, if deer select birth sites closer to development, topographic and vegetation diversity in the Piceance Basin might provide refuge from noise and human presence associated with development unlike the open, flat, sagebrush-dominated habitat in the Pinedale area. Moreover, the most disruptive phase of development, drilling of wells, was minimal during my study. Thus, the influence of drilling well pads on birth site selection could

be stronger with increased drilling and in areas with open, flat habitat. Ultimately, true before-after-control-impact studies (Manly 2001) are needed in areas with moderate to intense drilling activity to better understand the impacts of natural gas development on birth site selection.

Weakly, but in line with my predictions, parturient mule deer selected birth sites on moderately steep slopes in the high development study areas and on north-facing slopes relative to available sites in the low development study areas. Selection for these locations is likely the result of a trade-off between the decreased energetic cost of locomotion on these slopes (Parker et al. 1984) and increased protection from predators that tend to travel along routes with gentler slopes and less cover (Riley and Dood 1984, Bowyer 1987, Lingle 2000, Farmer et al. 2006) on south-facing slopes. Moreover, variable canopy cover and light penetration on moderately steep slopes can create patches of contrasting sun and shade, further minimizing detection by predators and provide a favorable microclimate for thermoregulation (Fox and Krausman 1994, Bowyer et al. 1999, Van Moorter et al. 2009, Pitman et al. 2014). Finally, avoidance of well pads restricted to flat ridge tops and canyons may have influenced selection of birth sites on moderately steep slopes to minimize detection by predators.

Parturient mule deer weakly selected birth sites farther from treed edges on the low development study areas. Habitat further into trees is dense and provides concealment cover and is not preferred habitat for cougars that stalk and ambush prey near edge habitat (Hornocker 1970, Beier et al. 1995) and open areas (Pierce et al. 2004) or coursing predators, such as coyotes and black bear (Riley and Dood 1984, Bowyer 1987, Turner et al. 2011). Alternatively, ungulates might make a trade-off between increased canopy cover and reduced forage availability (Myysterud and Ostbye 1999, Barten et al. 2001, Hebblewhite and Merrill 2009). Because birth sites are only used for several hours, important components of birth sites are likely

related to thermal microclimate and predation risk of neonates instead of nutritional demands of lactating females (Barten et al. 2001, Barbknecht et al. 2011, Freeman 2014). My results are similar to results found by others examining birth site selection by caribou (*Rangifer tarandus*; Barten et al. 2001, Gustine et al. 2006, Leclerc et al. 2012), elk (Barbknecht et al. 2011), and mule deer (Tull et al. 2001, Butler et al. 2009, Long et al. 2009, Freeman 2014).

Most predation in my study areas were of neonates ≤ 2 weeks old that are entirely dependent on a hiding strategy for survival (Walther 1965, Lent 1974, Geist 1981). Hence, I assumed neonates selected bed sites with certain habitat characteristics where predators then killed them. As predicted, predation sites were characterized as being in woodlands compared to shrubland-steppe and forbs-grasslands relative to available sites on the high development study areas. Neonates possibly avoided beds in shrubland-steppe and forb-grassland habitat providing little canopy or concealment cover and greater light penetration that increases predation risk and thermoregulation (Gerlach and Vaughan 1991, Van Moorter et al. 2009, Grovenburg et al. 2010, Pitman et al. 2014). In addition, shrubland-steppe and forb-grassland habitat is typified by easily traversable terrain that offers minimal hindrance to coursing predators (Riley and Dood 1984, Bowyer 1987, Lingle 2000, Farmer et al. 2006) and is relatively open and close to edge habitat favored by stalking predators (Hornocker 1970, Pierce et al. 2004, Rearden et al. 2011). Conversely, less concealment cover can increase visibility to reduce predation risk (Bowyer et al. 1999, Poole et al. 2007, Rearden et al. 2011, Pinard et al. 2012).

As predicted, predation sites were characterized as being in aspen-conifer stands relative to woodlands and available sites on the low development study areas. Aspen-conifer stands with variable canopy cover and a dense understory are important fawning areas (Anderson et al. 1992, Lutz et al. 2003), provide diverse and productive forage for lactating females (Pyke and Zamora

1982, Long et al. 2008, Kuhn et al. 2011), and provide favorable microclimates for neonates (Fox and Krausman 1994, Bowyer et al. 1998). Consequently, predators likely locate fawning areas in aspen-conifer stands by developing a search image to prey on vulnerable neonates during a birth pulse (Whittaker and Lindzey 1999, Testa 2002, Petroelje et al. 2014).

Contrary to my predictions, predation sites were characterized as being on north-facing slopes relative to south-facing slopes and available sites on the high development study areas. South-facing slopes are typified by increased solar radiation and primary production of vegetation in the spring (Bowyer et al. 1998, D'Eon and Serrouya 2005). However, vegetation senesces earlier on south-facing slopes possibly reducing concealment cover and availability of high quality forage (Long et al. 2009), particularly in the relatively dry climate of the Piceance Basin. Whereas, north-facing slopes are characterized by trees providing increased and variable canopy cover (Long et al. 2009) that hold winter moisture longer (Nicholson et al. 1997) and reduce solar radiation (Barbknecht et al. 2011) likely delaying spring green-up of understory vegetation. Further, young neonates avoid habitat with decreased canopy cover providing increased solar radiation (Van Moorter et al. 2009) and high visibility (Linnell et al. 1999, Pitman et al. 2014). Consequently, delayed green-up of vegetation on north-facing slopes could provide adult females with abundant and higher quality forage during lactation and neonates with cover and favorable microclimates. Thus, neonates dependent on hiding in cover providing favorable microclimates are likely to be killed by a predator if detected in preferred habitat (Roberts and Rubenstein 2014).

Weakly, but in line with my prediction, predation sites were characterized as being closer to producing well pads compared to available sites on the high development study areas. However, I note that predation sites were on average relatively far (2,057 m) from producing

well pads (Table 3.2) and I have difficulty proposing a mechanism to explain how well pads that far away can influence predation site characteristics. Constant noise and human activity is not associated with producing well pads unlike drilling well pads. Deer and elk have been shown to select habitat closer to producing well pads, especially at night (Dzialak et al. 2011a, Northrup et al. 2015) when predators are generally active (Rogers 1970, Anderson and Lindzey 2003). Perhaps, deer forage in openings closer to producing well pads and associated pipelines and that might provide abundant and higher quality forage (Webb et al. 2011c, Lendrum et al. 2012), but that might increase predation risk of hiding neonates (Rearden et al. 2011). Thus, habitat closer to producing well pads could be beneficial to adult females, but possibly detrimental to neonates, especially at night.

My study provides novel insights into whether natural gas development influences birth site selection by parturient mule deer and predation site characteristics of neonatal mule deer. Natural gas development appears to influence birth site selection with predation site characteristics possibly related to foraging habitat selection in my study system, thus development planning should focus on mitigation or avoidance of birth site habitats. Parturient mule deer selected birth sites in habitat farther from development that likely provided neonates with increased concealment cover and favorable microclimates and minimized predation risk of neonates. Most predation sites were characterized by habitat that possibly provided cover and favorable microclimates for neonates and abundant high quality forage to meet the nutritional demands of lactating females. However, I cannot be certain of my interpretation because I did not explicitly measure forage availability and used a coarse measure of forage quality (i.e., NDVI). I note that NDVI provides a better index of forage availability than quality because of annual variation in how precipitation influences vegetation green-up and desiccation. Birth site

selection and subsequent neonate survival can depend on macrohabitat and microhabitat scale characteristics (Van Moorter et al. 2009, Rearden et al. 2011, Pitman et al. 2014) and future studies should examine habitat selection at multiple scales (Bowyer and Kie 2006, Boyce 2006) to avoid using NDVI as an index for forage availability and quality. Ultimately, future studies should consider regional differences in topography, vegetation, predator assemblages and associated predation risk, and development intensity to fully comprehend the influence of natural gas development and environmental variables on birth site selection and habitat characteristics of predation sites.

MANAGEMENT IMPLICATIONS

My results suggest natural gas development and environmental variables can influence birth site selection by mule deer. Consequently, developers should consider strategies to minimize direct habitat loss and disturbances when planning projects, such as concentrating road and well pad development and minimizing removal of hiding cover when constructing well pads. Moreover, industry should consider strategies to minimize indirect habitat loss, such as reducing vehicle traffic to well pads particularly during June and July when most birth and predation events occur to minimize fitness consequences of mule deer. Further, managers should maintain habitat to provide cover for concealing neonates, potentially reducing mortality. Thus, I recommend that developers and managers apply my RSF model to develop maps that predict high and low use areas for birth sites when planning development or landscape manipulations (e.g., habitat treatments). Avoiding or mitigating impacts from development or other disturbances in high use areas could reduce direct and indirect habitat loss and help managers maintain critical habitat to enhance neonatal deer survival that is influential for ungulate population dynamics. However, I caution that my RSF models should only be used in areas with topographic and vegetation

composition similar to the Piceance Basin (see study area description) and may not be applicable to more open, less topographically diverse mule deer habitats. I also caution that my RSF model was developed using individual home ranges of deer (i.e., home range scale) and should not be applied at a landscape scale (Boyce 2006). Consequently, I suggest using a moving window analysis to maintain the correct scale when applying my RSF model.

TABLES

Table 3.1. List of variables and hypothesized results for birth site selection and habitat characteristics of predation sites in the Piceance Basin, Colorado, USA, 2012–2014.

Variable^a	Hypothesis	Variable definition
Elevation (m)	Deer will select birth sites at higher elevations and predation sites will occur at lower elevations.	Elevation (m) of birth and predation sites.
Slope (%)	Deer will select birth sites on moderately steep slopes and predation sites will be on gentler slopes.	Slope (%) of birth and predation sites.
Aspect	Birth sites will be on north-facing slopes and predation sites will be on south-facing slopes.	A categorical variable referenced to north for predation and birth sites.
VRM	Birth sites will be in rugged terrain and predation sites in flatter terrain.	Vector ruggedness measure (VRM), a measure of terrain ruggedness.
NDVI	Birth sites will be in areas with higher primary productivity of vegetation.	The normalized difference vegetation index (NDVI), a measure of primary productivity.
Habitat	Deer will select birth sites primarily in woodlands and secondarily in aspen-conifer stands, whereas predation sites will occur primarily in aspen-conifer stands and secondarily in woodlands.	A categorical variable including woodlands (reference group), shrubland-steppe, aspen-conifer stands, and forbs-grasslands habitat types.
Dist.edge (m)	Birth sites will be farther from treed edges and predation sites will be closer to treed edges.	Distance (m) to nearest treed edge (i.e., into trees).
Dist.drill (m)	Birth sites will be farther from drilling well pads and predation sites will be closer to drilling well pads.	Distance (m) to nearest drilling well pad.
Dist.prod (m)	Birth sites will be farther from producing well pads and predation sites will be closer to producing well pads.	Distance (m) to nearest producing well pad.
Dist.pipe (m)	Birth sites will be farther from pipelines and predation sites will be closer to pipelines.	Distance (m) to nearest pipeline.
Dist.road (m)	Birth sites will be farther from roads and predation sites will be closer to roads.	Distance (m) to nearest road.

Table 3.2. Mean and standard deviation (SD) of unstandardized continuous variables included in conditional logistic regression models of birth site selection by mule deer and habitat characteristics of predation sites on the high development ($n = 90$ birth and 900,000 available sites and $n = 56$ predation and 560,000 available sites) or low development ($n = 41$ birth and 410,000 available sites and $n = 24$ predation and 240,000 available sites) study areas. “—” indicates variables that were not included in models. Data collected in the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Variable ^a and study areas	Birth site		Available site		Predation site		Available site	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Dist.edge (m)								
High development	62.33	50.03	63.74	45.92	61.02	49.10	63.22	45.55
Low development	108.42	146.7	88.48	91.83	72.62	41.67	78.06	71.14
Dist.road (m)								
High development	182.16	141.96	182.32	163.28	176.82	130.11	167.93	155.89
Low development	574.33	1030.34	595.01	1074.87	540.77	689.00	484.13	603.00
Dist.drill (m)								
High development	7,420.36	5,652.49	7,477.67	5,908.53	7,170.46	5,104.32	7,240.82	4,995.41
Low development	—	—	—	—	—	—	—	—
Dist.prod (m)								
High development	2,429.29	1,936.58	2,297.03	1,872.53	2,056.85	1,919.28	2,156.00	1,927.76
Low development	—	—	—	—	—	—	—	—
NDVI								
High development	0.55	0.13	0.54	0.12	—	—	—	—
Low development	0.64	0.12	0.65	0.13	—	—	—	—
Elevation (m)								
High development	—	—	—	—	2,413.19	166.84	2,412.88	164.31
Low development	—	—	—	—	2,222.55	249.46	2,236.23	252.11
Slope (%)								
High development	27.70	14.60	30.11	16.26	33.84	15.46	30.36	15.25
Low development	21.67	12.68	24.97	16.16	22.76	15.71	24.71	17.00

VRM

High development	0.006	0.007	0.006	0.008	0.008	0.009	0.007	0.009
Low development	0.006	0.007	0.005	0.008	0.006	0.006	0.006	0.010

^a Variables are defined as in Table 3.1.

Table 3.3. Model selection results for birth site selection by adult female deer on the high or low development study areas. Only models within two ΔAICc units of the top-ranked model are shown. Data collected in the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Study areas and model^a	AICc	ΔAICc	AICc weight	K^b
High development				
Dist.prod + slope	1654.174	0.000	0.057	2
Dist.prod	1654.595	0.422	0.046	1
Dist.prod + slope + NDVI	1655.096	0.923	0.036	3
Dist.prod + NDVI	1655.337	1.163	0.032	2
Dist.prod + slope + VRM	1655.484	1.311	0.029	3
Dist.prod + slope + dist.drill	1655.537	1.364	0.029	3
Dist.prod + dist.drill	1655.889	1.715	0.024	2
Dist.prod + slope + dist.edge	1655.975	1.802	0.023	3
Dist.prod + slope + dist.road	1656.093	1.919	0.022	3
Dist.prod + VRM	1656.150	1.977	0.021	2
Low development				
Slope	754.852	0.000	0.059	1
Slope + dist.edge	754.861	0.008	0.058	2
Dist.edge	755.033	0.181	0.054	1
Slope + aspect	755.996	1.144	0.033	4
Slope + dist.edge + aspect	756.267	1.414	0.029	5
Slope + dist.edge + dist.road	756.318	1.466	0.028	3
Dist.edge + dist.road	756.340	1.488	0.028	2
Aspect	756.441	1.589	0.026	3
Dist.edge + aspect	756.617	1.764	0.024	4
Slope + dist.road	756.667	1.815	0.024	2
Slope + NDVI	756.717	1.865	0.023	2
Slope + NDVI + dist.edge	756.733	1.881	0.023	3
Slope + dist.edge + VRM	756.782	1.930	0.022	3
Slope + VRM	756.795	1.943	0.022	2

^a Variables are defined as in Table 3.1.

^b K is the number of parameters in the model.

Table 3.4. Cumulative AICc (Akaike Information Criterion adjusted for small sample size) weights for variables included in conditional logistic regression models of birth site selection by mule deer and habitat characteristics of predation sites on the high or low development study areas. “—” indicates variables that were not included in models. Data collected in the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Birth site		Predation site	
Study areas and variable^a	Cumulative AICc weight	Study area and variable^a	Cumulative AICc weight
High development		High development	
Dist.prod (m)	0.854	Habitat	0.970
Slope (%)	0.559	Aspect	0.532
NDVI	0.402	Slope (%)	0.500
VRM	0.332	Dist.prod (m)	0.486
Dist.drill (m)	0.343	VRM	0.320
Dist.edge (m)	0.288	Elevation (m)	0.298
Dist.road (m)	0.280	Dist.edge (m)	0.287
Aspect	0.066	Dist.road (m)	0.282
Habitat	0.062	Dist.drill (m)	0.277
Low development		Low development	
Slope (%)	0.572	Elevation (m)	0.429
Dist.edge (m)	0.535	Dist.road (m)	0.417
Aspect	0.360	Slope (%)	0.336
Dist.road (m)	0.333	Dist.edge (m)	0.325
NDVI	0.300	Habitat	0.317
VRM	0.288	VRM	0.292
Habitat	0.110	Aspect	0.280
Dist.drill (m)	—	Dist.drill (m)	—
Dist.prod (m)	—	Dist.prod (m)	—

^a Variables are defined as in Table 3.1.

Table 3.5. Model selection results for habitat characteristics of predation sites on the high or low development study areas. Only models within two ΔAICc units of the top-ranked model are shown. Data collected in the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Study areas and model ^a	AICc	ΔAICc	AICc weight	K ^b
High development				
Habitat + aspect	1021.484	0.000	0.026	6
Habitat + aspect + dist.prod	1021.628	0.143	0.024	7
Habitat + slope	1021.810	0.326	0.022	4
Habitat	1021.822	0.338	0.022	3
Habitat + dist.prod + slope	1021.931	0.447	0.021	5
Habitat + aspect + dist.prod + slope	1022.014	0.530	0.020	8
Habitat + aspect + slope	1022.025	0.541	0.020	7
Habitat + dist.prod	1022.067	0.583	0.019	4
Habitat + aspect + VRM	1023.133	1.649	0.011	7
Habitat + slope + elevation	1023.218	1.734	0.011	5
Habitat + aspect + dist.prod + slope + VRM	1023.224	1.740	0.011	9
Habitat + aspect + dist.prod + VRM	1023.230	1.746	0.011	8
Habitat + aspect + dist.edge	1023.319	1.835	0.010	7
Habitat + aspect + slope + VRM	1023.319	1.835	0.010	8
Habitat + aspect + dist.road	1023.338	1.853	0.010	7
Habitat + aspect + dist.prod + dist.road	1023.390	1.906	0.010	8
Habitat + aspect + dist.prod + dist.edge	1023.424	1.940	0.010	8
Habitat + aspect + elevation	1023.454	1.970	0.010	7
Habitat + slope + VRM	1023.458	1.974	0.010	5
Habitat + aspect + dist.prod + dist.drill	1023.472	1.988	0.010	8
Habitat + aspect + dist.drill	1023.481	1.997	0.010	7
Low development				
Dist.road	443.278	0.000	0.044	1
Elevation	443.408	0.130	0.041	1
Slope	443.559	0.281	0.038	1
Dist.road + elevation	443.737	0.459	0.035	2
Dist.edge	443.837	0.559	0.033	1
VRM	444.022	0.744	0.030	1
Habitat	444.054	0.776	0.030	3
Aspect	444.128	0.850	0.029	3
Dist.road + slope	444.757	1.479	0.021	2
Elevation + slope	445.012	1.734	0.019	2
Elevation + habitat	445.025	1.747	0.018	4
Elevation + dist.edge	445.106	1.828	0.018	2
Dist.road + elevation + habitat	445.155	1.877	0.017	5

Dist.road + dist.edge	445.214	1.936	0.017	2
Dist.road + VRM	445.277	1.999	0.016	2

^a Variables are defined as in Tables 3.1.

