POTENTIAL EFFECTS OF OIL AND GAS ENERGY DEVELOPMENT ON MULE DEER IN EASTERN MONTANA

by

Jesse L. Kolar
University of Missouri

Dr. Joshua J. Millspaugh
University of Montana

Chris P. Hansen
University of Montana

Ryan Williamson
Montana Fish, Wildlife & Parks

Melissa Foster
Montana Fish, Wildlife & Parks

Dr. Christopher T. Rota
West Virginia University

Brett P. Skelly
West Virginia University

Justin Gude
Montana Fish, Wildlife & Parks

Dr. Colter Chitwood
University of Montana

Helena, Montana
April
2018

This report fulfills the final requirement of RDGP grant # RIT-14-8768, Impacts of Energy Development and Leasing Stipulations on Mule Deer, to the Montana Department of Fish, Wildlife and Parks. Additional copies if this report can be obtained online at http://fwp.mt.gov/fishAndWildlife/diseasesAndResearch/research/deer/default.html or by contacting Justin Gude at 406-444-3767 or jgude@mt.gov.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

We thank Rod Weeding (pilot) for his assistance with reconnaissance flights before and during captures, and Quicksilver Air Inc. for capturing, radio-collaring, and collecting samples from the mule deer in this study.

The North Dakota Game and Fish veterinary lab assisted with necropsies, and we especially thank Dr. Dan Grove, Hannah Pritchert, Adam Pachl, and John Mortenson for help during necropsies and sample submission.

Several Montana Fish, Wildlife and Parks staff helped in the field, particularly with recovering mortalities promptly after notifications were received. We thank Ryan Karren and Ken Plourde for retrieving carcasses promptly so that laboratory necropsies could be conducted.

We appreciate the help from Rami Woods who performed stress hormone assays on all fecal samples for our physiological stress chapter.

Funding for this project was provided by the Research and Development Grant Program, Montana Department of Natural Resources. Justin Gude (FWP) secured the grant for this research.

ABSTRACT

Oil and gas energy development are becoming an integral part of the landscape in eastern Montana and western North Dakota. There will likely be continued development based on abundant oil reserves. Much of the oil reserve boundaries overlap with the mule deer (*Odocoileus hemionus*) range in the region. Mule deer are valued for hunting and wildlife viewing. For wildlife managers to identify appropriate mitigation strategies for addressing potential effects from energy development, it is necessary to understand the impacts of oil and gas energy development on mule deer demographics and behavior. This project was conducted simultaneously with a project in western North Dakota where high levels of oil and gas energy development were occurring. The goal of these two projects was to investigate the potential impacts of oil and gas energy development on mule deer resource selection, movements, physiological stress, and survival in western North Dakota and in eastern Montana, 2014-2016. This report summarizes the findings from the Montana portion of the study.

We captured 73 mule deer (30 does and 43 female fawns) in February 2014 and December 2014 and fitted deer with satellite GPS radio collars. We programmed collars to collect locations every 5 hours. We also programmed collars to transmit real-time locations if collars remained still for >6 hours, which allowed us to investigate mortality events. We conducted necropsies on all intact carcasses at the North Dakota Game and Fish Department (NDGF) veterinary laboratory. We collected 115,470 locations from collared mule deer from February 2014 - December 2015.

We used discrete choice models to compare used mule deer GPS locations to random available locations. We used predictor variables from three hypothesis sets: Vegetation (vegetation class, distance from wooded edge, interspersion juxtaposition index, Normalized

difference vegetation index [NDVI]), Topography (aspect, percent slope, ruggedness [vector ruggedness measure], and landforms), and Anthropogenic Development (distance to nearest road, road density, density of active well pads, and presence of drilling rig within 600m or 2500 m). We also included interaction terms for age (fawn, adult), season (spring, summer, winter, autumn) and period of day (day, night, or crepuscular).

Our top model was the global model which included all variables except distance to nearest road (which we removed due to correlation with road density) and presence of drilling rig (removed due to low frequency of drilling rigs in Montana). Unlike the results in North Dakota where drilling rigs were the strongest driver of resource selection, the most important predictors of resource selection in Montana were topographic features: landform and slope. Ridges, upper draws and slopes were used more than valley bottoms or flat areas. Road density and well pad density negatively influenced mule deer resource selection, but the relationship was not as strong as topographic or vegetation influences. Mule deer selected areas closer to wooded edges and wooded or shrubland vegetation types. Mule deer selected areas with low to moderate slopes and moderately high ruggedness indices. We generated a predictive map of relative probability of selection for mule deer in our study area that can be used to identify valuable mule deer habitat and comment on development proposals.

We summarized movement distances between summer and winter centroids to explain migration and seasonal range fidelity patterns. Movement data were strongly skewed, so we reported median distances for movements and fidelity. The median movement distance between winter and summer centroids was 608 m for adults (Range = 41 - 17,000 m), 1,273 m for yearlings (Range = 236 - 20,994 m), and 1,232 m for fawns (Range = 236 - 27,883 m). Regardless of movement distances between seasons, most deer showed fidelity to seasonal ranges. The median distance between successive seasonal centroids (e.g. summer to summer) was < 800 m for all ages and all seasons (Range 358 - 752 m). Although majority of the deer were non-migratory and showed strong fidelity to seasonal ranges, we documented one fawn that dispersed >160 km. It appears that a small proportion of the population, mainly fawns and yearlings, are responsible for dispersing and recolonizing previously occupied areas. Biologists in montane areas with migratory mule deer populations often focus on the potential for development as a barrier to movement corridors. We did not observe strong use of limited corridors. Rather, our findings that mule deer used smaller areas with shorter movement distances suggest that mitigation efforts should be focused on seasonal ranges identified as having high probability of selection.

We summarized seasonal and annual home range sizes using 95% minimum convex polygons to quantify how much space mule deer used on the landscape. Seasonal home ranges were slightly larger for fawns and yearlings than does, for all seasons and ranged from 417 ha to 842 ha. Seasonal home ranges were smallest during summer, and largest during autumn and winter. We were only able to analyze data from 30 deer for annual home ranges due to mortalities or collar failure. Median annual home ranges were 1,698 ha for fawn/yearlings and 952 ha for adults. The largest home ranges were observed for deer that made large movements between ranges or dispersal movements. Apart from dispersals and movements between ranges, all deer remained in ranges nearer to our median home range size (i.e., 900 - 1,500 ha).

We analyzed survival data for 73 mule deer using radio-tracking data. We observed 18 mortality events. We calculated bi-weekly utilization distributions (UDs; kernel density estimates) for each deer and classified UDs into survived or mortality categories depending on whether the deer survived that period. We assigned predictor variables to each UD for

background variables (age, season, temperature, biological year, snow depth, NDVI, and management unit), oil and gas energy development (distance to nearest rig, distance to nearest active well pad, rig density, well pad density, number of drilling rigs, and number of well pads) and road variables (distance to nearest road, road length and road density). We compared home ranges for periods where deer survived to home ranges where deer died using generalized linear models. The estimated annual adult survival probability was 82.6%, and overwinter fawn survival probability (Dec – May) was 77%. Survival probabilities were lowest in the winter season for adults and fawns. The leading known cause of mortality was malnutrition which accounted for 18.8% of doe mortalities and 30% of fawn mortalities. The most significant factors affecting survival were season and temperature, and we only detected weak effects of anthropogenic development features. However, we observed very low rates of hunting mortality, and increased road densities for future developments could have indirect impacts on hunter success and mule deer mortality.