^b K is the number of parameters in the model.

FIGURES

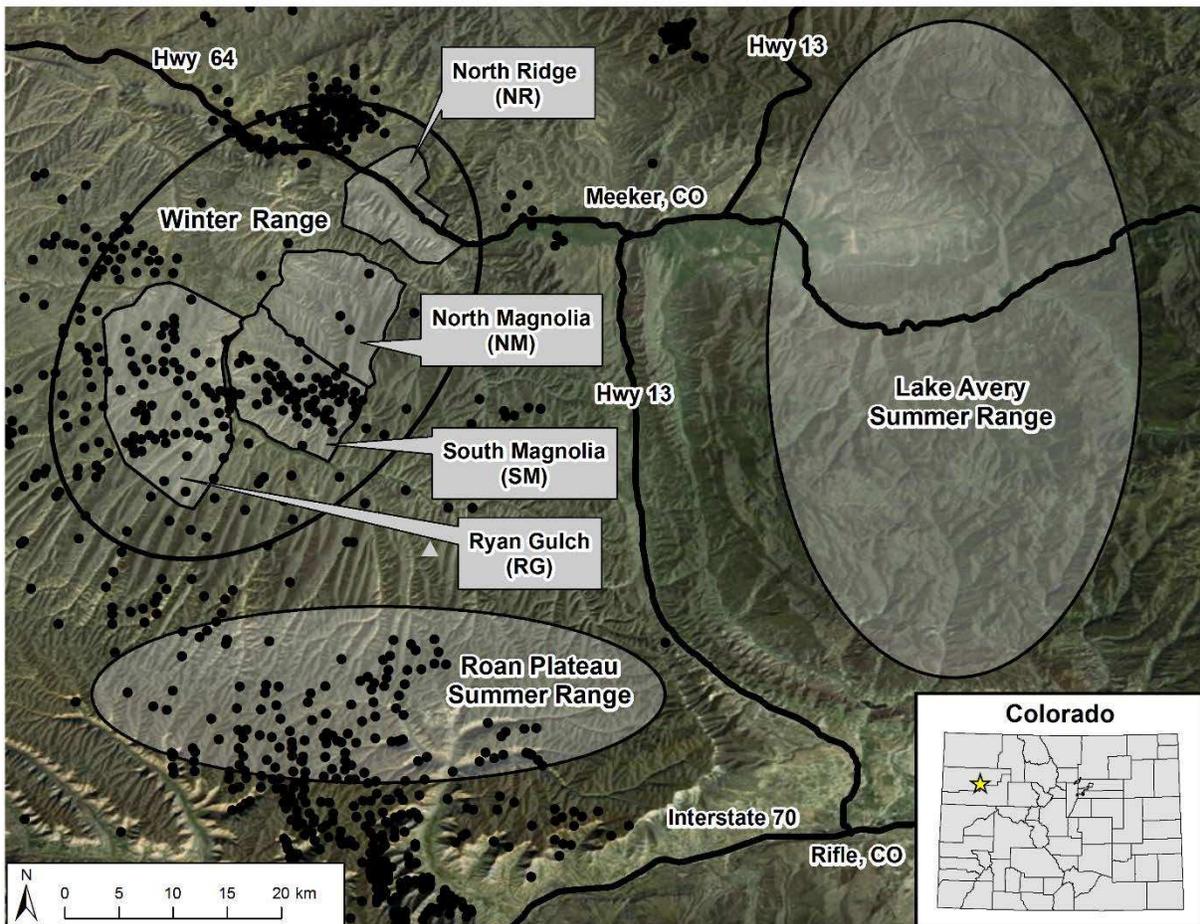


Figure 3.1. Mule deer winter and summer range study units in the Piceance Basin in northwestern Colorado, USA. Winter range study units were referenced as Ryan Gulch (RG), South Magnolia (SM), North Magnolia (NM), and North Ridge (NR). Summer range study units were referenced as Roan Plateau and Lake Avery. RG and SM deer generally migrated towards the Roan Plateau summer range, while NM and NR deer generally migrated towards the Lake Avery summer range. Overall, RG, SM, and Roan Plateau were considered the high development study areas, whereas NM, NR, and Lake Avery were considered the low development study areas. Drilling and producing natural gas well pads (●) and National Climatic Data Center weather station (▲).

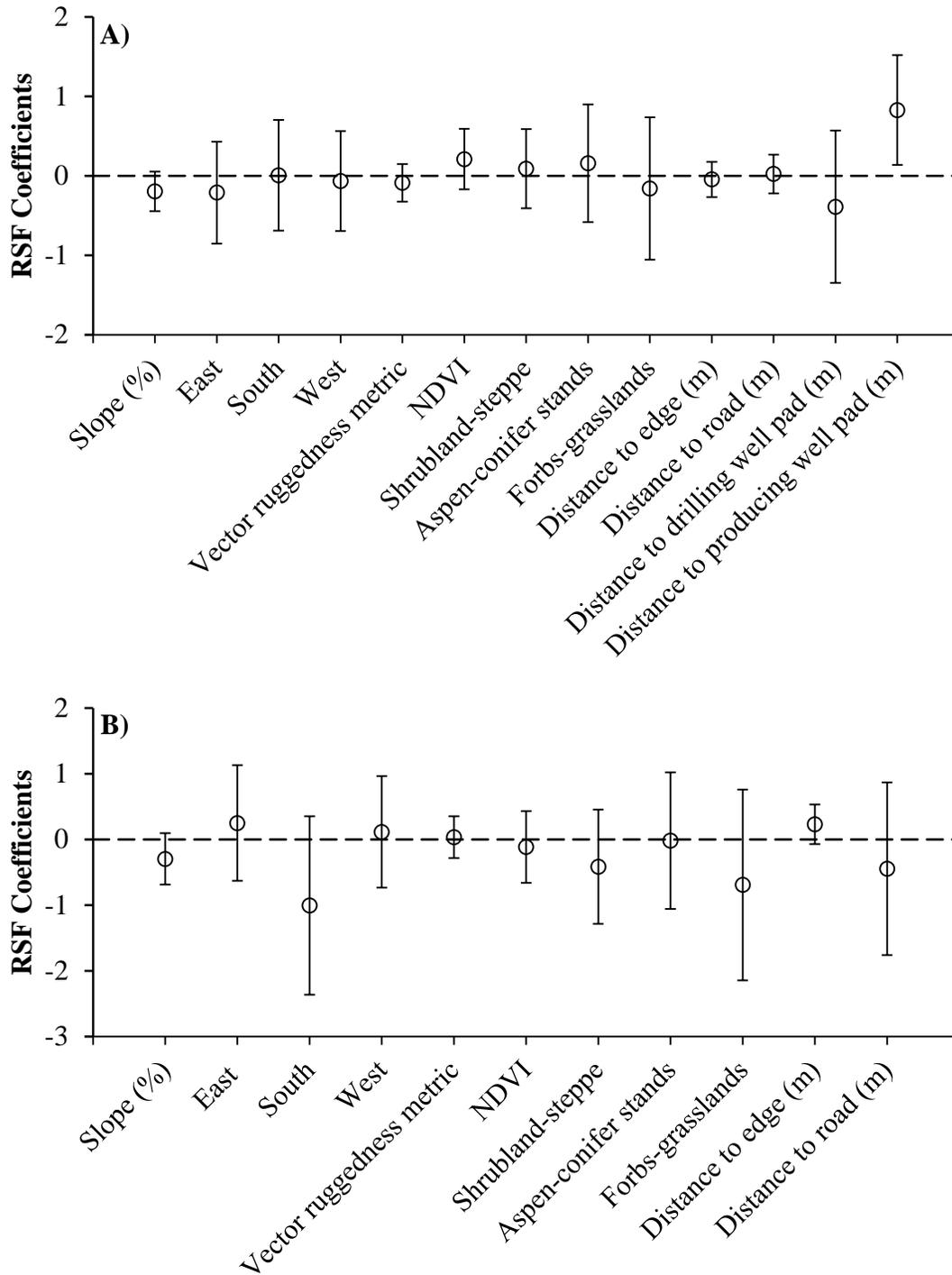


Figure 3.2. Model-averaged parameter estimates (\pm 95% CI) from resource selection functions for birth site selection by adult female mule deer on the high development (A) or the low development (B) study areas. Positive estimates signify selection of variable, whereas negative estimates signify avoidance. Continuous parameter estimates were calculated with standardized variables so they are directly comparable. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

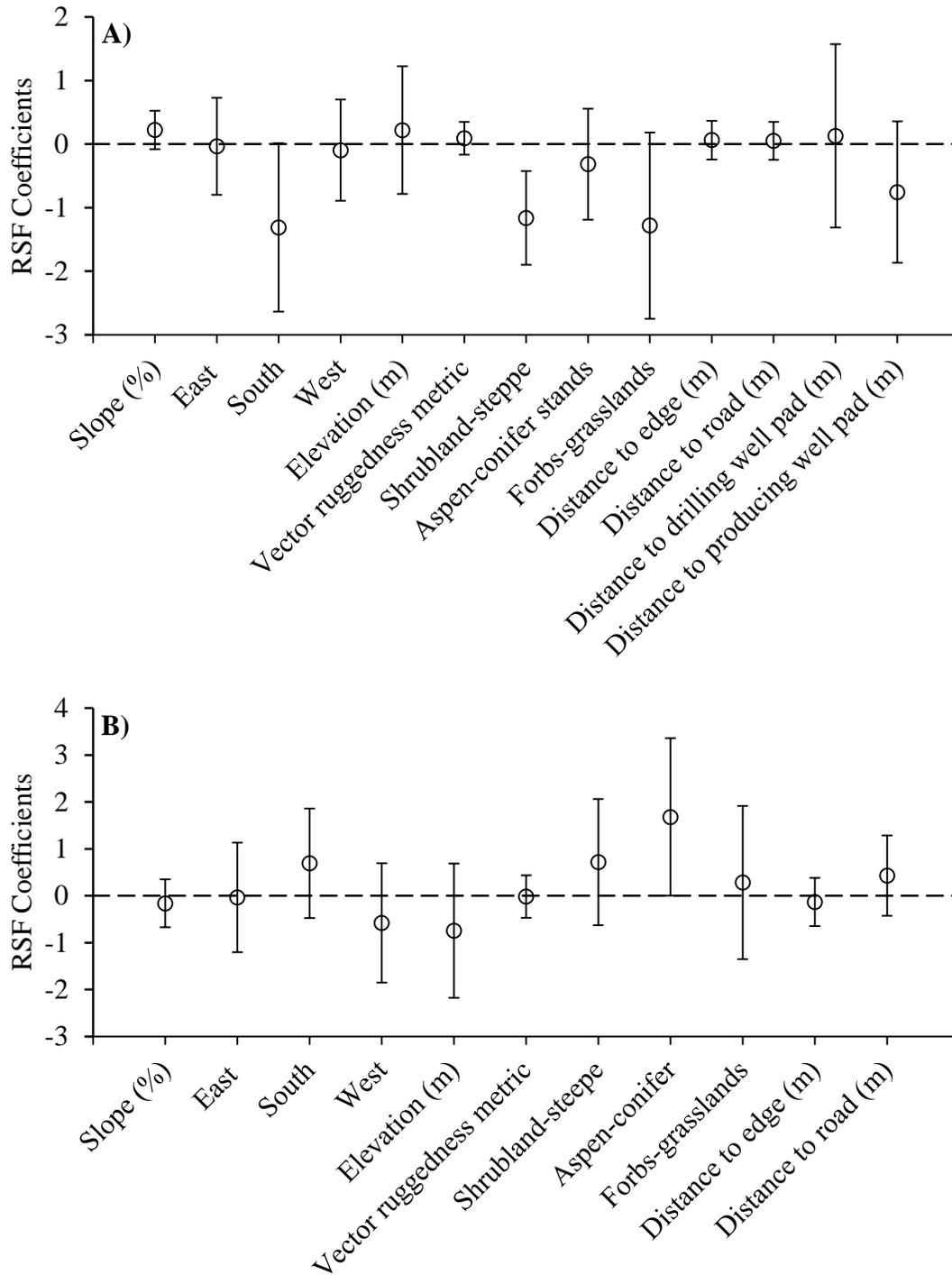


Figure 3.3. Model-averaged parameter estimates (\pm 95% CI) from resource selection functions for habitat characteristics of predation sites on the high development (A) or the low development (B) study areas. Positive estimates signify favorable characteristic, whereas negative estimate signify unfavorable characteristic. Continuous parameter estimates were calculated with standardized variables so they are directly comparable. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

CHAPTER 4:

FACTORS INFLUENCING NEONATAL MULE DEER MORTALITY IN A NATURAL GAS DEVELOPMENT AREA

Synopsis. Potential impacts of natural gas development on wildlife and their habitat has caused concern among wildlife managers, researchers, and stakeholders. Specifically, understanding how this development and other factors influence neonatal (i.e., 0–6 months old) mule deer (*Odocoileus hemionus*) mortality rates, recruitment, and population dynamics have been identified as knowledge gaps. Thus, I tested hypotheses about the influence of natural gas development, adult female, neonate, and temporal factors on neonatal mortality in the Piceance Basin in northwestern Colorado, USA from 2012–2014. I estimated apparent cause-specific mortality in areas with relatively high or low levels of natural gas development using a multi-state model. Predation and death by malnutrition decreased from 0–14 days old. Predation of neonates was positively correlated with rump fat thickness of adult females, but negatively correlated with the distance (0–0.4 km) from a female’s core area to a producing well pad on winter or summer range. Death by malnutrition was positively correlated with the distance from a female’s core area to a road on winter range and weakly, but negatively correlated with temperature. During my study, predation was the leading cause of neonatal mortality in both areas and mean daily predation probability was 9% higher in the high versus low development areas. However, black bear (*Ursus americanus*) predation was the leading cause of neonatal mortality in the high development areas (22% of all mortalities) compared to cougar (*Felis concolor*) predation in the low development areas (36% of all mortalities). Reduced precipitation

and patchy habitat further fragmented by development possibly contributed to less hiding cover or edge effects, potentially leading to increased predation in the high development areas.

Consequently, developers and managers should consider strategies to mitigate impacts from development and improve habitat to reduce mortality. Such strategies could include implementing habitat treatments to rehabilitate areas, as well as minimizing habitat fragmentation and minimizing removal of hiding cover when constructing well pads and roads.

INTRODUCTION

Wildlife managers, researchers, and public stakeholders have heightened concern about the potential impacts of natural gas development on wildlife and their habitat (Walker et al. 2007, Doherty et al. 2008, Webb et al. 2011a, Christie et al. 2015). Impacts on mule deer (*Odocoileus hemionus*) populations and their habitat are of particular interest due to their recreational, social, and economic importance as a game species (Sawyer et al. 2006, Lendrum et al. 2012, Northrup et al. 2015). Understanding neonatal (i.e., 0–6 months old) mule deer mortality rates and cause-specific mortality is helpful to comprehend mule deer population dynamics, especially where natural gas development disturbances are occurring. Ungulate juvenile (i.e., 0–1 year old) survival is typically low and variable, consequently annual variation in survival and recruitment can influence population dynamics (Gaillard et al. 1998, Gaillard et al. 2000, Forrester and Wittmer 2013). However, neonatal mule deer survival has been little studied, even though this time period may be when most mortality occurs (Bishop et al. 2009, Hurley et al. 2011, Monteith et al. 2014, Shallow et al. 2015).

Neonatal mortality can be influenced by distance an adult female's core area is from natural gas development and roads due to increased noise, human presence, and perceived predation risk. Past studies suggest deer tend to avoid roads (Rost and Bailey 1979, Webb et al.

2011c, Lendrum et al. 2012) and well pads (Sawyer et al. 2006, Sawyer et al. 2009, Northrup et al. 2015). However, deer have been shown to use habitat closer to well pads and during spring migration because disturbed topsoil near well pads possibly provided the first nutritious herbaceous vegetation of the growing season (Webb et al. 2011c, Lendrum et al. 2012). Increased human presence associated with development might provide a refuge from predators (Berger 2007, Dussault et al. 2012), although gas-developed areas have also been shown to cause higher perceived risk of predation and exposure to noise (Frid and Dill 2002, Barber et al. 2010, Dzialak et al. 2011b, Lynch et al. 2014). Consequently, neonatal mortality could be positively or negatively influenced by distance from development.

Adult female characteristics (e.g., body condition, fetal production, and age) may be affected by development and have the potential to influence neonatal mortality (Bishop et al. 2007, Lomas and Bender 2007, Bishop et al. 2011). Nutrition seems to be the driving force behind reproductive success of deer (Johnstone-Yellin et al. 2009, Parker et al. 2009, Tollefson et al. 2011) and can influence adult female body condition (Robinette et al. 1973). Availability of high quality forage is necessary to support fetal and neonatal growth (Keech et al. 2000, Tollefson et al. 2011), particularly during the critical periods of the last trimester and lactation (Robbins and Robbins 1979, Pekins et al. 1998). However, development may alter or enhance availability of nutritious forage on both winter and summer range and subsequently influence body condition of females, which has implications for neonate mortality (Keech et al. 2000, Cook et al. 2004, Monteith et al. 2014, Shallow et al. 2015). Litter size also has implications for neonate mortality as twins or triplets weigh less than singletons (Robinette et al. 1973, Robinette et al. 1977), thus increasing the risk of starvation for larger litters. In addition, twins and triplets tend to be more pretentious than singletons, thus increasing their risk of predation (Riley and

Dood 1984). Female age can also influence neonate mortality as white-tailed deer offspring produced by prime-aged and older females (3-10 years old) versus younger females had lower mortality due to improved rearing skills, anti-predator behavior, and selection of prime habitat (Ozoga and Verme 1986, Grovenburg et al. 2009, Grovenburg et al. 2012). Overall, maternal body condition, litter size, and maternal age can influence neonatal mortality.

Neonatal mortality can be influenced by neonate characteristics including mass, age, and date of birth. Neonate mass can also interact with age (Lomas and Bender 2007, Bishop et al. 2009) and date of birth (Testa 2002) in influencing survival. Neonates are most vulnerable to mortality events from birth to 8 weeks old (Lomas and Bender 2007, Monteith et al. 2014, Shallow et al. 2015). Earlier date of birth may allow adult females access to nutritious high quality forage during the early growing season (Parker et al. 2009, Lendrum et al. 2014), which increases neonate growth and strength to elude predators (Testa 2002). Thus, neonate characteristics and subsequent mortality are influenced by habitat and adult female body condition (Monteith et al. 2014, Simard et al. 2014, Shallow et al. 2015).

Temporal characteristics, namely winter precipitation (i.e., season before parturition), summer precipitation, and temperature can influence neonatal mortality. Neonatal mortality from 4–6 weeks after birth depends on maternal body condition, cryptic coloration, and hiding cover to minimize detection by predators (Walther 1965, Lent 1974, Geist 1981). Precipitation can indirectly affect maternal condition and subsequent neonate birth mass and mortality through forage growth and quality (Lomas and Bender 2007, Monteith et al. 2014, Shallow et al. 2015). Additionally, summer ambient temperatures can increase neonate mortality if exposure to cold, wet weather occurs shortly after birth (Gilbert and Raedeke 2004, Hurley et al. 2011).

The use of vaginal implant transmitters (VITs) allowed me to capture mule deer neonates from radio-collared females to test hypotheses about how natural gas development, adult female, neonate, and temporal characteristics influence neonatal mortality. The use of VITs aided capture of neonates at or close to birth and minimized unknown fates of very young neonates, which can cause biased mortality rates when using age-dependent models (Gilbert et al. 2014). I estimated cause-specific mortality in areas with relatively high (0.04–0.90 well pads/km²) or low (0.00–0.10 well pads/km²) levels of natural gas development using a multi-state model (White et al. 2006, Lebreton et al. 2009). My objective was to test predictions that neonatal mortality would be higher farther from producing well pads (e.g., less forage), closer to roads (e.g., less cover), for younger and lighter neonates (e.g., increased mortality risk and less strength), for late-born (e.g., decreased growth rate), male (e.g., more active), and twin neonates (e.g., lower mass and more active). I also predicted neonatal mortality would be higher for neonates produced by females with decreased rump fat thickness (i.e., body condition) and younger (≤ 3.5 years old) females (e.g., poor rearing skills), and with increased previous winter precipitation (e.g., poor body condition), and with decreased summer precipitation (e.g., less forage and cover) and temperature (e.g., increased thermoregulation). Additionally, I predicted that predation would be the primary cause of neonatal mortality and higher in the high versus low natural gas development study areas (e.g., less cover and fragmented habitat). My novel results can be used to comprehend mule deer population dynamics and address management decisions and mitigation strategies.

METHODS

Study Area

I examined neonatal mortality in the Piceance Basin in northwestern Colorado, USA, from 2012–2014 (Figure 4.1). The Piceance Basin provides crucial winter and transition range habitat for one of the largest migratory mule deer populations in North America (White and Lubow 2002), yet some of the largest natural gas reserves in North America reside beneath the Basin as part of the Green River Formation. My winter range study area included four study units in the Piceance Basin (Figure 4.1) and are part of a larger research project (Anderson 2015). My winter range study units were South Magnolia (83 km²; 39.898°N, –108.343°W), Ryan Gulch (141 km²; 39.894°N, –108.343°W), North Ridge (53 km²; 40.045°N, –108.153°W), and North Magnolia (79 km²; 39.966°N, –108.206°W). South Magnolia and Ryan Gulch study units had relatively high levels of natural gas development (0.6–0.9 well pads/km²; hereafter referenced as the high development study area), whereas North Magnolia and North Ridge study units had low levels of development (0.0–0.1 well pads/km²; hereafter referenced as the low development study area).

Winter range habitat was dominated by two-needle pinyon (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* Torr.) woodlands, big sagebrush (*Artemisia tridentate* Nutt.), Utah serviceberry (*Amelanchier utahensis* Koehne.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), antelope bitterbrush (*Purshia tridentate* Pursh.), rubber rabbitbrush (*Ericameria nauseosa* Pall ex. Pursh.), and mountain snowberry (*Symphoricarpos oreophilus* A. Gray; Bartmann 1983, Bartmann et al. 1992). Shrubs, forbs, and grasses common to the area are listed in Bartmann (1983) and Bartmann et al. (1992). Drainage bottoms bisected the study units and contained stands of big sagebrush, saltbush (*Atriplex* spp.), and greasewood

(*Sarcobatus vermiculatus* Hook.), with most of the primary drainage bottoms having been converted to irrigated, grass hay fields. Plant nomenclature follows the United States Department of Agriculture PLANTS Database (USDA and NRCS 2016). Winter study unit elevations ranged from 1,860 m to 2,250 m and the winter climate of the Piceance Basin is typified by cold temperatures with most of the moisture resulting from snow. During my study, winter (October–April) precipitation averaged 22.4 cm and mean winter temperatures ranged from -14°C to 14°C at the Rifle 23 NW weather station located at 2,301 m elevation (National Climatic Data Center 2015).

Summer range study units included parts of Garfield, Moffat, Rio Blanco, and Routt counties in northwestern Colorado (39.580°N , -107.961°W and 40.330°N , -107.028°W ; Figure 4.1). Ryan Gulch and South Magnolia deer generally migrated southeast and south to the Roan Plateau (Lendrum et al. 2013) where deer potentially encountered natural gas development (0.04–0.06 well pads/ km^2 ; hereafter referenced as the high development study area). North Magnolia and North Ridge deer generally migrated northeast and east across US Highway 13 towards Lake Avery and the Flat Tops Wilderness Area (Lendrum et al. 2013) where deer encountered minimal natural gas development (0.00–0.01 well pads/ km^2 ; hereafter referenced as the low development study area). Not all deer ($n = 8$) migrated to summer range and instead opted to remain residents on winter range.

Summer range habitat was dominated by Gambel oak (*Quercus gambeli* Nutt.), mountain mahogany, Utah serviceberry, mountain snowberry, chokecherry (*Prunus virginiana* L.), quaking aspen (*Populus tremuloides* Michx.), big sagebrush, pinyon pine, and Utah juniper. Dominant habitat was interspersed with Douglas-fir (*Pseudotsuga menziesii* Mirb.), Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), and subalpine fir (*Abies lasiocarpa* Hook.) forests

(Garrott et al. 1987). Summer study unit elevations ranged from 1,900 m to 3,150 m and the summer climate of the Piceance Basin is typified by warm temperatures with most of the moisture resulting from spring snow melt and brief summer monsoonal rainstorms. During my study, summer (May–September) precipitation averaged 20.3 cm and mean summer temperatures ranged from 2 °C to 31 °C at the Rifle 23 NW or Hunter Creek weather station (National Climatic Data Center 2015) depending on available weather data.

Adult Female Capture and Handling

During December 2011–2013, adult female mule deer (≥ 1.5 years old) were captured in each of the four winter range study units using helicopter net gunning techniques (Barrett et al. 1982, van Reenen 1982). Deer were blindfolded, hobbled, and chemically immobilized with 35 mg of Midazolam (a muscle relaxant) and 15 mg of Azapirone (an anti-anxiety drug) given intramuscularly. For each captured deer, age was estimated (Severinghaus 1949, Robinette et al. 1957b) and I fit each captured deer with a store-on-board GPS radio collar with a motion-sensitive mortality switch on an 8-hour delay and a timed released mechanism set to release 16 months after deployment (Model G2110D, Advanced Telemetry Systems, Inc., Isanti, MN, USA). Most GPS radio collars were programmed to attempt a fix every 5 hours, but some attempted a fix every 30 minutes between 1 September and 15 June and hourly between 16 June and 31 August to address different research objectives (Northrup 2015). I consolidated data to attain the same temporal scale of 5 hours for all deer.

During early March 2012–2014, radio-collared adult females were recaptured on winter ranges using helicopter net gunning techniques. I performed transabdominal ultrasonography to measure maximum subcutaneous fat thickness on the rump and thickness of the longissimus dorsi muscle of each adult female using a SonoVet 2000 portable ultrasound unit (Universal

Medical Systems, Inc., Bedford Hills, NY) with a 5 MHz linear transducer (Stephenson et al. 1998, Stephenson et al. 2002, Cook et al. 2010). I determined a body condition score for each deer by palpating the rump (Cook et al. 2007, Cook et al. 2010). I estimated percent ingesta-free body fat of each female by combing the ultrasonography measurements with the body condition score (Cook et al. 2010). I also performed transabdominal ultrasonography to determine pregnancy status and number of fetuses present with a 3 MHz linear transducer (Stephenson et al. 1995, Bishop et al. 2007). If an adult female was pregnant, I inserted a vaginal implant transmitter (VIT; Model M3930, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and followed VIT insertion procedures described in detail by Bishop et al. (2007) and Bishop et al. (2011). In 2012 and 2013, each VIT was equipped with a temperature-sensitive sensor (Bishop et al. 2011). In 2014, each VIT was equipped with a temperature- and photo-sensitive sensor, which changed the signal when the ambient temperature dropped below 32 °C or when ambient light was ≥ 0.01 lux (Cherry et al. 2013). The manufacturer programmed VITs to lock on 80 pulses per minute to minimize issues associated with hot ambient temperatures (Newbolt and Ditchkoff 2009).

Adult Female Monitoring and Neonate Capture

On winter range, field technicians monitored radio collar and VIT signals daily from the ground or a Cessna 182 or 185 (Cessna Aircraft Co., Wichita, KS, USA) fixed-wing aircraft. During the parturition period (late May–mid-July), I checked VIT signals daily by aerially locating each radio-collared female having a VIT, weather permitting. In 2014, ground crews also located adult females with VITs to aid in determining when parturition occurred because VIT photo-sensors malfunctioned. When I detected a fast (i.e., postpartum) pulse rate, ground crews used a coded telemetry receiver (Model R4520, Advanced Telemetry Systems, Inc., Isanti, MN, USA) and 3-

element Yagi antenna to simultaneously locate the VIT and radio-collared female. Ground crews searched for neonates and a birth site near (≤ 400 m) the female and expelled VIT. If a VIT was shed prior to parturition or malfunctioned (e.g., battery failure), crews located the female once per day, observed female behavior, and searched in the vicinity of the female to locate neonates and birth sites (Carstensen et al. 2003). All neonate searches lasted up to 1 hour. Crews retrieved VITs and recorded coordinates of birth sites using a hand-held GPS (Garmin GPSMAP 62S, Oregon 650, or Montana 650, Garmin International Inc., Olathe, KS, USA). Crews identified birth sites based on detection of neonates and VIT or by birth site characteristics, including placental remnants, a large deer bed with flattened vegetation radiating outward, browsed or grazed vegetation, moist soil, fresh fecal pellets, tracks, hair, and characteristic odor (Barbknecht et al. 2011, Bishop et al. 2011, Rearden et al. 2011).

Crews attempted to determine the fate of each female's fetus(es) documented in February/March as live or stillborn neonates. I assumed that no fetuses were resorbed based on past research (Robinette et al. 1955, Medin 1976, Carpenter et al. 1984). Unless evidence suggested a neonate was born alive at a birth site (e.g., milk in the abomasum), crews classified the neonate as stillborn. Crews collected and submitted stillborn neonates to the Colorado Parks and Wildlife's Health Laboratory (Fort Collins, CO) for necropsy to confirm that a neonate had died before breathing.

During 2012 and 2013, ground crews captured neonates and located birth sites in the high and low development study areas. In 2014, crews captured neonates and located birth sites predominantly in the high development study areas and sporadically in the low development study areas because VIT photo sensors malfunctioned. Each captured neonate was handled with nitrile latex gloves to minimize transfer of human scent, blindfolded, and placed in a cloth bag to

measure body mass (± 0.1 kg). Crews measured hind foot length (± 0.5 cm), sexed each neonate, and estimated neonate age (days) primarily based on VIT expulsion date and secondarily based on hoof characteristics, condition of the umbilical cord, pelage, and behavior (Haugen and Speake 1958, Sams et al. 1996). Crews fit each neonate with a radio collar (Model M4210, Advanced Telemetry Systems, Inc., Isanti MN, USA) equipped with an 8-hour mortality sensor. Crews modified radio collars for temporary attachment by cutting the collar in half and splicing the ends with two lengths of rubber surgical tubing (5.7 cm each). Handling time was ≤ 5 minutes per neonate and crews replaced neonates where initially found to reduce abandonment. Past neonatal deer studies have reported minimal or no marking-induced abandonment (Pojar and Bowden 2004, Powell et al. 2005, Bishop et al. 2007). All capture, handling, radio collaring, and VIT insertion procedures were approved by the Institutional Animal Care and Use Committee at Colorado Parks and Wildlife (protocol #17-2008 and #1-2012) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Neonate Monitoring and Cause-specific Mortality

From the air, field technicians or I monitored radio-collared neonates daily during the parturition period, weekly until deer migrated from summer range, and daily from the ground when deer arrived on winter range. Technicians or I monitored radio-collared neonates from birth until death, collars were shed, or the end of the neonate survival period (i.e., 0–6 months old) on 15 December 2012, 2013, or 2014. Daily monitoring during the parturition period, when a majority of mortalities occurred, allowed us to investigate mortalities typically within 24 hours, thus I am confident in our determination of cause-specific mortality. When I detected a mortality signal, ground crews located the neonate and/or radio collar and conducted a mortality site investigation and field necropsy, if possible, to determine cause-specific mortality. During the mortality site

investigation, crews documented GPS coordinates of the site, predator tracks, predator scat, drag trails, blood, hair, and any other signs (e.g., matted vegetation or broken shrub branches) that could help determine cause-specific mortality or scavenging. If no carcass was present, but site investigation suggested probable predation (i.e., blood at the site or on the radio collar), crews used predation site characteristics and predatory feeding behavior reported in the literature to help assign a specific predator (Wade and Bowns 1982, Acorn and Dorrance 1990, Stonehouse et al. *In prep*).

Crews classified cause-specific mortality into the following categories: predation by black bear (*Ursus americanus*), bobcat (*Lynx rufus*), cougar (*Puma concolor*), coyote (*Canis latrans*), domestic dog (*Canis familiaris*), raptor, unknown predation, malnutrition, accident, disease, or unknown mortality. Crews identified cause-specific predation based on characteristics detailed in Stonehouse et al. (*In prep*) and malnutrition as cause of death if the femur contained minimal or no marrow fat on an intact carcass (Riney 1955) and no sign indicated hemorrhaging, predation, disease, or scavenging. Accident mortalities included blunt force trauma and vehicle collisions. Lastly, disease mortalities included deaths caused by congenital deformities.

Mule Deer Core Area Estimation

Radio collars deployed on adult females were programmed to release 16 months post-capture. Technicians retrieved collars then, or from mortality sites, and downloaded GPS data. I imported data into ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA) to determine winter and summer range locations for each adult female. Using helicopter net gunning techniques to capture deer can potential impact mule deer behavior (Northrup et al. 2014), thus I censored location data for 4 days following capture. Deer in this area are migratory, thus I classified winter range locations as being from post-capture to departure from winter range

and summer range locations as being from arrival to departure or date of neonatal death. I determined migration patterns for each deer by examining GPS locations in ArcMap 10.2. I derived 50% kernel density estimates of core areas and centroids for each adult female on winter and summer ranges using the Geospatial Modeling Environment (Beyer 2012).

Multi-state Mark-recapture Mortality Analyses and Model Set

Because of the logistics of aerial telemetry flights and ground telemetry, migration patterns of mule deer, and transmitter failures, my data violated the fundamental assumptions of a known-fate study (White and Garrott 1990) that detection probability (p) equals 1.0 and all fates (alive or dead) are known (White and Garrott 1990). To overcome these violations, I used a multi-state model (Brownie et al. 1993, Lebreton and Pradel 2002, Lebreton et al. 2009) as implemented in Program MARK (White and Burnham 1999, White et al. 2006).

I analyzed apparent mortality daily from parturition until 15 December 2012–2014 by setting time intervals in MARK to one day during the parturition period and seven days (i.e., weekly) after the parturition period until 15 December to align with my monitoring protocols. I considered my encounter data to be in one of five states represented by alive in the high development study areas (H), alive in the low development study areas (L), death by predation (K), death by malnutrition (M), or death by unknown mortality (U ; Figure 4.2). In addition, each encounter history was assigned to one of three groups represented by 2012, 2013, or 2014. Lastly, prior to modeling, I calculated a correlation matrix to test for collinearity among covariates ($|r| \geq 0.6$). If two covariates were correlated, I retained the more biologically plausible covariate.

Multi-state models estimate three parameters including survival (S), detection, and transition probabilities (Lebreton et al. 2009). In my case, I modeled alive and dead states and

estimated apparent mortality rates as the transition probability ($\hat{\psi}$) from an alive to a dead state (Lebreton and Pradel 2002, Devineau et al. 2010). Because survival is the complement of mortality and I estimated mortality with the transition probabilities, I fixed survival rates in the high (S^H) and low (S^L) development area states to one and survival rates in the death by predation (S^K), malnutrition (S^M), and unknown mortality (S^U) states to zero (Devineau et al. 2010, Devineau et al. 2014). I modeled transitions from alive in the high or low development study areas to death by predation, malnutrition, or unknown mortality ($\hat{\psi}^{HK}, \hat{\psi}^{HM}, \hat{\psi}^{HU}, \hat{\psi}^{LK}, \hat{\psi}^{LM}, \hat{\psi}^{LU}$). I assumed transitions from a dead to an alive state or a dead to a dead state could not happen and fixed those to zero. In addition, transitions from an alive state in the high development areas to an alive state in the low development areas did not occur and I fixed those to zero.

I modeled mortality as function of winter range development, summer range development, adult female, neonate, and temporal covariates that I hypothesized would influence neonatal mule deer mortality (Table 4.1) based on previous deer studies (Pojar and Bowden 2004, Bishop et al. 2009, Johnstone-Yellin et al. 2009, Hurley et al. 2011, Monteith et al. 2014, Shallow et al. 2015). Winter and summer range development covariates included the distance (km) from a female's core area to the nearest drilling well pad, producing well pad, and road (Table 4.1). We acquired the location of natural gas wells from the Colorado Oil and Gas Conservation Commission (<http://cogcc.state.co.us>). We classified each well in the high development summer range as either actively being drilled or actively producing natural gas with no drilling activity using a procedure described in Northrup et al. (2015). Using the classified well pad data, we calculated mean distance (m) from the centroid of each adult female's core area to the nearest drilling and producing well pad on their specific winter and summer range

study areas. I fit models using a distance threshold model structure that accounted for distances that can illicit behavioral responses by deer (Northrup et al. 2015), specifically 0–0.8 km from a drilling well pad and 0–0.4 km from a producing well pad. We also created a road network map by digitizing all roads visible on NAIP imagery and calculated mean distance (m) from the centroid of each adult female’s core area to the nearest road on their specific winter and summer range study areas. We calculated mean distances from a female’s capture date to departure from winter range for winter range development covariates and calculated distance from summer range development covariates on a neonate’s date of birth using the R statistical software (R Core Team 2015).

Adult female-specific covariates included rump fat thickness (mm) of females in March, in utero fetal count in March, female age in December, and deer density (deer/km²; Table 4.1). Deer density in each study area was estimated using annual mark-resight helicopter surveys conducted in late March–early April (Anderson 2015).

Neonate-specific covariates included age (days old), estimated mass at birth (kg), date of birth (DOB), and sex (Table 4.1). I incorporated neonate age into models by fitting a model that allowed transition probabilities to vary by an age trend from 0–14 days old and constant thereafter. I estimated neonate mass at birth by regressing neonate capture mass as a function of age for each year separately (Bishop et al. 2008, Bishop et al. 2009) using a linear model in the R statistical software (R Core Team 2015). I defined date of birth (DOB) as the number of days following the first detected birth in a given year (Bishop et al. 2009).