We conducted aerial block surveys on six survey areas during spring in fall to evaluate mule deer abundance and herd composition, respectively. Uncorrected mule deer densities in our study area ranged from 0.82 to 2.26 deer/mile^2 and we observed an average of 1.56 deer/mile^2. We observed a small increase in density from 2014 to 2015 by 14%. We saw high fawn-to-doe ratios (0.76) and buck-to-doe ratios (0.58). The densities and composition we observed suggest that the mule deer population in our study area was growing during our study. The same trends for mule deer population change were observed in the high development areas in western North Dakota, suggesting mule populations are ultimately driven by weather and vegetation factors.

We collected fecal samples during capture events for physiological stress hormone analysis. To bolster our sample size, we included data from mule deer captured in both eastern

Montana and western North Dakota. We collected 190 fecal samples. All fecal samples were homogenized, frozen, and sent to the University of Missouri Wildlife Physiological Laboratory (Columbia, MO), where concentrations of fecal glucocorticoid metabolites (FGM; physiological stress hormones) were measured. We used generalized linear models to evaluate the relationship between FGM and vegetation, topography, and anthropogenic development metrics calculated around the capture location (1.91 km or 2.91 km buffer depending on the variable). We added temperature and gravel pits to our list of covariates. Our top model was the global model. Deer captured from areas with >3 gravel pits within 2.91 km or >1 drilling rig within 2.91 km had significantly higher FGM levels. We hypothesized that ruggedness would mitigate any disturbance impacts, but ruggedness only showed a slight, positive relationship. Temperature had a marginal effect, where FGM levels were higher when the temperature was below 0° C.

The low levels of energy development in the Montana portion of this study do not appear to be strongly influencing mule deer resource selection, survival, or movement patterns. However, across the border we documented mule deer avoidance of drilling rigs and areas with high road densities, increased physiological stress in areas with high gravel pit or drilling rig densities, and decreased survival in areas with high well pad density. In North Dakota, mule deer responded to oil and gas development by modifying behavior, initiating a physiological stress response, and reducing survival. Based on this study and results from the North Dakota study, we make the following recommendations for oil and gas energy development occurring in mule deer range in the region:

1) Create a new “primary mule deer range” map updated with information from resource selection models that incorporate: vegetation, topography, current oil and gas

infrastructure and road densities. This map should be adjusted based on local knowledge and historical trend data.

2) Minimize drilling rig locations and gravel pits in primary mule deer habitats during winter and fawning/fawn rearing seasons and select locations for drilling rigs that are more open (>1.1 km from wooded edge) and have lower slopes (<15%).

3) Maintain new development infrastructure near existing roads to avoid increases in overall road density, specifically to maintain road densities < 1.2 km/km^2.

4) In areas where multiple wells will be drilled, consolidate wells on fewer well pads to minimize the overall well pad density (i.e., maintain well pad densities < 5/mi^2).

INTRODUCTION

In North America, the exploration and production of hydrocarbons increased rapidly beginning in the early 2000s (United States Energy Information Administration [USEIA] 2012). Disturbance from such development can have negative effects on wildlife at the landscape-level, including spatial displacement and population declines (Northrup and Wittemyer 2013). As oil and gas production increased in North Dakota's Bakken Formation, speculators purchased mineral leases in much of eastern Montana. In 2014, Montana authorized 270 drilling permits, and subsequently, funding was secured to study the impacts of oil and gas development on mule deer in eastern Montana. However, as the Bakken oil boom developed, much of the extraction activity remained further east, and it became evident that many of the Montana leases would not be developed. The research goals for this grant shifted to parallel the methods of a concurrent study in North Dakota (Kolar et al. 2017), with the intention of using the Montana data as a baseline for comparisons. In this report we primarily examine the data collected in the Montana funded portion of the study. Much of the text is taken from the North Dakota report, as the methods were duplicated. We did not have sufficient data for the physiological stress chapter to separate the states, so the stress chapter is taken directly from the North Dakota report, which used both state's data.

Gas and oil production has become an important part of the economy and landscape in eastern Montana and western North Dakota. Currently, North Dakota is among the top oil producing states and much of the Bakken development expands into eastern Montana. Richland county is the leading oil producing county in Montana and produced and average of 42,000 barrels of oil per day during 2015. Copeland et al. (2009) identified portions of the region with extremely high potential for oil and gas development. In a 2008 report, the USGS estimated a mean of 3.65 billion barrels of oil could be recoverable in the Bakken Formation (http://www.usgs.gov/newsroom/article.asp?ID=1911). In 2013, the USGS raised that estimate to 7.4 billion barrels of oil and 6.7 trillion cubic feet of natural gas (http://pubs.usgs.gov/fs/2013/3013/fs2013-3013.pdf). Given recent technological developments in rock fracturing methods, recent estimates now suggest upwards of 18 billion barrels might be a more accurate estimate (http://www.nd.gov/ndic/ic-press/bakken-form-06.pdf). Such projections have resulted in considerable interest in oil and gas production in the region.

Energy development will continue to alter regional landscapes. As of January 2015, there were 11,892 wells producing 1.2 million barrels of oil/day in North Dakota (Helms 2015). Industry projections estimate that another 40,000 wells will be drilled in the next 18 years (North Dakota Industrial Commission [NDIC] presentation,14 February 2014). The average size of a well pad is 3.7 acres, including an average of 1.5 acres of access road development. Even larger, multi-well pads (typically 6-8 wells, and as many as 18 wells) are becoming more commonplace with the development of lateral drilling technology (Helms 2015). Multiple, directional wells—which can pump oil up to 4 miles, horizontally, from a well pad—can be positioned on a single well pad or along a narrow corridor, thus increasing the individual well pad size, but decreasing the overall footprint of each well. During the first year of development of each well, it takes roughly 2,000 vehicle visits to the well pad (NDIC Energy Presentation, Bismarck State College, 29 January 2014). In January 2014, 186 oil rigs were actively drilling in western North Dakota (vs. 78 in January of 2010). Also, in January 2015, 166 drilling rigs continued to drill for oil in western North Dakota despite lowest crude oil prices since 2009. Meanwhile, in Montana, the rig count in 2014 only peaked at 15, and has declined steadily since. Currently there is only one drilling rig in Montana, in Roosevelt County. Nonetheless, this scale of development has the potential to impact shared wildlife resources.

A primary concern with increased oil and gas energy development is the potential loss of important wildlife habitat through direct and indirect effects. Direct effects include direct loss of habitat through development of infrastructure (e.g., well pad, roads, gravel pits, water depots, storage sites, etc.). Indirect effects include factors associated with the infrastructure such as traffic and noise that might reduce suitability of an area. Most studies have identified negative impacts of oil and gas development on the habitat of a diversity of species through either direct loss or through displacement (Sawyer et al. 2006, Walker et al. 2007). Few studies concluded that there were no effects from energy development, but no studies have reported that all development metrics affected mule deer. For example, Lendrum et al. (2012) found an effect of well pad density on 5-hour movement distances during migration but did not detect avoidance of well pads during migration.

Researchers have documented both direct and indirect impacts of oil and gas energy development on mule deer (*Odocoileus hemionus*) in Wyoming (Sawyer et al. 2017), Colorado (Lendrum et al. 2012, Northrup et al. 2015), Montana (Ihsle 1982), and in North Dakota (Fox 1989, Ciuti et al. 2014, Kolar et al. 2017), but the responses vary by region and season. Currently, it is projected that about 18% of the primary mule deer range in North Dakota is moderately affected by oil and gas development; another 1.7% is highly impacted (NDGF, unpublished report). There are 1,123 active wells in the primary mule deer range, and 6,991 active wells in the primary and secondary mule deer range. Much of this development has occurred in the past 5 years (NDGF, unpublished report). Mule deer are a valuable component of the region’s landscape and are prized as a game species. Oil and gas energy development overlaps much of the mule deer range in North Dakota and has the potential to affect (directly or indirectly) mule deer habitat in the region.

Previously research in North Dakota found that mule deer fawn production was significantly affected by the interaction between number of oil wells and an index of coyote density (Ciuti et al. 2014). While the cause of this correlation is not well understood, Ciuti et al. (2014) hypothesized that it may be due to a behavioral response to oil and gas energy development that could reduce available fawning areas and increase predator efficiency. Researchers have studied the impacts of oil and gas energy development on mule deer space use in multiple oil and gas developments. Easterly et al. (1991) reported 29 mule deer fitted with VHF collars in eastern Wyoming used areas farther away from development during the drilling phase only. Sawyer (2009) also observed avoidance of wintering areas near active developments (up to 3.7 km from drilling rigs), but avoidance persisted after drilling phases (Sawyer et al. 2017). Avoidance behavior without acclimatization (i.e. displacement) is particularly significant if mule deer are displaced from important habitats that are limited in availability. Alternatively, Ihsle (1982) did not detect impacts of oil and gas development on mule deer space use in northwestern Montana, but energy development density was low. Northrup et al. (2015) found that mule deer on winter ranges in the Piceance region of northwestern Colorado avoided drilling rigs, producing well pads, and roads, but the avoidance distances (e.g. 600-800 m from drilling rigs) were not as high as in Wyoming. Mule deer in Colorado also showed that avoidance distances decreased after the drilling phase. It was suspected that increased vegetation and ruggedness might have helped to mitigate impacts of oil and gas energy development on mule deer in Colorado. Regional variation in both avoidance distance and avoidance persistence suggests that research from other regions may have limited inference for mule deer resource selection in the eastern portion of the specie's distribution.

Although there are links between oil and gas energy development and mule deer abundance (Sawyer et al. 2017), and fawn production (Ciuti et al. 2014), there is little available research investigating the relationship between survival and energy development. Over a 15-year period in western Wyoming, Sawyer et al. (2017) noted a difference of 20% between the reduction in mule deer abundance for the population that wintered in a gas development compared to the entire subherd (36% vs. 16% reduction). The source for the decline in abundance (decreased survival, reproduction or emigration) could not be identified, but authors suggested that strong fidelity to seasonal ranges likely precluded emigration. Although hunting success rates can increase with increasing well pad density (Dorning et al. 2016), the population decline in Wyoming occurred despite reductions in hunting permits. Using long-term survey data, Ciuti et al. (2014) found a negative relationship between well pad density and fawn production (fawn-to-doe ratio) in western North Dakota. However, the relationship was only significant when an interaction effect was included for coyote density. More work is still needed to investigate how impacts of oil and gas energy development might affect mule deer population dynamics via changes in survival or recruitment.

If oil and gas development have similar direct and indirect effects on mule deer in eastern Montana and western North Dakota as in other states, available habitat could be reduced by the ongoing oil and gas energy development. However, the effects in the region could be different due to the rugged topography and woody vegetation of the breaks habitats and non-migratory movement patterns. Managers require region-specific information on impacts to mule deer to protect priority areas and mitigate the potential effects appropriately. Further, mule deer in the region are at the eastern edge of their distribution (Remote Sensing and GIS Laboratory 2005). Species living near the edge of their distribution are often subjected to higher levels of ecological stress (Davies et al. 2013). Because mule deer are a valued species iconic of the region, it is imperative that their habitat is better delineated and protected from effects that detract from the overall suitability.

This research is designed to be part of a comprehensive assessment of oil and gas development on mule deer populations. In coordination with research from North Dakota (Kolar et al. 2017), we have identified key factors affecting mule deer, and recommend potential mitigation strategies to reduce and minimize impacts of future developments. This research and data are a valuable supplement to the previous studies on mule deer biology in the region (Jensen 1988, Fox 1989, Hamlin and Mackie 1989, Carnes 2009).

Goals and Objectives

Goal 1: Develop sightability models to evaluate mule deer abundance and composition.
NOTE: *This goal was not attainable due to large degrees of variation around detectability from the air, and limitations in distinguishing whether a collared deer was detected.*

Goal 2: Determine how energy development impacts mule deer habitat selection and distribution.
Objective 1: Establish baseline habitat selection and distribution patterns in each study area.

Goal 3: Determine how energy development impacts mule deer population dynamics.
Objective 1: Establish baseline doe survival rates in each study area.
Objective 2: Establish baseline female fawn overwinter survival rates in each study area.
Objective 3: Establish estimates of population trend in each study area using doe and fawn survival rates.
Objective 4: Establish estimates of population trend in each study area using aerial surveys and sightability corrections.

Goal 4: Develop a risk-assessment map to quantify influences that energy development might have on mule deer populations.
Objective 1: Combine mule deer demographic data and resource selection models with existing habitat data to create a map showing relative values of existing habitat for mule deer populations.

Goal 5: Ensure adequate communication and integration of project results and inferences.
Objective 1: Integrate results into natural resource management programs.

Methods for all Chapters

Study Area

The eastern Montana portion of our study included two study areas: (1) the Yellowstone River study area was located between the towns of Glendive and Sidney, Montana, bounded by the Yellowstone River to the west and the North Dakota border to the east, and (2) the Culbertson study area south of the town of Culbertson, Montana and adjacent to the Missouri River (Figure 1). These areas were selected as partial control areas for our larger study addressing the impacts of oil and gas development on mule deer (Kolar et al. 2017) because they contained similar habitat and landscape features but low levels of oil and gas energy development. Habitat in the study areas consisted primarily of highly-eroded, broken topography (badlands) and rolling hills. The Yellowstone study area comprised 1,221 km^2. The boundaries of the Yellowstone study area roughly followed Interstate 40 to the south (Latitude 47.00), the Yellowstone River to the west (Longitude -104.69), Montana Highway 23 to the north (Latitude 47.67), and the North Dakota state line to the east (Longitude -104.00). The Culbertson study area was 218 km^2 and bounded by Latitude 47.94 in the south, Longitude 104.26 in the west, Longitude 104.59 in the east, and the Missouri River to the North (Latitude 48.11).