Temporal covariates included total precipitation (cm) during the previous winter season before parturition (1 October–30 April), daily precipitation (cm) and daily temperature (°C)

during the parturition period, and the 7-day average of precipitation and temperature after the parturition period until 15 December (Table 4.1).

I used a two-stage modeling approach to assess covariate importance and used stage one to identify and exclude unsupported covariates from stage two. For stage one, I conducted separate mortality analyses for winter range development, summer range development, adult female, neonate, or temporal covariates while holding detection probabilities constant. I also ran a separate analysis where I modeled detection probability as a function of year and migration (i.e., different probability before and after autumn migration) while holding transition probabilities constant. Due to memory limitations in Program MARK, I fit all possible combinations of additive models (Doherty et al. 2012) with a maximum of 6 winter range development (Appendix 4.1), 3 summer range development (Appendix 4.2), 4 adult female (Appendix 4.3), 3 neonate (Appendix 4.4), and 4 temporal (Appendix 4.5) covariates. For the detection probability analysis, I fit all possible combinations of additive and interactive models (Appendix 4.6; Doherty et al. 2012). For each analysis, I calculated the sum of Akaike's Information Criterion adjusted for small sample size (AICc) weights for models containing each covariate of interest (Burnham and Anderson 2002). I considered covariates with a cumulative AICc weight ≥ 0.50 as important (Barbieri and Berger 2004) and retained these variable for stage two of model selection (Table 4.2).

For stage two of model selection (Table 4.3), I fit all possible combinations of additive models (Appendix 4.7; Doherty et al. 2012) and calculated cumulative quasi-likelihood using Akaike Information Criterion adjusted for small sample size (QAICc) weights to help identify important variables (Burnham and Anderson 2002). Following suggestions of Barbieri and Berger (2004), I constructed a prediction model that contained all covariates with a cumulative

QAICc weight ≥ 0.50 . Unless otherwise noted, I used the prediction model when presenting estimates.

Bootstrap Analyses

I attempted to capture and radio collar all neonates documented in utero for each radiocollared adult female. This potentially caused overdispersion because of sibling dependence (Bishop et al. 2008). I followed methods described by Bishop et al. (2008) to test for overdispersion (\hat{c}) and conducted a bootstrap analysis in Program MARK. I resampled litters of radio-collared adult females instead of individual radio-collared neonates and each analysis consisted of 1,000 replicates. I used the most parametrized model from stage two of model selection described above for the bootstrap and calculated the mean and standard deviation for each of the 1,000 mortality estimates using mean covariate values. The dependence among litters is reflected in the standard deviation of the mortality estimates and yielded an empirical sampling variance estimate. I estimated overdispersion by dividing the empirical (i.e., bootstrap) estimate of standard deviation ($[SD(\hat{S})]^2$) by the theoretical (i.e., observed) standard error ($[SE(\hat{S})]^2$) from the mortality estimate of the top model. If the mean estimate of \hat{c} was above 1.00, I adjusted \hat{c} in Program MARK and calculated QAICc weights (Burnham and Anderson 2002).

RESULTS

During 29 May–30 June 2012–2014, I captured and radio-collared 128 (2012, $n = 61$; 2013, $n = 33$; 2014, $n = 34$) and 56 neonates (2012, $n = 20$; 2013, $n = 31$; 2014, $n = 5$) in the high and low development study areas, respectively. Neonates were captured from 85 [43 or 42 with one or two collared neonate(s)] and 33 [21, 11, or 1 with one, two, or three collared neonate(s)] females in the high and low development study areas, respectively. In the high and low development study areas, mortality was attributed to black bear predation ($n = 17$ and 5), cougar predation (n

= 9 and 6), coyote predation ($n = 10$ and 1), bobcat predation ($n = 1$ and 4), felid predation ($n = 3$ and 1), raptor predation ($n = 1$ and 0), unknown predation ($n = 18$ and 5), malnutrition ($n = 4$ and 3), vehicle ($n = 1$ and 0), and unknown mortality ($n = 13$ and 5). I censored two neonates from the mortality analyses because their deaths were related to capture. I right-censored 13 additional neonates during the study, 12 because of slipped radio collars and one because of a capture-related (i.e., leg caught in collar) mortality attributed to predation at eight weeks old.

Cause-specific Mortality of Neonates

I estimated \hat{c} as 1.035 (SE = 0.153) and assessed relative importance of each covariate for predicting probability of predation using cumulative QAICc weights (Table 4.3). Rump fat thickness of adult females, distance (0–0.4 km) an adult female’s core area was from a producing well pad on winter or summer range, and a 14-day neonate age trend and constant thereafter all had a cumulative QAICc weight > 0.5 (Table 4.3), suggesting support for influencing predation of neonates. The daily predation probability of neonates increased as female rump fat thickness increased ($\hat{\beta} = 0.196$, 95% CI: 0.072 to 0.321; Figure 4.3). In addition, predation of neonates decreased as the distance from a female’s core area to a producing well pad on winter ($\hat{\beta} = -2.135$, 95% CI: -4.207 to -0.064; Figure 4.4) or summer ($\hat{\beta} = -6.215$, 95% CI: -10.587 to -1.844; Figure 4.5) range increased from 0–0.4 km, and decreased as neonate age increased from 0–14 days old ($\hat{\beta} = -0.054$, 95% CI: -0.102 to -0.007; Figure 4.6). Overall, predation was the leading cause of neonatal mortality in both areas and mean daily predation probability of neonates was 9% higher in the high development areas (0.012, SE = 0.002) than the low development areas (0.011, SE = 0.001; Figure 4.7).

I also assessed relative importance of each covariate for predicting probability of death by malnutrition using cumulative QAICc weights (Table 4.3). A 14-day neonate age trend and

constant thereafter, distance an adult female's core area was from a road on winter range, and temperature all had a cumulative QAICc weight > 0.5 (Table 4.3), suggesting support for influencing death by malnutrition. The daily probability of death by malnutrition decreased as neonate age increased from 0–14 days old ($\hat{\beta} = -0.78$, 95% CI: -0.364 to 0.008; Figure 4.8), increased as the distance from a female's core area to a road on winter range increased ($\hat{\beta} = 2.171$, 95% CI: 0.347 to 3.995; Figure 4.9), and decreased as temperature increased ($\hat{\beta} = -0.116$, 95% CI: -0.246 to 0.014). Overall, mean daily probability of death by malnutrition ranged from 0.001 (SE = 8.163×10^{-5}) to 0.003 (SE = 0.002) in the high development areas and from 0.001 (SE = 9.171×10^{-5}) to 0.003 (SE = 0.002) in the low development areas (Figure 4.7).

Lastly, variation in detection probability was best explained by an interaction between year and an autumn migration effect (cumulative QAICc weight = 1.000; Table 4.3). Detection probability ranged from 0.931 (SE = 0.009) to 0.986 (SE = 0.003) before migration and from 0.517 (SE = 0.043) to 0.810 (SE = 0.042) after migration (Table 4.4).

DISCUSSION

Predation was the primary cause of neonatal mule deer mortality in both the high and low development areas, but decreased as neonate age increased from 0–14 days old. However, black bear predation was the leading cause of neonatal mortality in the high development areas (22% of all mortalities) compared to cougar predation in the low development areas (36% of all mortalities). Neonates ≤ 14 days old rely on a hiding strategy with cryptic coloration and sedentary behavior to minimize predation risk (Walther 1965, Lent 1974, Geist 1981). Consequently, an annual birth pulse of neonates provides predators with an irruption of vulnerable prey after predators develop a search image (Whittaker and Lindzey 1999, Testa 2002, Petroelje et al. 2014). Bears and cougars are known to prey on mule deer neonates during

the first few weeks after birth when neonates are most vulnerable (Monteith et al. 2014, Marescot et al. 2015, Shallow et al. 2015), but hiding cover can reduce predation (Panzacchi et al. 2010, Shallow et al. 2015). Decreased precipitation, particularly in 2012, possibly reduced hiding cover leading to increased predation (Lomas and Bender 2007). Moreover, patchy habitat further fragmented by development contributing to increased edge effects in the high development areas might increase predators' capture success, especially for bears during dry years when vulnerable neonates were likely more visible as compared to the low development areas where neonates could have quickly found dense cover (Rohm et al. 2007). My result of age-specific vulnerability to predation is similar to other studies examining mortality of neonatal mule deer (Bishop et al. 2009, Hurley et al. 2011, Monteith et al. 2014, Shallow et al. 2015). In contrast to my predation findings, coyote predation (Whittaker and Lindzey 1999, Bishop et al. 2009, Hurley et al. 2011) or malnutrition (Pojar and Bowden 2004, Lomas and Bender 2007) has been found to be the primary cause of neonatal mortality in other studies. Of note, I monitored neonates weekly instead of daily after mid-July. Weekly surveys increased the time between checks and increased the likelihood of unknown mortality. Consequently, I suspect many unknown mortalities of neonates were from predation, particularly by bears, due to neonate's reduced mobility (Ozoga and Verme 1982, Mathews and Porter 1988, Kunkel and Mech 1994).

Contrary to my prediction, predation of neonates was negatively correlated with the distance from a female's core area to a producing well pad on winter or summer range. Deer can temporarily alter their behavior to select for areas closer to producing well pads during the night (Northrup et al. 2015) possibly for foraging benefits (Webb et al. 2011c, Lendrum et al. 2012). Deer foraging in openings closer to producing well pads and associated pipelines could positively influence maternal nutrition and condition and subsequently birth mass and growth

rate of neonates (Lomas and Bender 2007, Monteith et al. 2014, Shallow et al. 2015). However, deer foraging in openings can increase predation risk of hiding neonates (Rearden et al. 2011), especially at night when predators are generally active (Rogers 1970, Anderson and Lindzey 2003). Thus, habitat closer to producing well pads could be beneficial to adult females, but detrimental to neonates, especially at night. However, deer have been shown to reduce habitat use within 200 m of producing well pads at night on winter range (Northrup et al. 2015), potentially limiting access to high quality forage. Whether similar behavioral processes or other unknown processes influence neonatal mortality around producing well pads on summer range is unknown.

As predicted, death by malnutrition decreased as neonate age increased from 0–14 days old. Contrary to my prediction, rump fat thickness of adult females was positively correlated with predation of neonates. Poor nutritional condition of maternal females contributes to lower birth mass (Robinette et al. 1973), which inhibits neonate growth (Tollefson et al. 2011, Shallow et al. 2015) and increases neonatal mortality (Bishop et al. 2009, Hurley et al. 2011, Monteith et al. 2014). However, a nutrition treatment has been shown to only marginally decrease neonate mortality (Bishop et al. 2009). Further, my rump fat thickness findings may be spurious as some predation of vulnerable neonates (< 28 days old) is expected regardless of maternal condition (Hamlin et al. 1984, Ballard et al. 2001) and others suggest the influence of maternal condition on neonatal mortality primarily occurs when lactation demands increase (≥ 28 days old; Monteith et al. 2014).

Contrary to my prediction, death by malnutrition was positively correlated with the distance from a female's core area to a road on winter range. Road edges provide habitat where deer forage on abundant and high quality forage (Ager et al. 2003). Thus, foraging in habitat

farther from roads could negatively impact maternal nutrition and condition contributing to lower birth mass and increased malnutrition of neonates (Lomas and Bender 2007, Monteith et al. 2014, Shallow et al. 2015). However, death by malnutrition was minimal during my study (Figure 4.7) and my findings suggest body condition of females did not influence malnutrition of neonates, thus I am uncertain of how roads influence malnutrition.

Weakly, but in line with my prediction, death by malnutrition was negatively correlated with temperature. Death by malnutrition was 2% higher in 2013 when mean temperature was 3 °C cooler than 2012 and 2014 particularly during the peak birthing period. Consequently, cooler temperatures might have predisposed vulnerable neonates to malnutrition by increasing thermoregulatory energetic needs (Gilbert and Raedeke 2004, Hurley et al. 2011).

My study provides novel insights into what factors influence cause-specific mortality of neonates in a natural gas developed area. Natural gas development, adult female, and neonate characteristics appear to influence predation of neonates, whereas, development, neonate, and temporal characteristics appear to influence death by malnutrition. However, I cannot be certain of my interpretations because I did not explicitly measure forage availability and quality or hiding cover and habitat in these study areas might be different. Ultimately, future studies should quantify vegetative characteristics and their influence on maternal body condition and subsequently neonate mass to fully comprehend the influence of development and others factors on neonatal mortality.

MANAGEMENT IMPLICATIONS

My results suggest natural gas development may increase neonatal mortality, especially through predation, although inherent habitat and climate differences between the study areas may have also influenced neonatal mortality. Increased neonatal mortality can have implications for mule

deer recruitment and population dynamics. Consequently, developers should consider strategies to minimize habitat loss and fragmentation when planning projects, such as concentrating road and well pad development and minimizing removal of hiding cover when constructing well pads and roads. Developers and managers should also consider strategies to mitigate habitat loss, such as implementing habitat treatments to provide abundant and high quality forage for deer and cover for concealing neonates. Mitigating impacts from development could enhance neonatal deer survival that is influential for ungulate population dynamics and minimize fitness consequences of deer.

TABLES

Table 4.1. List of covariates (mean \pm SD) and hypothesized effects on cause-specific mortality of neonatal mule deer and detection probability in the Piceance Basin, Colorado, USA, 2012–2014. “—” indicates categorical variables.

Covariate	Mean (\pm SD)	Covariate definition	Hypothesis
Winter range (WR) development characteristics			
WR dist.drill 0–0.8 km	8.36 \pm 5.89	Distance (km) from nearest drilling well pad on winter range.	Neonates from adult females with a core area 0–0.8 km from a drilling well pad will have lower mortality in the summer as distance increases from 0–0.8 km.
WR dist.prod 0–0.4 km	1.57 \pm 1.56	Distance (km) from nearest producing well pad on winter range.	Neonates from adult females with a core area 0–0.4 km from a producing well pad will have higher mortality in the summer as distance increases from 0–0.4 km.
WR dist.rd	0.24 \pm 0.22	Distance (km) from nearest road on winter range.	Neonates from adult females with a core area closer to a road will have higher mortality in the summer than neonates from females with a core area farther from a road.
Summer range (SR) development characteristics			
SR dist.drill 0–0.8 km	18.49 \pm 18.33	Distance (km) from nearest drilling well pad on summer range.	Neonates from adult females with a core area 0–0.8 km from a drilling well pad will have lower mortality as distance increases from 0–0.8 km.
SR dist.prod 0–0.4 km	7.34 \pm 11.92	Distance (km) from nearest producing well pad on summer range.	Neonates from adult females with a core area 0–0.4 km from a producing well pad will have higher mortality as distance increases from 0–0.4 km.

SR dist.rd	0.24 ± 0.33	Distance (km) from nearest road on summer range.	Neonates from adult females with a core area closer to a road will have higher mortality than neonates from females with a core area farther from a road.
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Adult female characteristics

Rump fat	2.17 ± 1.45	Rump fat thickness (mm) of adult females measured in March.	Rump fat thickness will be negatively correlated with mortality.
Fetal count	—	In utero fetal count documented in March during adult female capture.	Twin and triplet neonates will have higher mortality compared to a singleton neonate.
Female age	4.95 ± 2.17	Age of adult females documented in December during capture.	Neonates from adult females (≥ 3.5 years) will have lower mortality than neonates from younger females.
Deer density	10.51 ± 3.40	Estimated deer density in each winter range study area derived from annual mark-resight helicopter surveys conducted in late March–early.	Deer density on winter range will be positively correlated with mortality.

Neonate characteristics

Neonate age 0–14 days old	—	Age trend from 0–14 days old and constant thereafter.	Predation and malnutrition will decrease as neonate age increases from 0–14 days old, whereas unknown mortality will increase as neonate age increases from 0–14 days old.
Mass	3.32 ± 0.70	Estimated birth mass (kg) of neonates.	Neonate mass will be negatively correlated with mortality.
DOB	11.68 ± 6.60	Date of birth was the number of days from the first detected birth in a given year.	Date of birth will be positively correlated with mortality.

Sex	—	Sex of captured neonates.	Females will have lower mortality than males.
Temporal characteristics			
Prev.precip	20.73 ± 6.31	Total precipitation (cm) during the previous winter season before parturition (1 October–30 April).	Higher precipitation in the winter before parturition will be positively correlated with mortality.
Precip	0.39 ± 0.86	Daily precipitation (cm) during the parturition period and 7–day average of precipitation after the parturition period until 15 December.	Higher precipitation will be negatively correlated with mortality.
Temp	23.54 ± 8.18	Daily temperature (°C) during the parturition period and 7–day average of temperature after the parturition period until 15 December.	Higher temperature will be negatively correlated with mortality.
Transition probability			
Study area (alive states)	—	High and low development study areas.	Mortality will be higher in the high versus the low development study areas.
Dead states	—	Predation, malnutrition, and unknown mortality.	Predation will be the primary cause of mortality followed by malnutrition.
Detection probability			
Year	—	Each year of the study.	Detection probability of neonates will vary annually.
Migration	—	Before and after autumn migration.	Detection probability of neonates will be lower after autumn migration.

Year * migration

—

An interaction between year and migration.

Yearly variation will occur before and after autumn migration.

Table 4.2. Cumulative weights for Akaike Information Criterion adjusted for small sample size (AICc), for all variables included in the first stage analysis of neonatal mule deer mortality. Parameters were probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Bold numbers indicate cumulative AICc weights above 0.500. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Parameters	Covariate ^a	Cumulative AICc weight
Winter range (WR) development characteristics		
Predation (ψ^K)	WR dist.prod 0–0.4 km	0.923
	WR dist.rd	0.498
Malnutrition (ψ^M)	WR dist.rd	0.734
	WR dist.prod 0–0.4 km	0.483
Unknown mortality (ψ^U)	WR dist.prod 0–0.4 km	0.326
	WR dist.rd	0.272
Summer range (SR) development characteristics		
Predation (ψ^K)	SR dist.prod 0–0.4 km	0.946
Malnutrition (ψ^M)	SR dist.prod 0–0.4 km	0.298
Unknown mortality (ψ^U)	SR dist.prod 0–0.4 km	0.346
Adult female characteristics		
Predation (ψ^K)	Rump fat	0.979
	Female age	0.217
	Fetal count	0.205
Malnutrition (ψ^M)	Fetal count	0.350
	Rump fat	0.248
	Female age	0.205
Unknown mortality (ψ^U)	Female age	0.371

	Rump fat	0.214
	Fetal	0.213
Neonate characteristics		
Predation (ψ^K)	Neonate age 0–14 days old	0.610
	Mass	0.127
	DOB	0.050
	Sex	0.036
Malnutrition (ψ^M)	Neonate age 0–14 days old	0.979
	Mass	0.261
	Sex	0.089
	DOB	0.034
Unknown mortality (ψ^U)	Neonate age 0–14 days old	0.306
	DOB	0.208
	Mass	0.104
	Sex	0.097
Temporal characteristics		
Predation (ψ^K)	Temp	0.616
	Prev.precip	0.493
	Precip	0.309
Malnutrition (ψ^M)	Temp	0.986
	Prev.precip	0.207
	Precip	0.183
Unknown mortality (ψ^U)	Temp	0.263
	Precip	0.165

Prev.precip

0.153

^a Covariates are defined as in Table 4.1.

Table 4.3. Cumulative weights for quasi-likelihood Akaike Information Criterion adjusted for small sample size (QAICc), for all variables included in the second stage analysis of neonatal mule deer mortality. Parameters were probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K) or malnutrition (ψ^M) state and detection probability (p). Bold numbers indicate cumulative AICc weights above 0.500. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

Parameters	Covariate ^a	Cumulative QAICc weight
Predation (ψ^K)	Rump fat	0.956
	SR dist.prod 0–0.4 km	0.890
	Neonate age 0–14 days old	0.707
	WR dist.prod 0–0.4 km	0.679
	Temp	0.409
Malnutrition (ψ^M)	Neonate age 0–14 days old	0.880
	WR dist.rd	0.677
	Temp	0.613
Detection probability (p)	Year	1.000
	Migration	1.000
	Year * migration	1.000

^a Covariates are defined as in Table 4.1.

Table 4.4. Estimated detection probability before (p) and after autumn migration ($p_{\text{migration}}$), associated standard error (SE), and upper and lower 95% confidence limits (CL) of mule deer neonates, Piceance Basin in northwestern Colorado, USA, 2012–2014.

Year	Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
2012	p	0.953	0.005	0.943	0.962
2012	$p_{\text{migration}}$	0.561	0.042	0.478	0.641
2013	p	0.986	0.003	0.977	0.991
2013	$p_{\text{migration}}$	0.517	0.043	0.433	0.599
2014	p	0.931	0.009	0.910	0.947
2014	$p_{\text{migration}}$	0.810	0.042	0.715	0.879

FIGURES

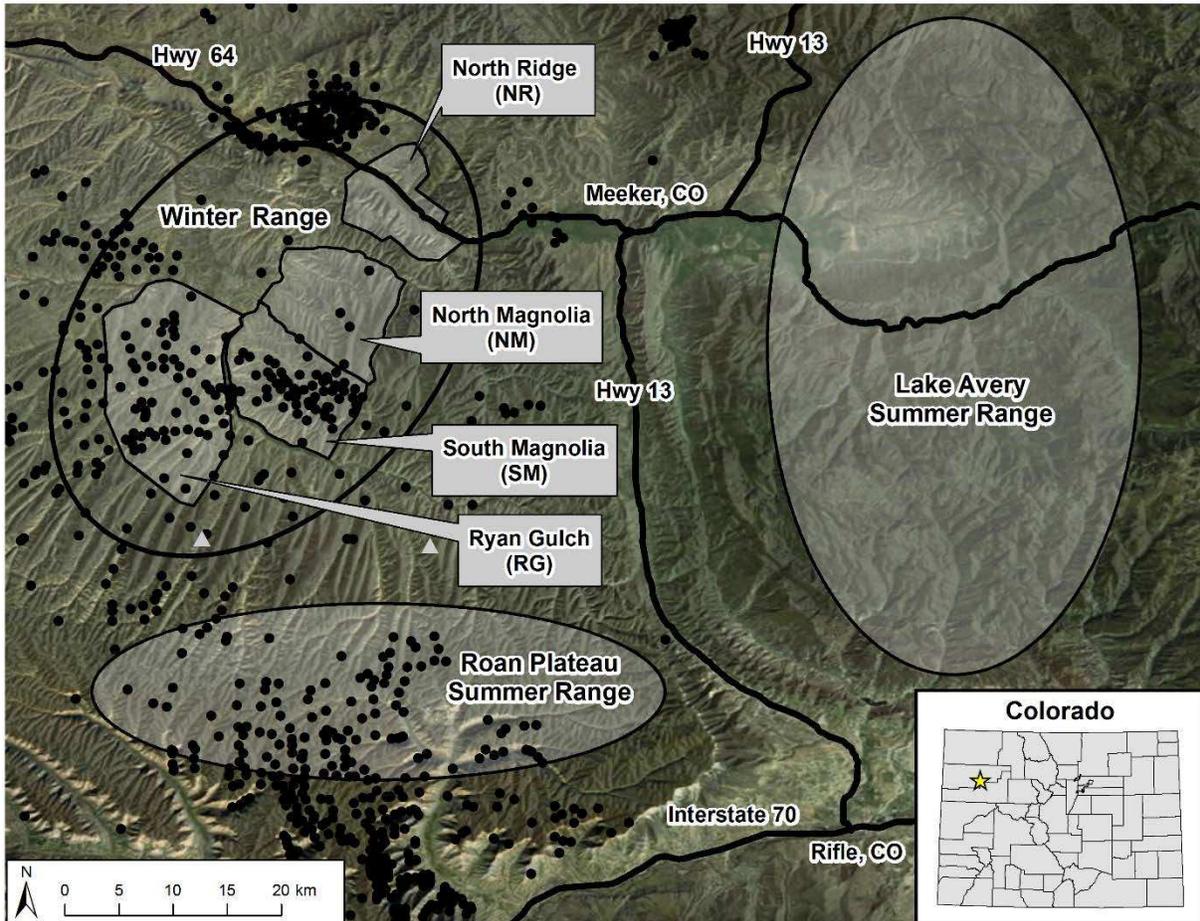


Figure 4.1. Mule deer winter and summer range study units in the Piceance Basin in northwestern Colorado, USA. Winter range study units were Ryan Gulch (RG), South Magnolia (SM), North Magnolia (NM), and North Ridge (NR). Summer range study units were Roan Plateau and Lake Avery. RG and SM deer generally migrated towards the Roan Plateau summer range, while NM and NR deer generally migrated towards the Lake Avery summer range. Overall, RG, SM, and Roan Plateau were considered high development study areas, whereas NM, NR, and Lake Avery were considered low development study areas. Drilling and producing natural gas well pads (●) and National Climatic Data Center weather stations (▲).

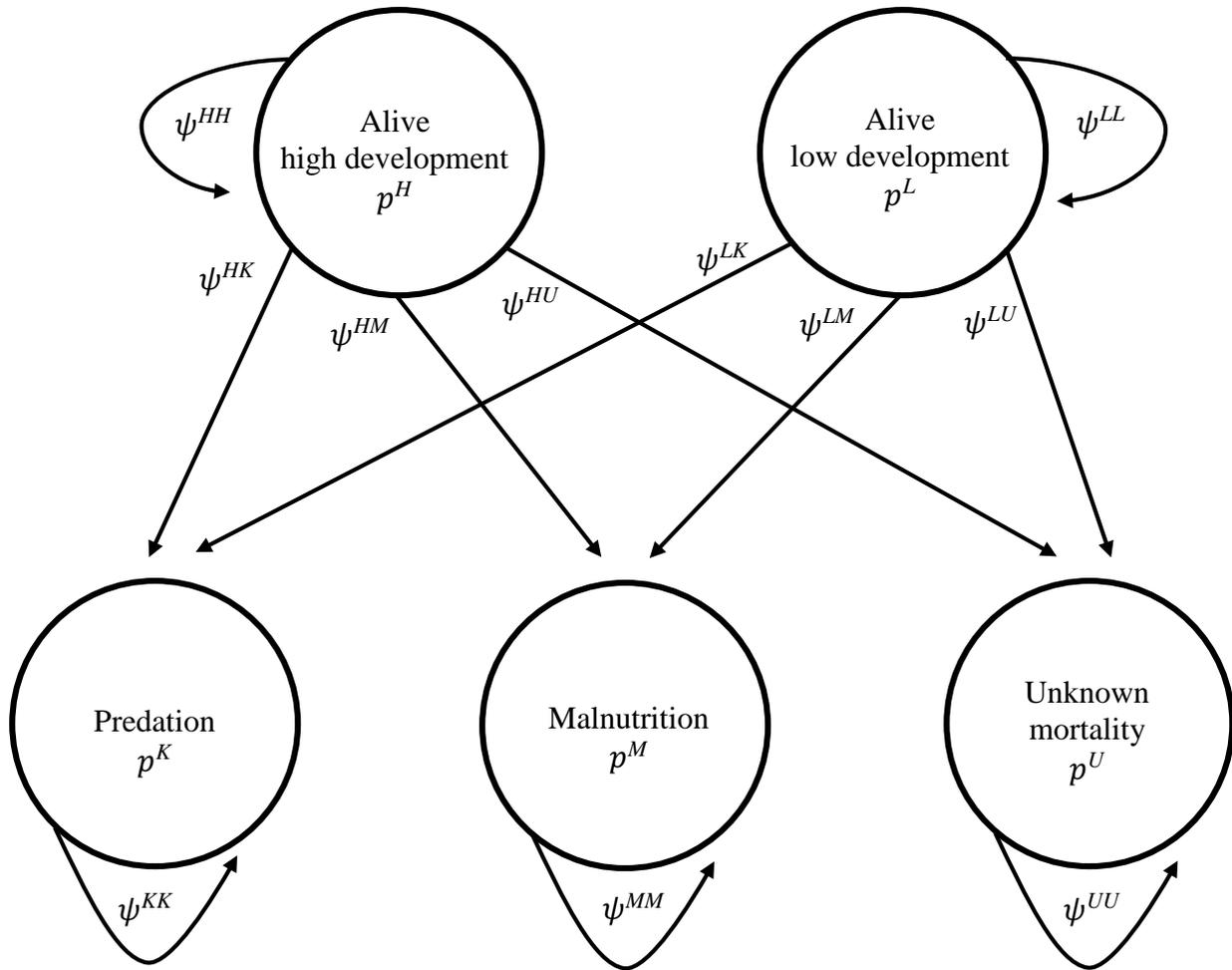


Figure 4.2. Multi-state model schematic representing alive and dead states for neonatal mule deer. Neonates transitioned to a cause-specific death by predation (K), malnutrition (M), or unknown mortality (U) state in the high (H) or low (L) development study areas ($\psi^{HK}, \psi^{HM}, \psi^{HU}, \psi^{LK}, \psi^{LM},$ or ψ^{LU}). Neonates remained in an alive (ψ^{HH}, ψ^{LL}) state or in a cause-specific death by predation, malnutrition, or unknown mortality ($\psi^{KK}, \psi^{MM},$ or ψ^{UU}) state in the high or low development study areas with parameter estimates obtained by subtraction. Neonates were captured at ≤ 3 days old and recaptured in an alive state or cause-specific death state ($p^H, p^L, p^K, p^M,$ or p^U).

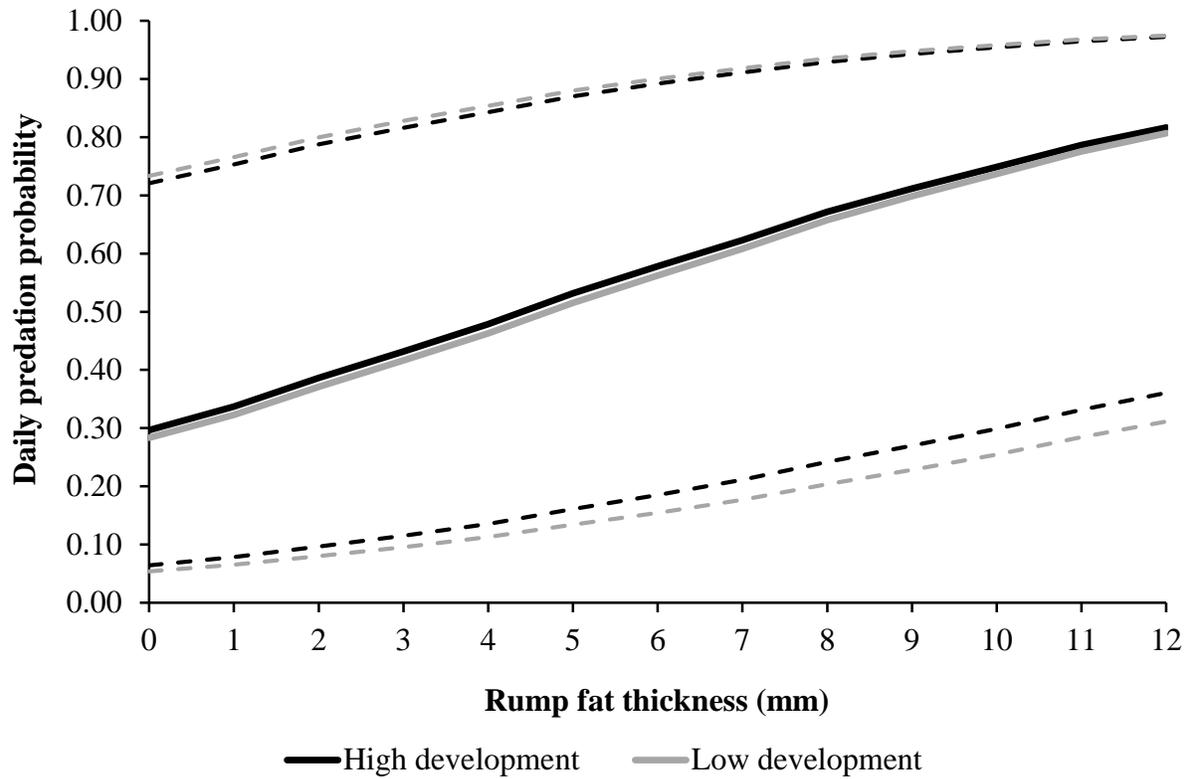


Figure 4.3. Estimated daily predation probability (\pm 95% CI) of mule deer neonates as a function of rump fat thickness of adult females in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

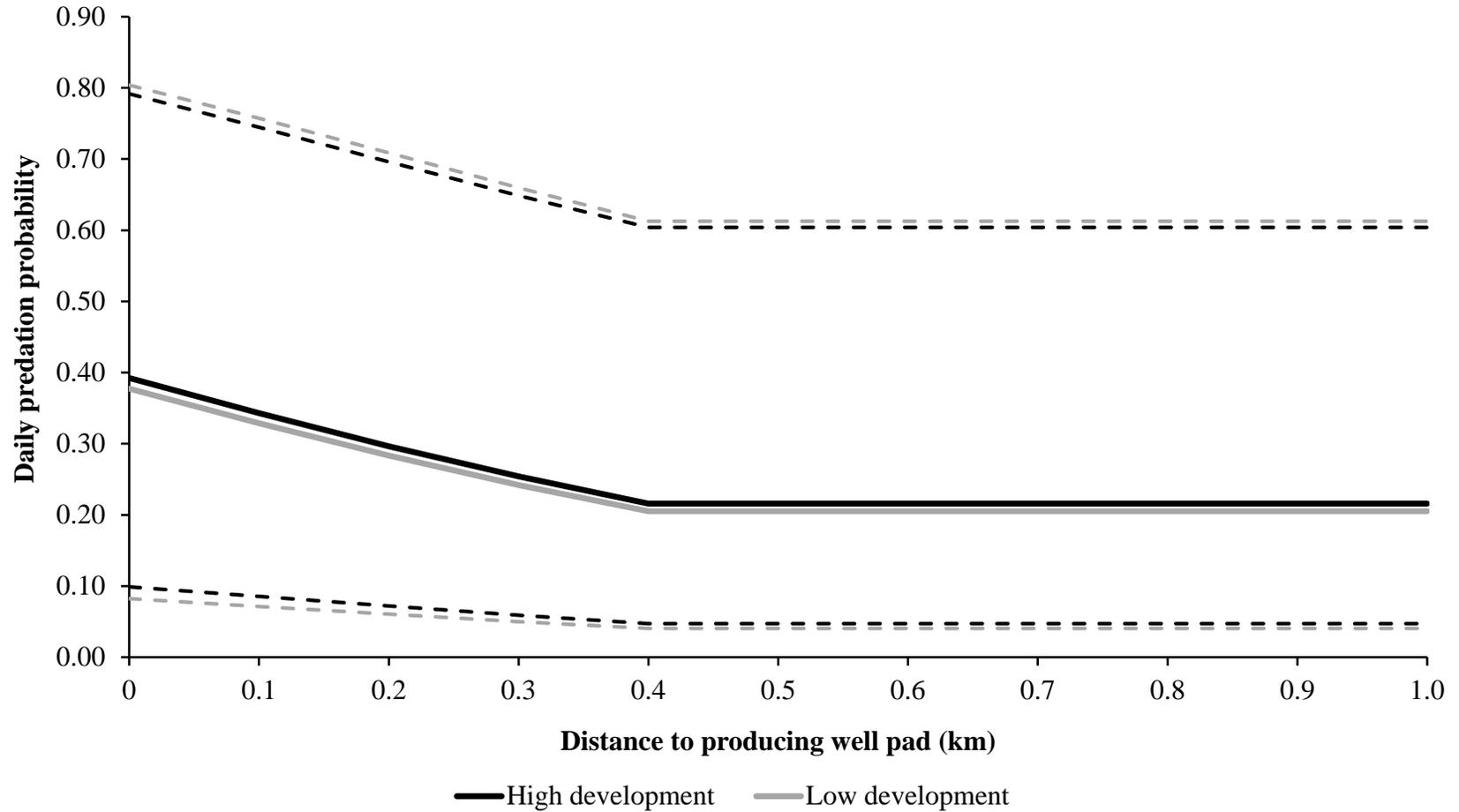


Figure 4.4. Estimated daily predation probability (\pm 95% CI) of mule deer neonates as a function of distance an adult female’s core area was from a producing well pad on winter range in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