Ecology. The primary vegetation type was mixed-grass prairie with pockets of shrubs and wooded north-facing slopes, draws and floodplains. North-facing, wooded slopes were dominated by Rocky Mountain juniper (*Juniperus scopulorum*), common juniper (*Juniperus communis*), horizontal juniper (*Juniperus horizontalis*), chokecherry (*Prunus virginianus*), skunkbrush (*Rhus trilobata*), and woods rose (*Rosa woodsii*). Wooded draws often contained green ash (*Fraxinus pennsylvanica*) with chokecherry and woods rose understory. Wide, well-drained valley bottoms contained mostly silver sage (*Artemisia cana*) and western wheatgrass

(*Agropyron smithii*). Shrub patches included: buffaloberry (*Shepherdia argentea*), buckbrush (*Symphoricarpos occidentalis*), chokecherry and skunkbrush (*Rhus trilobata*). South-facing, eroded clay slopes were typically bare, but did have rabbitbrush (*Chrysothamnus nauseosus*), shadscale saltbush (*Atriplex confertifolia*), and greasewood (*Sarcobatus vermiculatus*). Major grasslands included western wheatgrass, little bluestem (*Andropogon scoparius*), blue grama (*Bouteloua gracilis*), needle-and-thread (Stipa comata), green needlegrass (*Stipa viridula*), and prairie junegrass (*Koeleria cristata*). Introduced grasses included smooth brome (*Bromus inermis*), crested wheatgrass (*Agropyron cristatum*), Kentucky bluegrass (Poa pratensis) and cheatgrass (*Bromus tectorum*).

Other ungulate species present in the study areas included: white-tailed deer (*Odocoileus virginianus*) and pronghorn (*Antilocapra americana*). Elk (*Cervus elaphus*) occur in both study areas at low density. A small band of bighorn sheep (*Ovis Canadensis*) occupy a small portion of the Lower Yellowstone study area. Cattle were the dominant livestock species present. Potential predators of mule deer included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx* rufus) and golden eagles (*Aquila chrysaetos*).

Climate. We collected daily summaries of weather data from the Culbertson, MT (station ID: USC00242122), Sidney, MT (station ID USC00247560) and Glendive, MT (station ID: USC00243581) weather stations for summer 2013 through spring 2017 (National Oceanic and Atmospheric Administration [NOAA] 2017). Temperatures from 2013-2017 ranged from -37.2 C to 40 C. Temperatures and precipitation were similar among weather stations and years. The average seasonal high/low daily temperatures were: spring 18.3/2.6, summer 27.6/11.7, autumn 11.2/-2.0, winter 1.1/-10.6. Annual precipitation averaged 33.3 cm, seasonal precipitation totals were spring: 7.3 cm, summer: 21.1 cm, autumn: 3.1 cm, and winter: 1.8 cm.

Geology. The topography is generally eroded badlands habitats, and elevation ranges from approximately 580 m to 935 m above sea level. Soils are clayey, with sandy loam draws and sandy hilltops. Bedrock layers are primarily sandstone, and eroded areas contain exposed sandstone, coal veins and scoria layers.

Land Use. Land ownership is intermingled with 16% public (State Trust Lands and Bureau of Land Management) and 84% private in the Yellowstone study area, and 38% public and 62% private in the Culbertson study area. Due to the arid climate and availability of affordable grazing leases on public lands, private lands are typically managed for livestock production. Roughly 5% of the Yellowstone and 10% of the Culbertson study areas are cultivated, consisting of irrigated crops along the Yellowstone and Missouri Rivers, dryland crops in flat areas away from rivers (e.g., Belle Prairie within the Yellowstone study area), and alfalfa for hay.

The Yellowstone study area was located in FWP Region 7 hunting district 703 (HD 703). The Culbertson study area was located in FWP Region 6 hunting district 651 (HD 651). Archery seasons in Montana run from the first Saturday in September for 44 days. General rifle seasons run for 37 days, starting in late October and ending on the Sunday after Thanksgiving. Hunting opportunity within the study area was highly variable. Nearly all private landowners allow some level of hunting, but the amount varies from very restricted hunting on some properties (e.g., limited to the landowner and close family members) to properties that are open to extensive amounts of public access, either to hunters who ask permission or through the Montana Fish, Wildlife, and Parks (FWP) Block Management hunter access program. Hunting opportunity was unlimited on accessible public lands.

Deer numbers in Region 7 reached a recent low after back-to-back severe winters 2009-10 and 2010-11, and because of this decline antlerless seasons were closed statewide in Montana during the first hunting season that occurred during this study in fall of 2014. The general license in Montana is the only license valid for an antlered deer; to harvest a doe on this license (if legal to do so in a given hunting district) would mean relinquishing the opportunity to harvest a buck in that year in Montana. The general license remained antlered-only for mule deer in Hunting District 703 in 2015, but antlerless "B" licenses became available. In Hunting District 651, the general license became either-sex for mule deer in 2015, but no additional antlerless "B" licenses were issued. For the 2016 hunting season, both Hunting District 703 and 651 were either-sex for mule deer on the general license, and additional antlerless "B" licenses were available in both hunting districts. In Hunting District 703, it is estimated that 14 antlerless mule deer were harvested in 2014, 286 in 2015, and 826 in 2016. The Yellowstone study area represents 8.6% of Hunting District 703. Assuming even harvest distribution, it is estimated that 1 antlerless mule deer was harvested in 2014 in the Yellowstone study area, 25 in 2015, and 71 in 2016. In Hunting District 651, it is estimated that 11 antlerless mule deer were harvested in 2014, 36 in 2015, and 70 in 2016. The Culbertson study area represents 3.4% of Hunting District 651. Assuming even harvest distribution it is estimated that 0 antlerless mule deer were harvested in the Culbertson study area in 2014, 1 in 2015, and 3 in 2016. Harvest data are from telephone surveys of hunters (Montana Department of Fish, Wildlife, and Parks, unpublished data).

The Bakken and Three Forks Shale Formations largely overlapped with our study area (Figure 2), and oil and gas development, including drilling rigs and actively producing wells, occurred prior to and during our study (Figure 3). Although development levels were low in Montana, the North Dakota study area encompassed areas with more than 1.93 active well pads/km^2 (5 active well pads/mi^2), which the Western Association of Fish and Wildlife Agencies guidelines (WAFWA; Lutz et al. 2011) considered a high level of development for mule deer habitat.

Field Methods

To guide our capture effort, we identified target locations for adult and fawn dispersed across the study area. We used a coarse grid (4.8 x 4.8 km) to stratify our study area. We chose 4.8 km as a conservative estimate for an area that would contain an annual home range for a non-migratory, female, adult mule deer, 17.8 km^2 (Hamlin and Mackie 1989), and because the distance (3 miles) allowed us to overlay our grid on legal description lines to correspond with lands where we had permission to capture deer. To minimize the potential for auto-correlation, we attempted to maintain 4.8 km between any two capture target locations (i.e. 1 point per grid cell).

Mule deer densities are low in parts of eastern Montana (Figure 23 A & B), so we flew reconnaissance flights prior to capture to search for deer near target locations, beginning January 2014. We recorded waypoints for each deer group (or abundant tracks in snow) and adjusted the random target capture locations to match the nearest waypoint where deer were found. We could not find and capture deer at every target location, but we attempted to stratify captures across our study areas.

We captured mule deer February 2014 and December 2014 using helicopter net-gunning (Quicksilver Air Inc., Fairbanks, AK). In each study area, we captured and fitted 10 does (≥ 1.5 years old) and 10 female fawns with satellite GPS collars (G2110E Iridium and G2110L Iridium; Advanced Telemetry Systems Inc. [ATS], Isanti, Minnesota), for a total of 40 GPS-collared deer. We programmed collars to collect GPS locations every 5 hours to ensure sampling from all times of the day. Data were transmitted via satellite every 4 days; satellite technology allowed us to collect locations without disturbing deer during monitoring activities. Further, satellites attained locations regardless of access to the deer location. We programmed collars to transmit notifications if the collar was inactive for >6 hours, which enabled us to inspect carcasses promptly after mortality events. A built-in VHF transmitter aided in real-time tracking of deer, which was necessary to quickly recover carcasses after mortality events. Battery expectancy for this GPS fix schedule was 3.5 years and 2 years for G2110E and G2110L collars, respectively.

We conducted subsequent captures annually to maintain a radio-marked sample of 20 does and 20 female fawns. We captured new fawns each winter because fawns captured the previous year graduated to yearlings on 01 June (the approximate parturition date in North Dakota; Jensen 1988). We captured additional does to account for mortalities and collar failures. All animal use activities were reviewed and approved by the University of Missouri Institutional Animal Care and Use Committee (Protocol 7552).

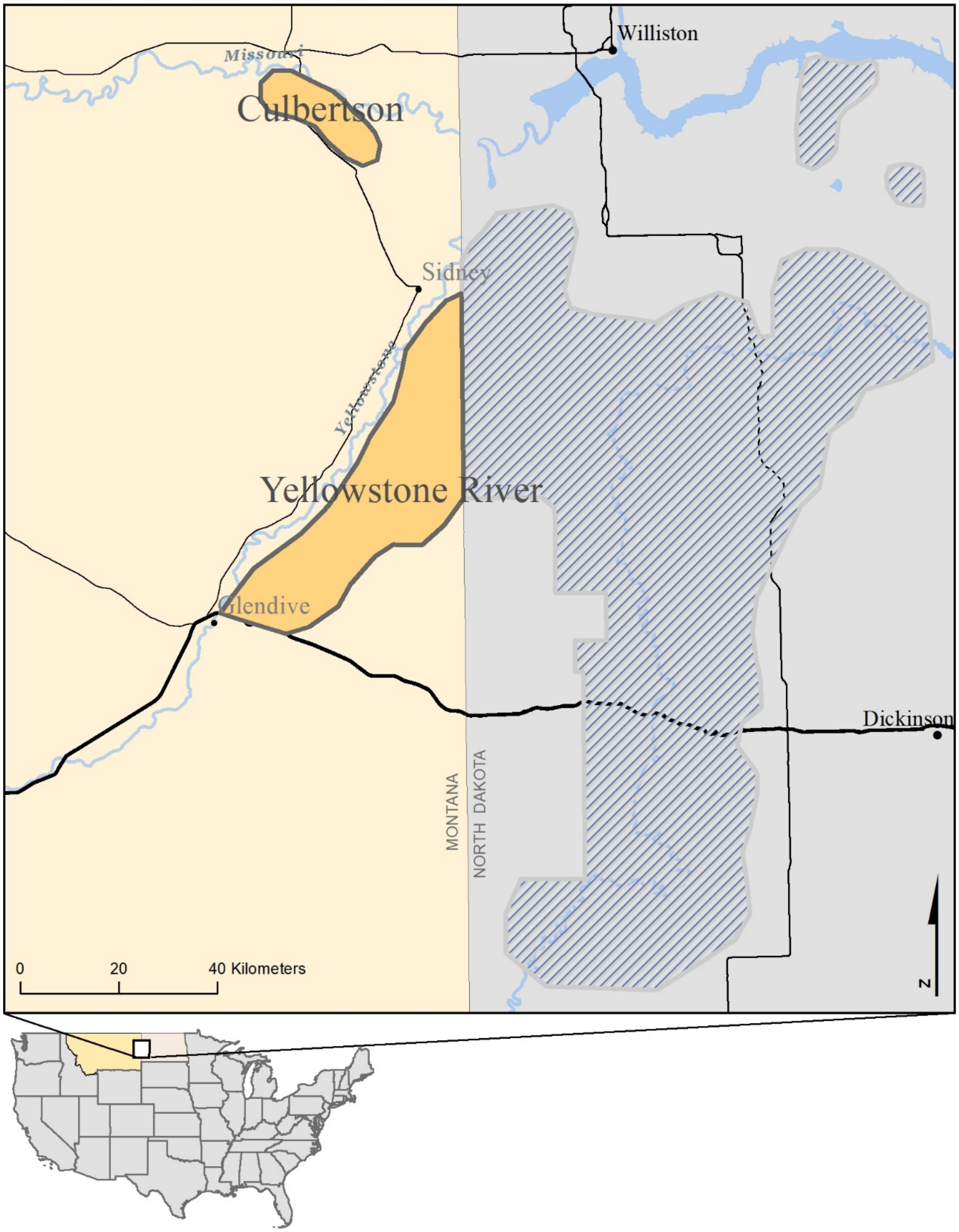


Figure 1. Map of mule deer study areas in eastern Montana (orange) along the Yellowstone River and southeast of Culbertson, MT, and sister study in western North Dakota (hashed lines).