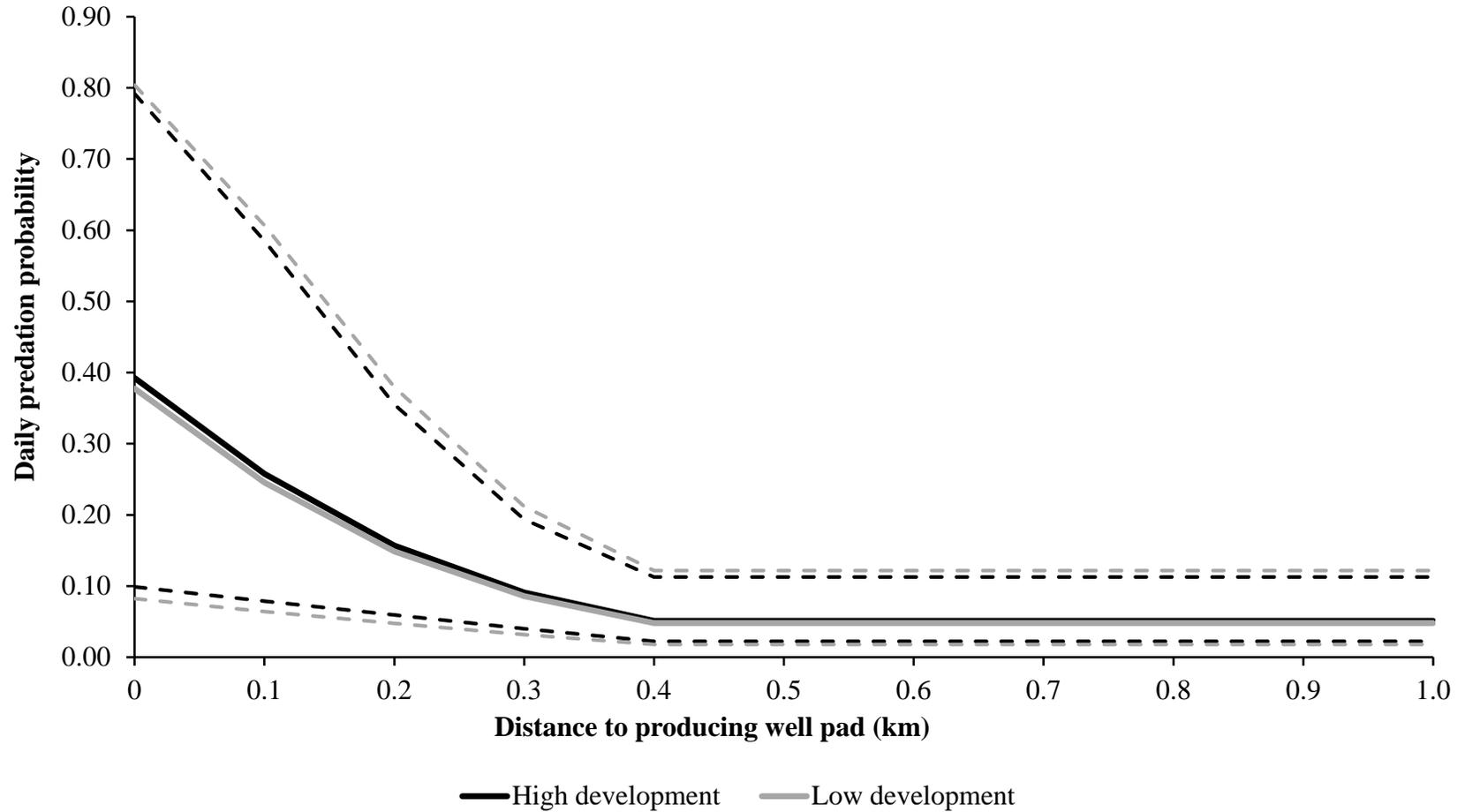


Figure 4.5. Estimated daily predation probability (\pm 95% CI) of mule deer neonates as a function of distance an adult female’s core area was from a producing well pad on summer range in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

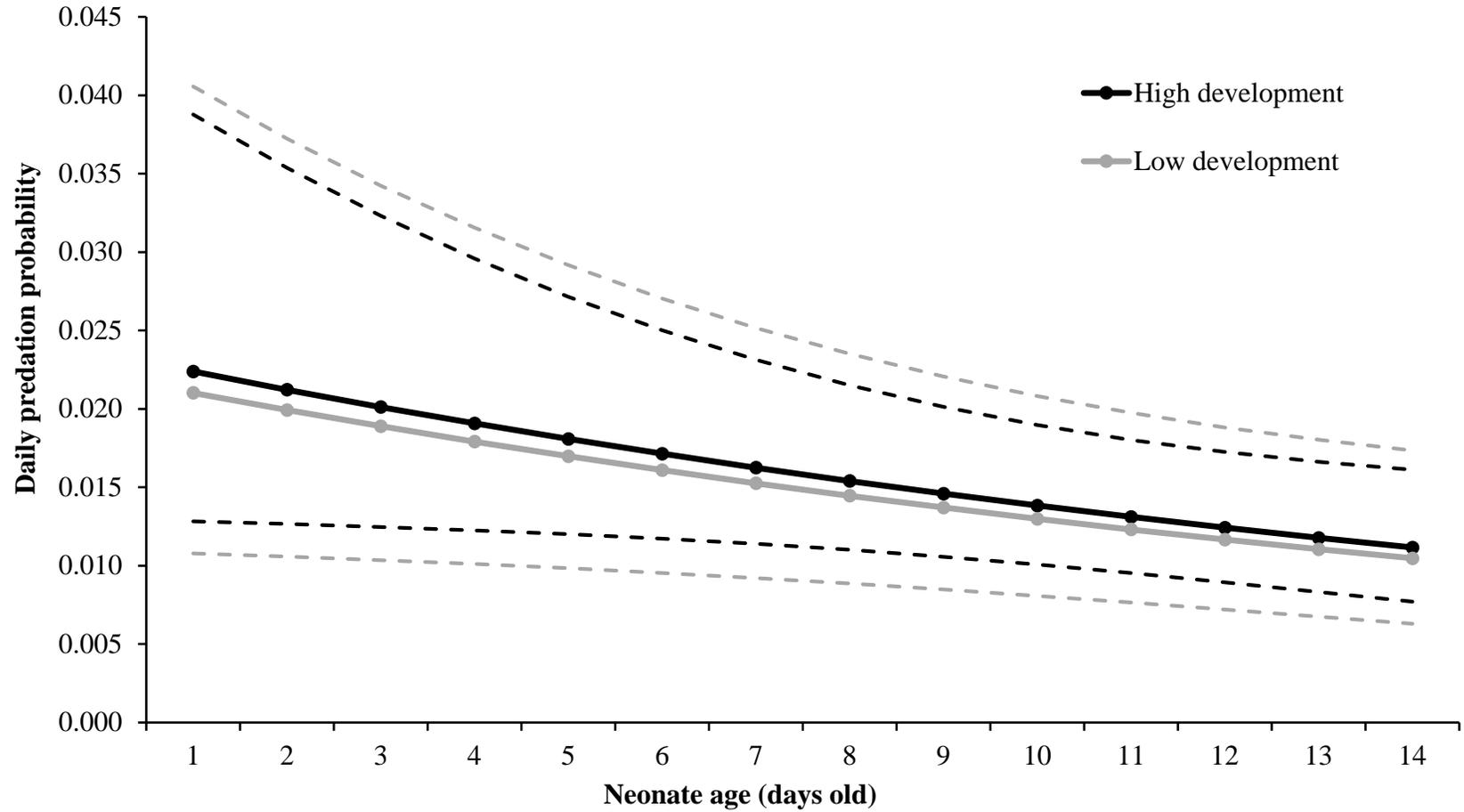


Figure 4.6. Estimated daily predation probability (\pm 95% CI) of mule deer neonates from 0–14 days old in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

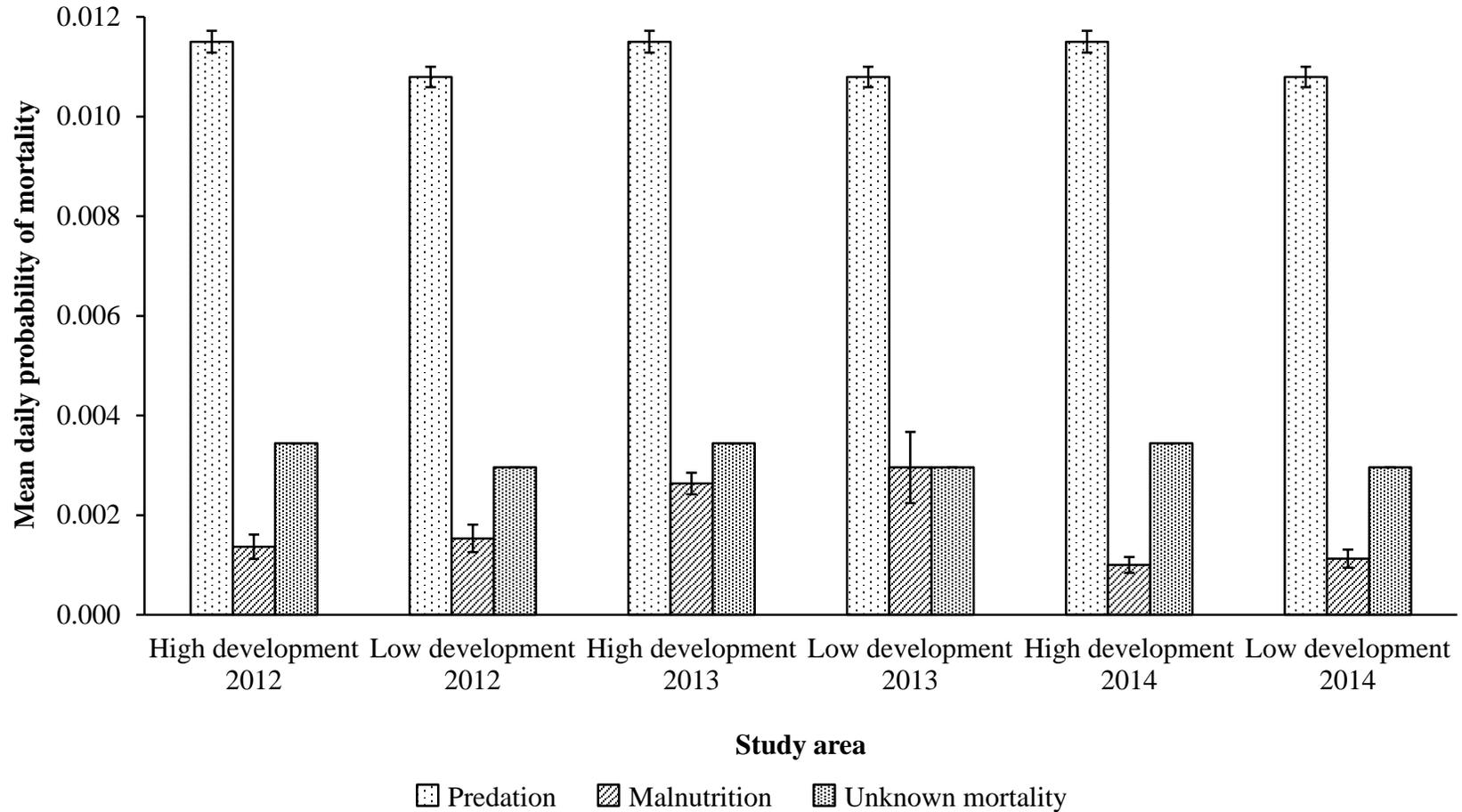
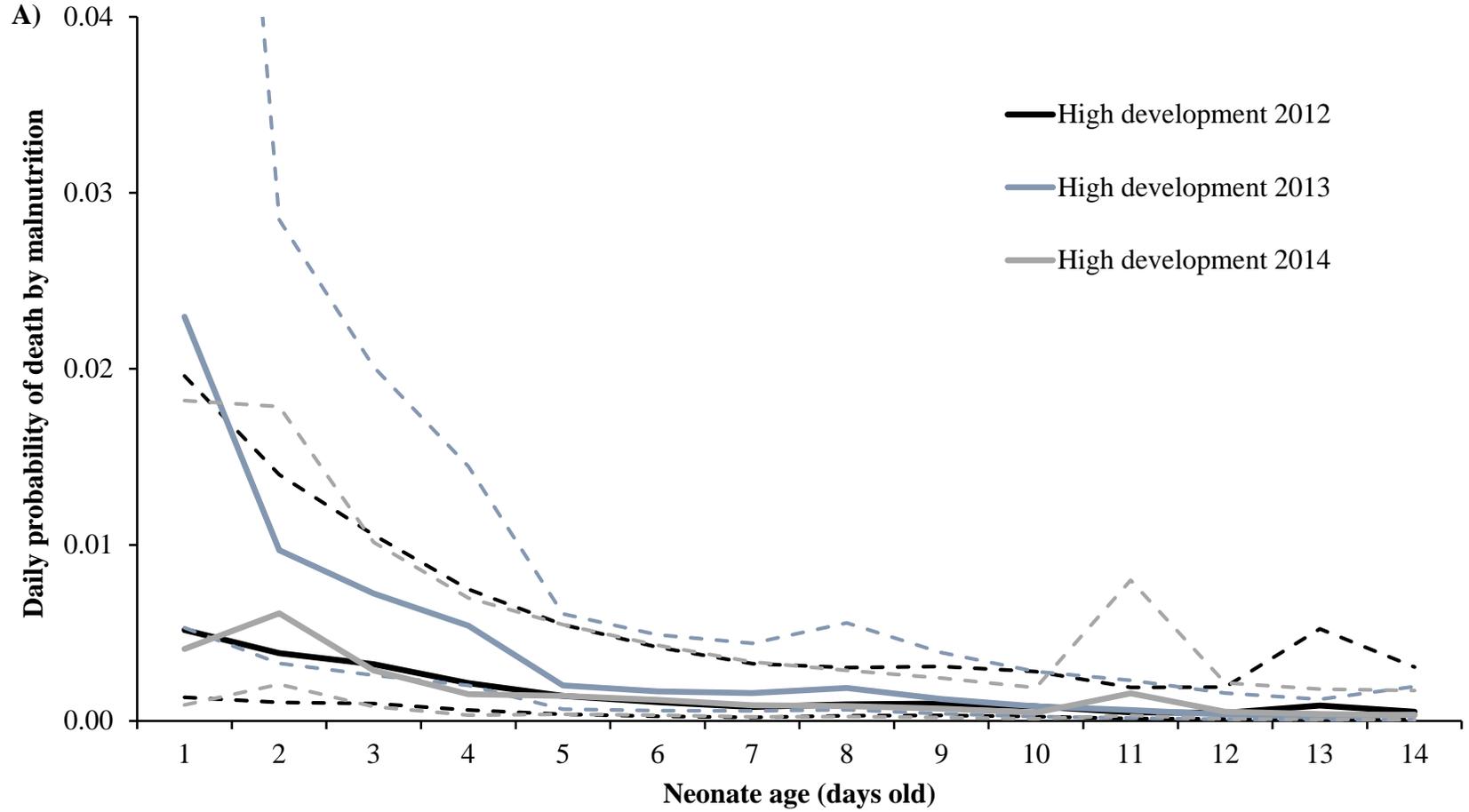


Figure 4.7. Mean daily probability of death by predation, malnutrition, or unknown mortality (\pm 95% CI) of mule deer neonates from 0–6 months old in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.



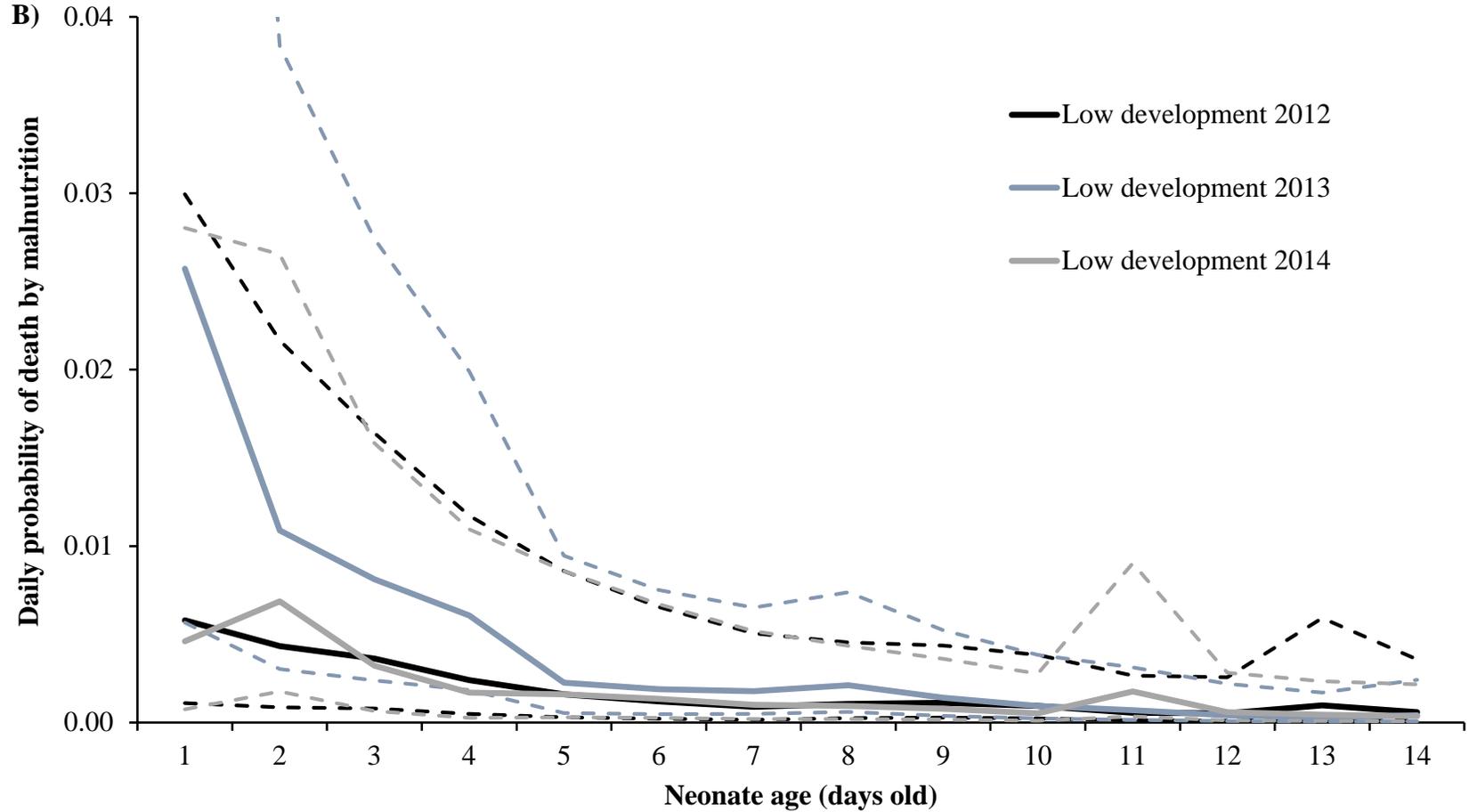


Figure 4.8. Estimated daily probability of death by malnutrition (\pm 95% CI) of mule deer neonates from 0–14 days old in the high (A) and low (B) development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

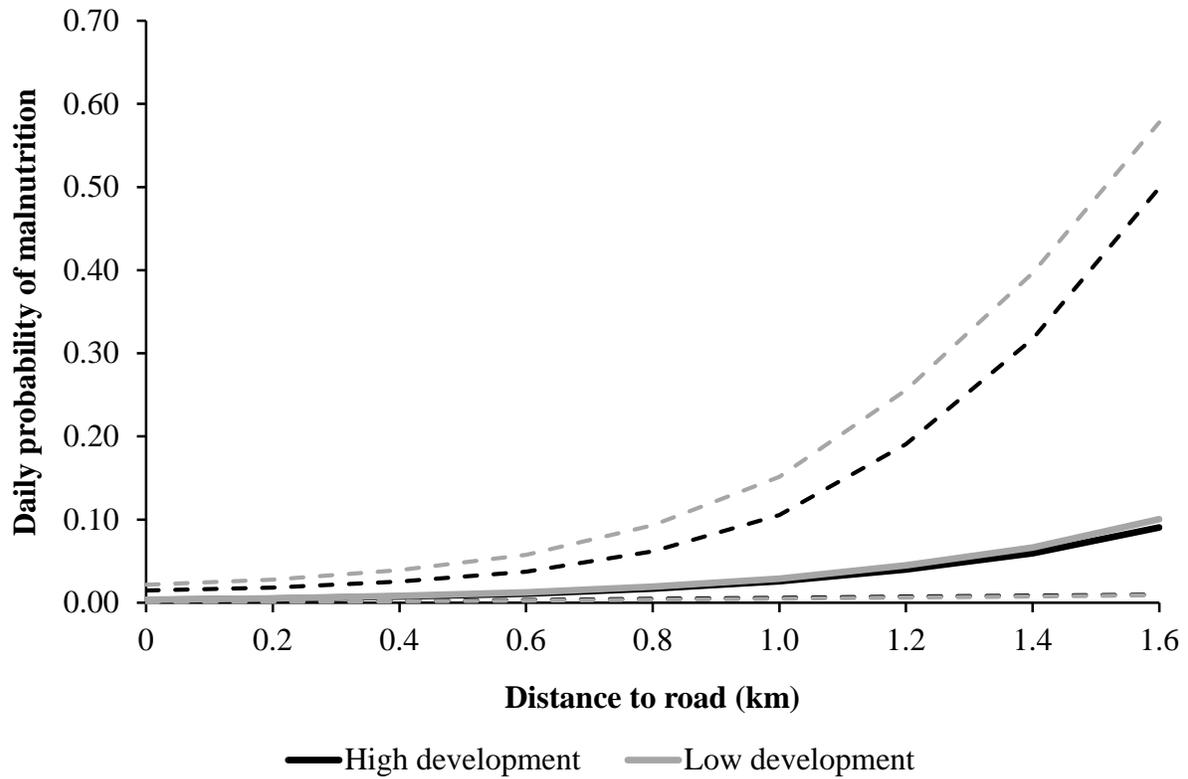


Figure 4.9. Estimated daily probability of death by malnutrition (\pm 95% CI) of neonatal mule deer as a function of distance an adult female’s core area was from a road on winter range in the high and low development study areas. Data obtained from the Piceance Basin in northwestern Colorado, USA, 2012–2014.