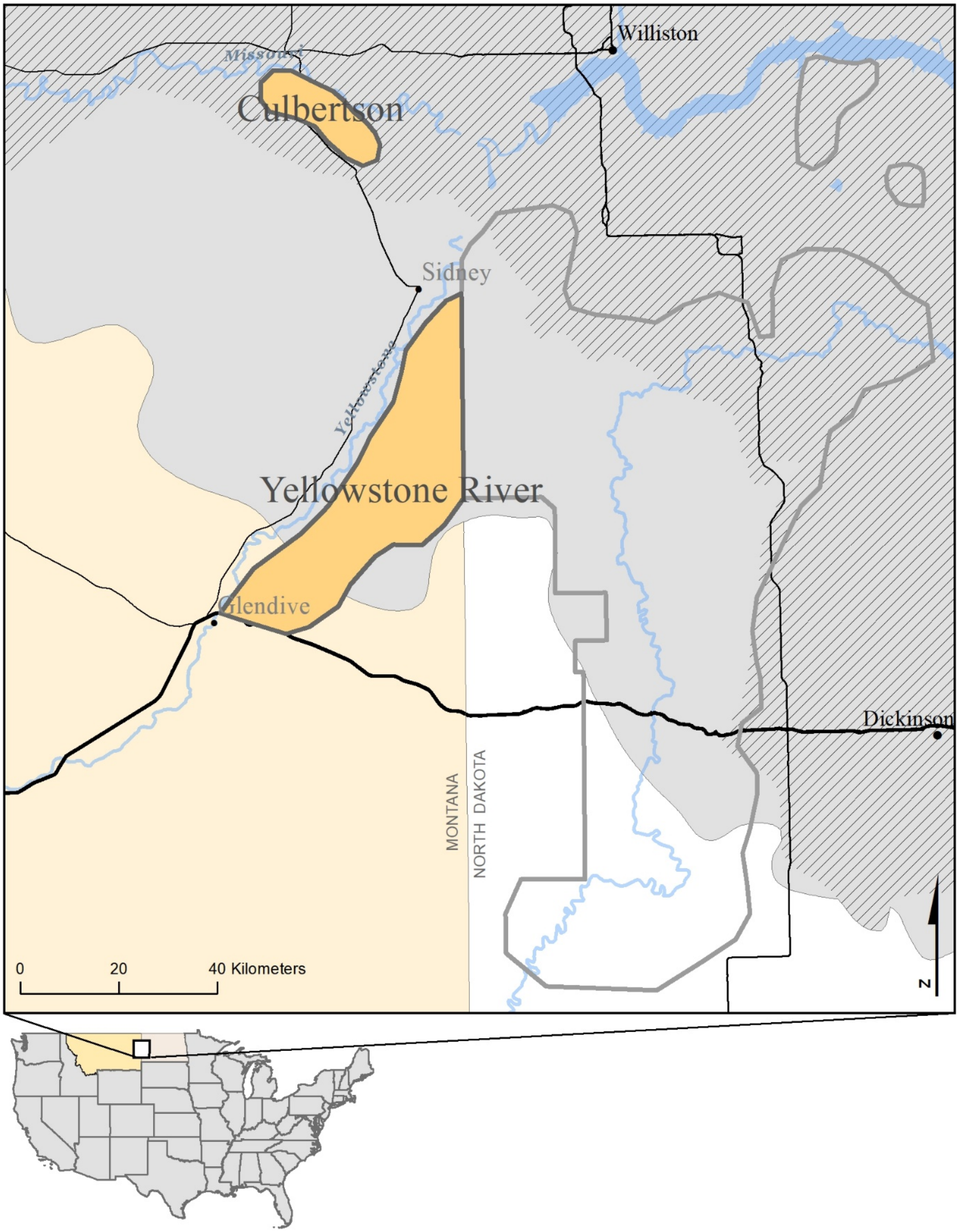


Figure 2. Map of mule deer study area and the overlapping Bakken (hashed lines) and Three Forks oil formations (gray) in western North Dakota and eastern Montana.

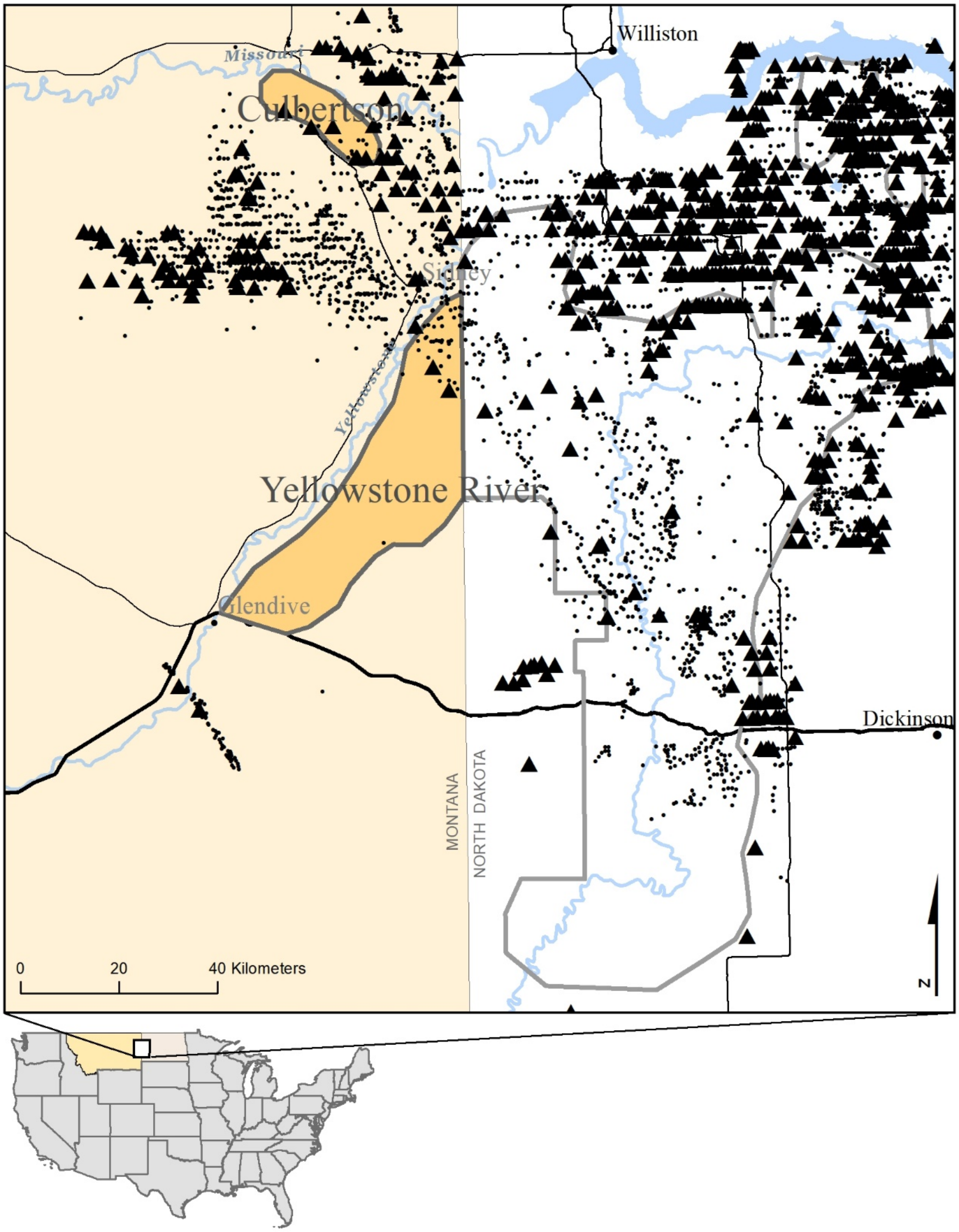


Figure 3. Map showing distribution of active drilling rigs (black triangles) and producing well pads (black dots) in eastern Montana and western North Dakota from 2014-2015.

Literature Cited

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

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009. Mapping oil and gas development potential in the U.S. Intermountain West and estimating impacts to species. PLoS One 4(10): e7400. doi:10.1371/journal.pone.0007400.

Davies, N. A., G. Gramotnev, C. McAlpine, L. Seabrook, G. Baxter, D. Lunney, J. R. Rhodes, and A. Bradley. 2013. Physiological stress in koala populations near the arid edge of their distribution. PLoS One 8(11):e79136.

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

Easterly, T.A.A.W. T.L. 1991. Responses of Pronghorn and Mule Deer to Petroleum Development on Crucial Winter Range in the Rattlesnake Hills. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Fox, R. A. 1989. Mule deer (Odocoileus hemionus) home range and habitat use in an energy-impacted area of the North Dakota Badlands. Thesis. University of North Dakota. Grand Forks, USA. 88 pp.

Hamlin, Kenneth L.; Mackie, Richard J. 1989. Mule deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. Final Report. Helena, MT: Montana Department of Fish, Wildlife, and Parks. 401 p.

Helms L. 2015. North Dakota Mineral Resources Status and Outlook. Report to the House Natural Resources Committee. <https://www.dmr.nd.gov/oilgas/presentations/HENR010915.pdf> January 9, 2015.

Ihsle, H. B. 1982. Population ecology of mule deer with emphasis on potential impacts of gas and oil development along the east front of the Rocky Mountains, northcentral Montana. Thesis. Montana State University, Bozeman, USA. 85pp.

Jensen, W.F. 1988. Summer and fall ecology of mule deer in the North Dakota badlands. Dissertation. University of North Dakota. Grand Forks, USA. 220 pp.

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

Lendrum, P. E., C. R. Anderson, Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3(9):82. http://dx.doi.org/10.1890/ES12-00165.1

Lutz, D. W., J. R. Heffelfinger, S. A. Tessmann, R. S. Gamo, and S. Siegel. 2011. Energy development guidelines for mule deer. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

National Oceanic and Atmospheric Administration. 2017. 2012-2016 Daily Summaries. https://www.ncdc.noaa.gov/cdo-web/datasets/. Accessed 2 February 2017.

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

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

Remote Sensing and GIS Laboratory. 2005. Mule deer habitat in the western United States. Utah State University, Logan, Utah. Retrieved from http://www.fs.fed.us/database/feis/animals/mammal/odhe/all.html#DistributionAndOccurrence

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

Sawyer H, N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer and energy development—Long-term trends of habituation and abundance. Global Change Biology 00:1–9.

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

U.S. Energy Information Administration [USEIA]. 2012. Energy explained: your guide to understanding energy. U.S. Department of Energy, Energy Information Administration, Washington, DC. <http://www.eia.gov/energyexplained/index.cfm> Accessed 04 Aug 2017.

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

CHAPTER I. RESOURCE SELECTION OF MULE DEER IN EASTERN MONTANA

Introduction

Animals distribute themselves across the landscape which is a fundamental ecological process that serves to maximize fitness (Fretwell and Lucas 1969). Understanding habitat selection can provide insight into numerous, individual-level ecological processes (e.g., site fidelity [Creel et al. 2005], foraging and predation risk [Switzer 1997]), as well as landscape-scale processes that affect population distribution and abundance (e.g., population dynamics [Pulliam and Danielson 1991], speciation [Rice 1987], dispersal [Shafer et al. 2012]). As noted by Sawyer et al. (2006), human development can change habitat selection patterns; however, different species may be affected in different and complex ways. Human activity may directly convert habitat into unusable area, but some activities may also lead to functional habitat loss in a disproportionately larger area that that which was developed directly (e.g., Sawyer et al. 2006). Animal responses to human activities also can be more nuanced, whereupon humans can be perceived as predators, prompting behavioral shifts that stem from tradeoffs between security and foraging or reproduction (Frid and Dill 2002, Hebblewhite and Merrill 2008). In contrast, animals can be attracted to areas of human development if vegetation disturbance stimulates new plant growth (Lutz et al. 2011) or through protection against predation (i.e., “human shield” [Berger 2007]). Such responses to anthropogenic changes can yield positive results for animals, though they can also lead to greater potential for negative encounters via human-wildlife conflict (Johnson et al. 2004) and the formation of evolutionary traps (e.g., Northrup et al. 2012, Chitwood et al. 2017). Given the myriad and complex responses of animals to human development, quantifying the mechanisms driving changes in wildlife behavior continue to be critical for developing appropriate management and mitigation strategies.

Throughout the western United States, energy development has occurred on mule deer (*Odocoileus hemionus*) winter range, which can result in decreased access to high quality forage (Parker et al. 1984). Moreover, across much of their range, mule deer have experienced major population declines (Unsworth et al. 1999), and recent studies indicate that mule deer have been displaced by and altered their habitat selection patterns in response to oil and gas energy development (Sawyer et al. 2006, 2009). Given that energy extraction is projected to continue to increase over the next several decades (USEIA 2014), assessing the effects of energy development on mule deer resource selection continues to be a major management priority. Thus, our objective was to identify the anthropogenic, vegetative, and topographic drivers of mule deer resource selection in a landscape that was undergoing rapid development due to energy extraction.

Methods

We analyzed mule deer landscape-scale selection (Johnson et al. 1980) in eastern Montana from Feb 2014 to Dec 2016 by employing a used vs. paired-available, discrete choice design (Cooper and Millspaugh 1999). We designated each mule deer location as a used site and selected 5 paired-available locations for each used site, without replacement, from a pool of random locations we created throughout the study area. To create the pool of random locations, we first defined the study area extent as a composite of buffers around capture locations with radii representing the mean of the maximum distances mule deer traveled from their capture site. Thus, we buffered 71 capture locations with a radius of 11 km to define available space. Only two deer crossed the Missouri or Yellowstone River, so we did not include areas east of the Yellowstone River or north of the Missouri River as available (Figure 4). Then, because mule deer use was not uniform across the study area, we stratified the study area extent into 22 km x

22 km grid cells and placed 5 times the number of random locations as used locations within each grid cell. At each used and paired-available mule deer location, we identified vegetation, topographic, and anthropogenic development variables (Table 1) that may influence mule deer selection and hypothesized how each variable may be related to selection (e.g., linear, quadratic, or pseudo-threshold relationship; Franklin et al. 2000).