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APPENDIX 1.1:

MULE DEER LIFE HISTORY

RANGE

Mule deer are ungulates belonging to the family Cervidae and are distributed across much of western North America ranging from the coastal islands of southern Alaska, down the Pacific Coast of California to southern Baja Mexico and from the extreme northern portion of the Mexican state of San Luis Potosí (Cowan 1956), northward through the Great Plains to the Canadian provinces of Saskatchewan, Alberta, British Columbia, the southern Yukon Territory (Wallmo 1981) and the island of Kauai, Hawaii (Telfer 1988). Due to the species' range, mule deer occupy a diversity of biomes and associated vegetation regimes including boreal forest, chaparral, desert, grassland, and temperate deciduous forest. Mule deer can be considered habitat generalists due to the variety of adaptations they have to persist in many diverse ecosystems.

DIGESTIVE SYSTEM

Mule deer are ruminants possessing a digestive system including four major chambers. The rumen is the first and largest followed by the reticulum, omasum, and abomasum. As compared to elk (Short et al. 1965), mule deer require highly digestible forage due to low rumen to body size ratio, small intestinal length, low small intestine to large intestine ratio, and higher metabolic rate. In addition, food is often retained in the rumen of mule deer for less than 1 day (Short 1981). Deer are classified as opportunistic concentrate selectors meaning they can precisely select forage high in energy and containing low levels of cellulose (Hofmann 1985). During late

spring, summer, and autumn, rapid rates of food consumption and passage of easily digestible foods through the gastrointestinal tract produce abundant assimilable nutrients in contrast with diminished levels in late autumn and winter (Short 1981).

FORAGE AND HABITAT REQUIREMENTS

Nutritious vegetation is an important component of a deer's daily quest for survival to meet dietary requirements. Mule deer mainly forage on new woody growth of various shrubs (e.g., antelope bitterbrush (*Purshia tridentata* Pursh.), alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), rubber rabbitbrush (*Ericameria nauseosa* Pall ex. Pursh.), forbs, berries, and a few grasses (Wallmo et al. 1977, Wallmo 1981). Quaking aspen (*Populus tremuloides* Michx.) stands provide highly preferred nutritious forage during the summer (Lutz et al. 2003). Food preferences vary with season, forage quality, and availability.

In addition to food, vegetation plays other important roles for deer including cover and habitat. Brushy areas, edge habitat, and tree thickets are important for escape cover. Vegetation cover is critical for thermal regulation in winter and summer such that deer use south-facing slopes more in cold weather and north-facing slopes more in hot weather. Aspen stands provide important thermoregulatory hiding cover and critical parturition habitat (Lutz et al. 2003). Overall, vegetation provides deer forage, cover, and habitat to promote survival.

REPRODUCTION

Mule deer breeding season (i.e., the rut) occurs in late autumn, and peaks from mid to late November, when males compete to establish dominance for the right to breed with females. Mule deer are polygynous with a tending-bond system characterized by males generally mating with several females (Geist 1981). Males search for a female near estrous and once he is

accepted by a female he tends her while fending off other males or until he is displaced by a rival. When a female enters estrous, breeding usually occurs by the dominant male, but he needs to be accepted by the female. Females seek out dominant males possibly to avoid constant harassment from subordinate males (Heffelfinger 2006). Timing and synchrony of the rut may be an adaptation to long-term climatic patterns that help ensure females have adequate nutrition during late gestation and parturition and that neonates are born at an optimal time of year (Bowyer 1991). Birth during the optimal time of year should be favored due to investment of time and energy during and following gestation.

Neonates are generally born in June after a mean gestation period of 200–208 days (Anderson 1981) and males are not involved in raising or caring for offspring. Yearling females usually produce a single neonate, whereas adult females generally produce twins and rarely triplets (Robinette et al. 1973). Neonates are altricial, requiring nourishment within the first hour of birth. Mean birth mass for wild deer is 3.27–3.70 kg (Robinette and Olsen 1944, Robinette et al. 1977). Fawning occurs in moderately dense shrublands and forests, dense herbaceous stands, and high-elevation riparian and mountain shrub habitats, with available water and abundant forage (Wallmo 1981). After birth, females groom the neonate(s) and rid the birth site of scent by consuming the placenta, feces, and urine (Geist 1981). Neonates are born nearly odorless and with white spots that act as camouflage, which will disappear after ~3 months.

Neonate survival depends on their ability to stay hidden from predators in protective cover for their first 4–6 weeks of life (Geist 1981, Ozoga et al. 1982). Predation is highest during the first 4–6 weeks because neonate mobility and strength is limited. Predators seem to locate newborn deer birth areas and develop a search image to locate neonates when available (Whittaker and Lindzey 1999, Testa 2002). Females generally forage or rest in the vicinity of

neonates (≤ 500 m) and only visit the neonate for nursing 3 or 4 times a day to minimize the chance of predation (Geist 1981). Dams with marginal quality forage may produce milk high in fats, but low in protein, which negatively affects growth of neonates (Wallmo 1981). The stomach of fawns less than 5 weeks old contains an esophageal groove, which causes the stomach to function as monogastric, consisting of the abomasum, an efficient organ for utilizing milk (Short 1981). Over the next 11 weeks, the digestive system develops into a highly specialized, four-compartment ruminant stomach with the same relative volume, functions, and appearance of adult deer (Short 1981). Weaning begins at about 5 weeks of age and usually is completed by 16 weeks (Short 1981).

MIGRATION

Mule deer can be year-round residents of an area if resources are abundant. However, deer usually migrate to high elevation summer ranges, consisting of montane forests, wet meadows, riparian areas, or aspen stands, to take advantage of seasonally abundant woody stems and forbs and return to low elevation ranges in winter when snow starts to accumulate and temperatures decrease (Nicholson et al. 1997, Rittenhouse et al. 2015). Migration may also be influenced by increasing photoperiod in the spring and decreasing photoperiod in autumn or winter (Nicholson et al. 1997) and vegetation changes (Garrott et al. 1987, Lendrum et al. 2014). Predation may be elevated during migration, but the benefits (e.g., better access to forage and avoidance of starvation) of migration are thought to outweigh predation risk (Nicholson et al. 1997).

Females contend with varying body condition depending on the time of the year and forage availability by migrating. Adult females are usually in their poorest condition when migrating from winter range to summer range. Winter range consists of shrub-dominated habitats with lower quality forage when compared to summer range. Females generally benefit from

spring green up and high forage quality during the time of their poorest condition while on summer range compared to winter range. Therefore, females are in their best condition when migrating from summer range to winter range. However, females must contend with the nutritional demands associated with producing and nursing neonates during their third trimester of gestation and especially during lactation while on summer range (Robbins and Robbins 1979, Pekins et al. 1998). Furthermore, in preparation for facing the rigors of winter conditions (Parker et al. 1984, Parker et al. 1999), females need to build fat reserves to enhance survival (Torbit et al. 1985).



Figure A1.1. Range map of mule deer (from Mackie et al. 2003).

APPENDIX 1.2:

NUMBER OF ADULT FEMALES EXCLUDED FROM IN UTERO FETAL RATE AND FETAL SURVIVAL RATE ANALYSES

Appendix 1.2. Number of adult females excluded from in utero fetal rate and fetal survival rate analyses in the Piceance Basin, northwest Colorado, USA, 2012–2014.

Reason	Number of females excluded
Not pregnant	17
Inaccurate fetal count	3
Denied permission to access private property	50
Myopathy	15
Mortality before birth	20
VIT malfunctioned	35
Inaccessible land	2
Could not locate following spring migration	2

APPENDIX 3.1:

LAND COVER CLASSIFICATION AND RECLASSIFIED LAND COVER CATEGORIES

Appendix 3.1. Colorado Vegetation Classification Project (CVCP) land cover classification and reclassified land cover categories.

CVCP code	Reclassified code	Class name	Description
0	0	Null	No value
1	4	Urban/Built Up	High density commercial or high density residential areas.
11	4	Residential	High density residential areas, lawns, planted trees.
12	4	Commercial	High density urban areas, parking lots, buildings, etc.
2	4	Agriculture Land	Row crops, irrigated pasture, dry farm crops.
21	4	Dryland Ag	Dryland crops and fields.
22	4	Irrigated Ag	Irrigated crops and fields.
23	4	Orchard	Cropland consisting of orchards.
31	4	Grass/Forb Rangeland	Perennial and annual grasslands and/or mixed forbs.
3101	2	Snakeweed/Shrub Mix	Shrubland codominated by snakeweed and mixed shrubs.
3102	4	Grass Dominated	Rangeland dominated by annual and perennial grasses.
3103	4	Forb Dominated	Rangeland dominated by forbs.
3104	4	Grass/Forb Mix	Rangeland codominated by grasses and forbs.
3109	4	Foothill and Mountain Grasses	Species include Parry's oatgrass, Arizona fescue, Idaho fescue, Thurber's fescue, slimstem muhly, mountain muhly, bluebunch wheatgrass, heartleaf twistflower, and prairie Junegrass.
3110	4	Disturbed Rangeland	Disturbed or overgrazed rangeland.

3111	4	Sparse Grass (Blowouts)	Sparsely vegetated grasslands, 10–40% vegetation, indicative of blowouts.
32	2	Shrub/Brush Rangeland	Consists of sagebrush, saltbrush, greasewood, snakeweed, etc.
3201	2	Sagebrush Community	Sagebrush with rabbitbrush and bitterbrush.
3202	2	Saltbush Community	Saltbrush on alkaline soils associated with snakeweed, sagebrush.
3203	2	Greasewood	Low elevation shrubland dominated by greasewood.
3204	1	Sagebrush/Gambel Oak Mix	Shrubland codominated by big sagebrush and Gambel oak.
3206	1	Snowberry	Deciduous shrubland dominated by mountain snowberry.
3207	1	Snowberry/Shrub Mix	Deciduous shrubland codominated by mountain snowberry and mixed shrubs.
3208	2	Bitterbrush Community	Shrubland dominated by bitterbrush.
3209	2	Salt Desert Shrub Community	Low-elevation shrublands found on alluvial salt fans or flats.
3210	2	Sagebrush/Greasewood	Shrubland codominated by sagebrush and greasewood, with some rabbitbrush.
33	4	Shrub/Grass/Forb Mix	Mixed grass/forb and shrub/grass rangeland.
3301	2	Sagebrush/Grass Mix	Codominant sagebrush shrubland and perennial grassland.
3302	2	Rabbitbrush/Grass Mix	Codominant rabbitbrush and perennial grassland.
3303	2	Sagebrush/Mesic Mtn Shrub Mix	Codominant sagebrush/mesic mountain shrub mixed with grass/forb.
3306	2	Bitterbrush/Grass Mix	Codominant bitterbrush shrubland and perennial grassland.
3308	2	Sagebrush/Rabbitbrush Mix	Codominant shrubland of sagebrush and rabbitbrush.
4101	1	Pinon-Juniper	Pinon-Juniper woodland with mixed understory.
4102	1	Juniper	Woodland principally dominated by Utah juniper and/or Rocky Mountain juniper.
4201	1	Gambel Oak	Deciduous woodland dominated by Gambel oak.
4202	1	Xeric Mountain Shrub Mix	Deciduous woodland dominated by mountain mahogany.
4203	1	Mesic Mountain Shrub Mix	Oak dominant with sagebrush, snowberry, grass.
4204	1	Serviceberry/Shrub Mix	Deciduous woodland dominated by serviceberry.

4205	1	Upland Willow/Shrub Mix	High elevation shrubland dominated by willow and mixed shrubs.
4206	1	Manzanita	Deciduous shrubland dominated by Manzanita
4301	1	PJ-Oak Mix	Codominant Gambel oak and pinyon/juniper woodland.
4302	1	PJ-Sagebrush Mix	Codominant pinyon-juniper and sagebrush.
4303	1	PJ-Mtn Shrub Mix	Codominant pinyon-juniper and oak, mountain mahogany or other deciduous shrubs.
4304	4	Sparse PJ/Shrub/Rock Mix	< 25% pinyon-juniper with sagebrush and rock.
4305	4	Sparse Juniper/Shrub/Rock Mix	< 25% juniper with sagebrush and rock.
4306	1	Juniper/Sagebrush Mix	Codominant juniper and sagebrush.
4307	1	Juniper/Mtn Shrub Mix	Codominant juniper and oak, mountain mahogany or other deciduous shrubs.
5101	3	Aspen	Deciduous forest dominated by aspen.
5102	3	Aspen/Mesic Mountain Shrub Mix	Codominant aspen and Gambel oak deciduous woodland.
5201	3	Ponderosa Pine	Coniferous forest dominated by ponderosa pine.
5202	3	Engelmann Spruce/Fir Mix	Coniferous forest codominated by Engelmann spruce and subalpine fir.
5203	3	Douglas Fir	Coniferous forest dominated by Douglas fir.
5204	3	Lodgepole Pine	Coniferous forest dominated by lodgepole pine.
5205	3	Sub-Alpine Fir	Coniferous forest dominated by sub-alpine fir.
5206	3	Spruce/Fir Regeneration	Harvested PIEN/ABLA sites, in regeneration.
5207	3	Spruce/Lodgepole Pine Mix	Coniferous forest codominated by lodgepole pine and spruce.
5211	3	Limber Pine	Coniferous forest dominated by limber pine.
5213	3	Lodgepole/Spruce/Fir Mix	Coniferous forest co-dominated by lodgepole pine, Engelmann spruce, and white fir.
5214	3	Fir/Lodgepole Pine Mix	Coniferous forest codominated by sub-alpine fir and lodgepole pine.
5215	3	Douglas Fir/Engelmann Spruce Mix	Coniferous forest co-dominated by Douglas fir and Engelmann spruce.

53	3	Mixed Forest Land	Forests of spruce/fir, pine/oak, fir/aspens or pine/aspens mix.
5301	3	Spruce/Fir/Aspens Mix	Mixed forest codominated by Engelmann spruce, sub-alpine fir, and aspens.
5304	3	Douglas Fir/Aspens Mix	Mixed forest codominated by Douglas fir and aspens.
5306	3	Lodgepole Pine/Aspens Mix	Mixed forest codominated by aspens and lodgepole pine.
5307	3	Spruce/Fir/Lodgepole/Aspens Mix	Mixed coniferous/deciduous forest codominated with Engelmann spruce, white fir, lodgepole pine, and aspens.
6	4	Barren Land	< 10% vegetation.
61	4	Rock	< 10% vegetation, rock outcrops, red sandstones, etc.
6101	4	Talus Slopes & Rock Outcrops	Talus and scree slopes, nearly 100% rock.
62	4	Soil	Bare soil and fallow agriculture fields.
6201	4	Disturbed Soil	Areas where human activities have created bare ground, i.e. mine tailings.
71	2	Alpine Meadow	> 11,500' tundra vegetation including grasses, forbs, sedges.
7101	2	Alpine Forb Dominated	> 11,500' meadow dominated by alpine forbs.
7102	2	Alpine Grass Dominated	> 11,500' meadow dominated by alpine grasses.
7103	2	Alpine Grass/Forb Mix	> 11,500' mixed meadow codominated by alpine grasses and forbs.
72	2	SubAlpine Shrub Community	7,000' to 11,500' tundra shrubs.
74	4	Subalpine Meadow	Herbaceous vegetation below timberline (9,000–11,500).
7401	4	Subalpine Grass/Forb Mix	High elevation meadows co-dominated by grass and forbs (9,000–11,500).
8	4	Riparian	Cottonwood, willow, sedges along waterways.
81	4	Forested Riparian	Wooded riparian areas consisting primarily of poplars.
8101	4	Cottonwood	Wooded riparian areas dominated by cottonwood.
8103	4	Conifer Riparian	Wooded riparian areas in mid-upper elevations with mixed coniferous species.
82	4	Shrub Riparian	Shrub riparian areas consisting primarily of shrub willows.
8201	4	Willow	Shrub riparian areas dominated by shrub willow species.

8202	4	Exotic Riparian Shrubs	Shrub Riparian area dominated by salt cedar and Russian olive.
83	4	Herbaceous Riparian	Non-woody riparian areas consisting primarily of sedges.
8301	4	Sedge	Herbaceous riparian areas dominated by sedges.
9	5	Water	Lakes, reservoirs, rivers, streams.

APPENDIX 4.1:

**MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE INFLUENCE OF WINTER RANGE
DEVELOPMENT CHARACTERISTICS ON DAILY NEONATAL MULE DEER MORTALITY**

Appendix 4.1. Multi-state mark-recapture model selection results for stage one analysis evaluating the influence of winter range development characteristics on daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Detection probabilities were held constant for all these models (not shown). Only models with an AICc weight ≥ 0.010 are shown.

Model^a	AICc^b	ΔAICc	AICc weight	K^c
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.rd) ψ^U (study area)	3501.472	0.000	0.095	10
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd) ψ^U (study area)	3501.714	0.242	0.084	9
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area)	3501.810	0.338	0.080	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area)	3502.009	0.537	0.072	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km)	3502.898	1.426	0.046	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km)	3503.148	1.676	0.041	10

ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km)	3503.190	1.718	0.040	12
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km) ψ^U (study area)	3503.439	1.967	0.035	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.rd)	3503.443	1.971	0.035	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km)	3503.449	1.977	0.035	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.rd)	3503.676	2.204	0.031	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.rd)	3503.729	2.257	0.031	12
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km) ψ^U (study area)	3503.783	2.311	0.030	9
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area) ψ^U (study area)	3503.802	2.330	0.029	9
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.rd)	3503.971	2.499	0.027	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area)	3504.113	2.641	0.025	8
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km) ψ^U (study area+WR dist.prod 0–0.4 km)	3504.868	3.396	0.017	11
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km+WR dist.rd)	3504.906	3.434	0.017	12
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km+WR dist.rd)	3505.152	3.680	0.015	11

ψ^K (study area+WR dist.prod 0–0.4 km) v (study area+WR dist.prod 0–0.4 km) ψ^U (study area+WR dist.prod 0–0.4 km)	3505.194	3.722	0.015	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km+WR dist.rd)	3505.211	3.739	0.015	13
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area) ψ^U (study area+WR dist.prod 0–0.4 km)	3505.228	3.756	0.014	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area+WR dist.prod 0–0.4 km) ψ^U (study area+WR dist.rd)	3505.400	3.928	0.013	11
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^U (study area+WR dist.prod 0–0.4 km+WR dist.rd)	3505.454	3.982	0.013	12
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area+WR dist.prod 0–0.4 km)	3505.545	4.073	0.012	9
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area+WR dist.prod 0–0.4 km) ψ^U (study area+WR dist.rd)	3505.710	4.238	0.011	10
ψ^K (study area+WR dist.prod 0–0.4 km+WR dist.rd) ψ^M (study area) ψ^U (study area+WR dist.rd)	3505.769	4.297	0.011	10
ψ^K (study area) ψ^M (study area+WR dist.rd) ψ^U (study area)	3505.884	4.412	0.010	8
ψ^K (study area+WR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area+WR dist.rd)	3506.069	4.597	0.009	9

^a Covariates are defined as in Table 4.1.

^b Akaike's Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.2:

**MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE INFLUENCE OF SUMMER RANGE
DEVELOPMENT CHARACTERISTICS ON DAILY NEONATAL MULE DEER MORTALITY**

Appendix 4.2. Multi-state mark-recapture model selection results for stage one analysis evaluating the influence of summer range development characteristics on daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Detection probabilities were held constant for all these models (not shown).

Model^a	AICc^b	ΔAICc	AICc weight	K^c
ψ^K (study area+SR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area)	3502.506	0.000	0.432	8
ψ^K (study area+SR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area+SR dist.prod 0–0.4 km)	3503.737	1.231	0.233	9
ψ^K (study area+SR dist.prod 0–0.4 km) ψ^M (study area+SR dist.prod 0–0.4 km) ψ^U (study area)	3504.176	1.670	0.187	9
ψ^K (study area+SR dist.prod 0–0.4 km) ψ^M (study area+SR dist.prod 0–0.4 km) ψ^U (study area+SR dist.prod 0–0.4 km)	3505.549	3.043	0.094	10
ψ^K (study area) ψ^M (study area) ψ^U (study area)	3508.257	5.751	0.024	7
ψ^K (study area) ψ^M (study area) ψ^U (study area+SR dist.prod 0–0.4 km)	3509.527	7.021	0.013	8
ψ^K (study area) ψ^M (study area+SR dist.prod 0–0.4 km) ψ^U (study area)	3509.935	7.429	0.011	8

ψ^K (study area)	ψ^M (study area+SR dist.prod 0–0.4 km)	ψ^U (study area+SR dist.prod 0–0.4 km)	3511.139	8.633	0.006	9
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^a Covariates are defined as in Table 4.1.

^b Akaike’s Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.3:

MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE INFLUENCE OF ADULT FEMALE CHARACTERISTICS ON DAILY NEONATAL MULE DEER MORTALITY

Appendix 4.3. Multi-state mark-recapture model selection results for stage one analysis evaluating the influence of adult female characteristics on daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study area to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Detection probabilities were held constant for all these models (not shown). Only models with an AICc weight ≥ 0.010 are shown.

Model^a	AICc^b	ΔAICc	AICc weight	K^c
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area)	3500.231	0.000	0.056	8
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area+female age)	3500.684	0.453	0.045	9
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area)	3500.871	0.640	0.041	9
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area+female age)	3501.331	1.099	0.032	10
ψ^K (study area+rump fat) ψ^M (study area+rump fat) ψ^U (study area)	3501.794	1.562	0.026	9
ψ^K (study area+rump fat+female age) ψ^M (study area) ψ^U (study area)	3502.088	1.856	0.022	9
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area+fetal count)	3502.130	1.899	0.022	9
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area+rump fat)	3502.148	1.916	0.021	9
ψ^K (study area+rump fat) ψ^M (study area+female age) ψ^U (study area)	3502.227	1.996	0.021	9
ψ^K (study area+rump fat+fetal count) ψ^M (study area) ψ^U (study area)	3502.232	2.000	0.021	9

ψ^K (study area+rump fat) ψ^M (study area+rump fat) ψ^U (study area+female age)	3502.249	2.017	0.020	10
ψ^K (study area+rump fat) ψ^M (study area+rump fat+fetal count) ψ^U (study area)	3502.345	2.114	0.019	10
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area+rump fat+female age)	3502.525	2.294	0.018	10
ψ^K (study area+rump fat+female age) ψ^M (study area) ψ^U (study area+female age)	3502.557	2.325	0.017	10
ψ^K (study area+rump fat) ψ^M (study area) ψ^U (study area+fetal count+female age)	3502.622	2.390	0.017	10
ψ^K (study area+rump fat) ψ^M (study area+female age) ψ^U (study area+female age)	3502.679	2.448	0.016	10
ψ^K (study area+rump fat+fetal count) ψ^M (study area) ψ^U (study area+female age)	3502.687	2.456	0.016	10
ψ^K (study area+rump fat+female age) ψ^M (study area+fetal count) ψ^U (study area)	3502.732	2.501	0.016	10
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area+fetal count)	3502.762	2.531	0.016	10
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area+rump fat)	3502.789	2.558	0.016	10
ψ^K (study area+rump fat) ψ^M (study area+rump fat+fetal count) ψ^U (study area+female age)	3502.808	2.576	0.015	11
ψ^K (study area+rump fat+fetal count) ψ^M (study area+fetal count) ψ^U (study area)	3502.876	2.645	0.015	10
ψ^K (study area+rump fat) ψ^M (study area+fetal count+female age) ψ^U (study area)	3502.880	2.648	0.015	10
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area+rump fat+female age)	3503.174	2.942	0.013	11
ψ^K (study area+rump fat+female age) ψ^M (study area+fetal count) ψ^U (study area+female age)	3503.208	2.977	0.013	11
ψ^K (study area+rump fat) ψ^M (study area+fetal count) ψ^U (study area+fetal count+female age)	3503.262	3.030	0.012	11
ψ^K (study area+rump fat+fetal count) ψ^M (study area+fetal count) ψ^U (study area+female age)	3503.338	3.107	0.012	11

ψ^K (study area+rump fat) ψ^M (study area+fetal count+female age) ψ^U (study area+female age)	3503.341	3.109	0.012	11
ψ^K (study area+rump fat+female age) ψ^M (study area+rump fat) ψ^U (study area)	3503.652	3.421	0.010	10

^a Covariates are defined as in Table 4.1.

^b Akaike's Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.4:

MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE INFLUENCE OF NEONATE CHARACTERISTICS ON DAILY NEONATAL MULE DEER MORTALITY

Appendix 4.4. Multi-state mark-recapture model selection results for stage one analysis evaluating the influence of neonate characteristics on daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Detection probabilities were held constant for all these models (not shown). Only models with an AICc weight ≥ 0.010 are shown.

Model^a	AICc^b	ΔAICc	AICc weight	K^c
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old)	3488.684	0.000	0.137	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area)	3489.012	0.327	0.116	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+DOB)	3489.587	0.903	0.087	10
ψ^K (study area+neonate age 0–14 days old+mass) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	3490.763	2.079	0.048	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+mass)	3490.903	2.219	0.045	10

ψ^K (study area) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old+DOB)	3490.928	2.244	0.044	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+sex)	3491.028	2.343	0.042	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	3491.257	2.573	0.038	9
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old+sex) ψ^U (study area)	3491.420	2.735	0.035	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area+neonate age 0–14 days old)	3491.496	2.811	0.033	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area+DOB)	3492.323	3.639	0.022	10
ψ^K (study area+neonate age 0–14 days old+DOB) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	3492.684	4.000	0.018	10
ψ^K (study area+mass) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old)	3492.752	4.068	0.018	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old+mass)	3492.971	4.287	0.016	10
ψ^K (study area+mass) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area)	3492.986	4.302	0.016	10
ψ^K (study area+neonate age 0–14 days old+sex) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	3493.134	4.450	0.015	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass+sex) ψ^U (study area)	3493.209	4.525	0.014	10
ψ^K (study area+neonate age 0–14 days old) ψ^M (study area+neonate age 0–14 days old+DOB) ψ^U (study area)	3493.247	4.563	0.014	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old+sex)	3493.521	4.837	0.012	10

ψ^K (study area+mass) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+DOB)	3493.606	4.922	0.012	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area+sex)	3493.607	4.923	0.012	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area+mass)	3493.647	4.963	0.011	10
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area+neonate age 0–14 days old)	3493.706	5.022	0.011	9
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+mass) ψ^U (study area)	3493.866	5.182	0.010	9
ψ^K (study area) ψ^M (study area+neonate age 0–14 days old+sex) ψ^U (study area+neonate age 0–14 days old)	3493.869	5.185	0.010	10

^a Covariates are defined as in Table 4.1.

^b Akaike's Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.5:

MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE INFLUENCE OF TEMPORAL CHARACTERISTICS ON DAILY NEONATAL MULE DEER MORTALITY

Appendix 4.5. Multi-state mark-recapture model selection results for stage one analysis evaluating the influence of temporal characteristics on daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. Detection probabilities were held constant for all these models (not shown). Only models with an AICc weight ≥ 0.010 are shown.

Model^a	AICc^b	ΔAICc	AICc weight	K^c
ψ^K (study area+prev.precip+temp) ψ^M (study area+temp) ψ^U (study area)	3495.797	0.000	0.073	10
ψ^K (study area+prev.precip+precip+temp) ψ^M (study area+temp) ψ^U (study area)	3496.163	0.366	0.061	11
ψ^K (study area+prev.precip+temp) ψ^M (study area+temp) ψ^U (study area+temp)	3496.467	0.670	0.052	11
ψ^K (study area+temp) ψ^M (study area+temp) ψ^U (study area)	3497.135	1.339	0.037	9
ψ^K (study area+prev.precip+temp) ψ^M (study area+prev.precip+temp) ψ^U (study area)	3497.137	1.341	0.037	11
ψ^K (study area+prev.precip+temp) ψ^M (study area+precip+temp) ψ^U (study area)	3497.374	1.578	0.033	11
ψ^K (study area+prev.precip+temp) ψ^M (study area+temp) ψ^U (study area+precip)	3497.593	1.796	0.030	11
ψ^K (study area+prev.precip+temp) ψ^M (study area+temp) ψ^U (study area+prev.precip)	3497.802	2.005	0.027	11
ψ^K (study area+temp) ψ^M (study area+temp) v (study area+temp)	3497.807	2.011	0.027	10

ψ^K (study area+prev.precip+precip) ψ^M (study area+temp) ψ^U (study area)	3497.904	2.107	0.025	10
ψ^K (study area+precip+temp) ψ^M (study area+temp) ψ^U (study area)	3498.276	2.479	0.021	10
ψ^K (study area+temp) ψ^M (study area+prev.precip+temp) ψ^U (study area)	3498.386	2.590	0.020	10
ψ^K (study area+prev.precip) ψ^M (study area+temp) ψ^U (study area)	3498.596	2.799	0.018	9
ψ^K (study area+prev.precip+precip) ψ^M (study area+temp) ψ^U (study area+temp)	3498.665	2.868	0.017	11
ψ^K (study area+temp) ψ^M (study area+precip+temp) ψ^U (study area)	3498.723	2.926	0.017	10
ψ^K (study area) ψ^M (study area+temp) ψ^U (study area)	3498.877	3.081	0.016	8
ψ^K (study area+precip+temp) ψ^M (study area+temp) ψ^U (study area+temp)	3498.947	3.150	0.015	11
ψ^K (study area+temp) ψ^M (study area+temp) ψ^U (study area+precip)	3498.950	3.153	0.015	10
ψ^K (study area+temp) ψ^M (study area+prev.precip+temp) ψ^U (study area+temp)	3499.055	3.258	0.014	11
ψ^K (study area+precip) ψ^M (study area+temp) ψ^U (study area)	3499.103	3.306	0.014	9
ψ^K (study area+temp) ψ^M (study area+temp) ψ^U (study area+prev.precip)	3499.130	3.333	0.014	10
ψ^K (study area+prev.precip+precip) ψ^M (study area+prev.precip+temp) ψ^U (study area)	3499.218	3.421	0.013	11
ψ^K (study area+prev.precip) ψ^M (study area+temp) ψ^U (study area+temp)	3499.374	3.577	0.012	10
ψ^K (study area+temp) ψ^M (study area+precip+temp) ψ^U (study area+temp)	3499.394	3.598	0.012	11
ψ^K (study area+prev.precip+precip) ψ^M (study area+precip+temp) ψ^U (study area)	3499.433	3.636	0.012	11
ψ^K (study area+precip+temp) ψ^M (study area+prev.precip+temp) ψ^U (study area)	3499.531	3.734	0.011	11
ψ^K (study area) ψ^M (study area+temp) ψ^U (study area+temp)	3499.647	3.850	0.011	9
ψ^K (study area+prev.precip+precip) ψ^M (study area+temp) ψ^U (study area+precip)	3499.665	3.869	0.011	11
ψ^K (study area+temp) ψ^M (study area+temp) ψ^U (study area+precip+temp)	3499.774	3.977	0.010	11

^a Covariates are defined as in Table 4.1.

^b Akaike's Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.6:

**MODEL SELECTION RESULTS FOR STAGE ONE ANALYSIS EVALUATING THE
DETECTION OF NEONATAL MULE DEER**

Appendix 4.6. Multi-state mark-recapture model selection results for stage one analysis evaluating detection of neonatal mule deer, Piceance Basin in northwestern Colorado, USA, 2012–2014. Transition probabilities were held constant for all these models (not shown).

Model^a	AICc^b	ΔAICc	AICc weight	K^c
<i>p</i> (year*migration)	3078.005	0.000	1.000	12
<i>p</i> (year+migration)	3134.276	56.271	0.000	10
<i>p</i> (migration)	3138.408	60.403	0.000	8
<i>p</i> (.)	3508.257	430.252	0.000	7
<i>p</i> (year)	3509.102	431.098	0.000	9

^a Covariates are defined as in Table 4.1.

^b Akaike’s Information Criterion adjusted for small sample size.

^c K is the number of parameters in the model.

APPENDIX 4.7:

MODEL SELECTION RESULTS FOR STAGE TWO ANALYSIS OF DAILY NEONATAL MULE DEER MORTALITY

Appendix 4.7. Multi-state mark-recapture model selection results for stage two analysis of daily neonatal mule deer mortality, Piceance Basin in northwestern Colorado, USA, 2012–2014. Each model provided a parameter estimate for probability of transitioning from an alive state in the high or low development study areas to a death by predation (ψ^K), malnutrition (ψ^M), or unknown mortality (ψ^U) state. All these models included detection probability as an interaction between year and an autumn migration effect (not shown). Only models with a QAICc weight ≥ 0.010 are shown.

Model^a	QAICc^b	ΔQAICc	QAICc weight	K^c
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2942.363	0.000	0.092	19
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2943.094	0.731	0.064	18
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2943.841	1.477	0.044	18
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2943.940	1.577	0.042	20
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2943.975	1.612	0.041	18

ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area)	2944.068	1.704	0.039	17
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2944.251	1.888	0.036	19
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2944.578	2.214	0.030	17
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2944.647	2.284	0.029	19
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd+temp) ψ^U (study area)	2944.866	2.503	0.026	18
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2944.937	2.574	0.025	18
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2945.094	2.731	0.024	18
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2945.150	2.787	0.023	19
ψ^K (study area+rump fat+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2945.400	3.037	0.020	18
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2945.443	3.080	0.020	17
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area) ψ^U (study area)	2945.544	3.180	0.019	16
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2945.550	3.187	0.019	19

ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area) ψ^U (study area)	2945.621	3.258	0.018	18
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2945.824	3.461	0.016	17
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2945.858	3.494	0.016	18
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2945.859	3.496	0.016	18
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area) ψ^U (study area)	2945.912	3.549	0.016	17
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2945.971	3.608	0.015	18
ψ^K (study area+rump fat+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2946.087	3.723	0.014	17
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area+WR dist.rd+temp) ψ^U (study area)	2946.354	3.991	0.013	17
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km+temp) ψ^M (study area+WR dist.rd+temp) ψ^U (study area)	2946.469	4.106	0.012	19
ψ^K (study area+neonate age 0–14 days old+rump fat+WR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old) ψ^U (study area)	2946.694	4.331	0.011	17
ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2946.703	4.340	0.011	17
ψ^K (study area+rump fat+SR dist.prod 0–0.4 km) ψ^M (study area+neonate age 0–14 days old+WR dist.rd+temp) ψ^U (study area)	2946.731	4.368	0.010	17
ψ^K (study area+neonate age 0–14 days old+rump fat+SR dist.prod 0–0.4 km+temp) ψ^M (study area+neonate age 0–14 days old+temp) ψ^U (study area)	2946.751	4.387	0.010	18

ψ^K (study area+rump fat+WR dist.prod 0–0.4 km+SR dist.prod 0–0.4 km)	ψ^M (study area)	ψ^U (study area)	2946.795	4.432	0.010	16
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^a Covariates are defined as in Table 4.1.

^b Quasi-likelihood using Akaike's Information Criterion adjusted for small sample size and model selection results were based on an estimated \hat{c} of 1.035.

^c K is the number of parameters in the model