We used the United States Department of Agriculture (USDA) National Agricultural Statistics Service (NASS) 30-m United States Cropland layer (USDA NASS 2013-2016) in ArcInfo 10.5 (Environmental Research Systems Institute, Redlands, CA) to identify vegetation types across the study area. To reduce the number of vegetation classes, we grouped NASS vegetation types into 7 dominant categories including "wooded" (deciduous and evergreen forest and woody wetlands—we grouped deciduous and evergreen because remote sensing data did not appear to accurately differentiate juniper from deciduous trees), "shrub" (shrublands), "grass" (grasslands), "hay" (hay fields and fallow/idle croplands), "legume" (alfalfa, peas, and other legume crops), "crop" (non-legume crops), and "barren" (areas devoid of vegetation). We dissolved pixels identified as "disturbance" into the majority vegetation category within a 0.09 km^2 square neighborhood around the pixel because disturbance categories, primarily consisting of unpaved roads, were relatively rare throughout our study area (<2% of pixels) and we already included road density as a variable in our model. If "disturbance" was the majority category in the 0.09 km^2 neighborhood, we reclassified the pixel as "barren." Also, we acquired monthly normalized difference vegetation index (NDVI) layers with 250-m resolution from eMODIS (Jenkerson et al. 2010) to quantify vegetation greenness because NDVI can be used as an indicator of forage availability for ungulates in open habitats (Borowik et al. 2013).

We included two vegetation-based variables that characterized landscape patterns: distance to the nearest wooded edge (Northrup et al. 2015, like maximum structural contrast: Kie et al. 2002) and interspersion and juxtaposition index (IJI; McGarigal et al. 2012). To calculate distance to wooded edge, we first “smoothed” the wooded category from our vegetation layer. Occasionally, pixels classified as something other than “wooded” occurred within contiguous wooded areas. We reclassified pixels as “wooded” if ≥ 75% of the surrounding pixels were classified as “wooded” to ensure pixels surrounded by contiguous forest were not classified as wooded edge. Next, we designated a pixel as “wooded edge” if the pixel had at least one neighboring “wooded” pixel but was not completely surrounded by “wooded” pixels. Last, we calculated the Euclidean distance from each pixel across the study area to the nearest “wooded edge” pixel to create a spatial map of distances to wooded edge. We used the moving window option in FRAGSTATS (McGarigal et al. 2012) to calculate the IJI within a 2-km buffer around each pixel of the 30-m 2011 National Land Cover Database layer (Homer et al. 2015). The IJI values ranged from 0 to 100, with higher values representing a vegetation patch type being equally adjacent to all other patch types. We hypothesized mule deer would select for moderate IJI levels, so we included the quadratic form of this variable in our model.

We used a 30-m digital elevation model (DEM) raster layer to calculate slope, northness, ruggedness index, and landforms based on the topographic position index (landform TPI). We created slope and aspect layers from the DEM layer using the Spatial Analyst toolbox in ArcInfo 10.5 and calculated topographic northness by taking the cosine of the aspect in radians, which results in values ranging from -1 (sloping directly south) to 1 (sloping directly north). We calculated the ruggedness index using equations provided in Sappington et al. (2007), who determined that a 3 x 3-pixel neighborhood (8,100 m^2) captured the complexity of the landscape without over-smoothing it. Ruggedness values ranged from 0 to 1, with greater values representing greater ruggedness. We calculated landform TPI using the Topography Toolbox for ArcGIS 10.1 and Earlier (Dilts 2015), and classified landform TPI values developed at 180-m and 2000-m scales into 4 landforms: ridges and heads of draws; mid to upper slopes; flat, lower slopes; and valleys. We hypothesized mule deer would select moderate values for slope and ruggedness (moderate slopes: Sawyer et al. 2009; mule deer selected lower slopes: Lendrum et al. 2012, Horncastle et al. 2013; greater slopes: Northrup et al. 2015), so we included the quadratic form for these variables.

We created line shapefiles for all roads by using City and County Roads and State and Federal Roads (ND Department of Transportation 2016), combined with a road shapefile digitized manually from 2015 NAIP aerial imagery, at a 1:5,000 scale. We used this roads layer to estimate distance to primary or secondary roads and road densities by dividing the total length of roads within 2 km by 12.57 (area within 2 km). We determined the number of drilling rigs and active wells each month using spatial data from the Montana Board of Oil and Gas Conservation. We consolidated multiple wells if they occurred on the same well pad (Northrup et al. 2015), so we used active well pads in our models. If a drilling rig and well were present on the same active well pad, we consolidated them as a drilling rig (Northrup et al. 2015) to avoid duplication of development points at a single well pad. The effects of drilling rigs and active well pads on selection may be scale-dependent, so we included the presence/absence of drilling rigs within 2.5 km (Sawyer et al. 2009) and 600 m (Northrup et al. 2015), as well as the number of active well pads within 2 km (Sawyer et al. 2009), 900 m (Fox et al. 2009), 400 m (Northrup et al. 2015), and 100 m (Fox 1989).

We hypothesized the influence of variables on selection would be dependent on season (summer [Jun. 1 – Sep. 31], autumn [Oct. 1 – Nov. 30], winter [Dec. 1 – Mar. 31], spring [Apr. 1 – May 31]), time of day (day, night, crepuscular [within 2 hours of sunrise or sunset]), and age (adult [≥1 year old], fawn [<1 year old]). Thus, we included interactions between each variable and season, time of day, and age in our analysis. We checked for multicollinearity between variables by calculating Pearson's correlation coefficient (*r*) using the cor() function in R (R Core Team 2016). If $r > 0.65$, we removed the correlated variable that explained the least variation in selection. Distance to road and number of active well pads within 2 km were correlated with other variables so we removed them from the model analysis.

We fit conditional logistic models using the "clogit" package in R with unique mule deer identification as a "cluster" variable, which accounts for potential dependence among locations when calculating variance (Therneau 2015). First, we ran single-parameter models that included only active well pad variables at each scale (2,000 m, 900 m, 400 m, 100 m). We used only the most supported scale for the active well pad variable (i.e., number of active well pads within 2000 m) in future modeling to reduce the number of parameters in our final model. Next, we ran a vegetation model that included vegetation and IJI covariates; a topographic model with slope, northness, ruggedness, and landform TPI covariates; a development model that included road, rig, and active well pad covariates; and a full global model with all covariates. We compared Akaike's Information Criterion values (Akaike 1973) among models and assumed the model with the lowest AIC value was the most supported (Burnham and Anderson 2002).

We demonstrated the effect of variables on mule deer selection by using model results to calculate and plot the changes in relative probability of selection across the range of values of the variable of interest while keeping all other variables in the model at their average value. We used the facet grid option in the “ggplot2” package in R (Wickham 2009) to facilitate the identification of differences among seasons, times of day, and ages. We also created a predictive map of mule deer selection across the study area using Raster Calculator in ArcMap 10.5.

Results

We captured 73 mule deer (30 does and 43 fawns) during 2 captures: February 2014 and December 2014 (Table 2). We used 115,470 used mule deer locations and 577,350 random locations of 30 adults and 40 fawns (Table 3). The full global selection model failed to converge due to no used locations within 2000 m of the nearest drilling rig. We removed presence of drilling rig from the global model. The modified global model had a lower AIC value (AIC = 317,150) than the vegetation model (AIC = 368,855), topographic model (AIC = 343,871), and anthropogenic development model (AIC = 396,791). Thus, we used the global model to predict mule deer selection.

TPI Landform had the greatest impact on mule deer selection (Figure 5, Table 4). Ridges (also included heads of draws) were the most likely landforms to be used by mule deer. Mule deer also selected areas with low to moderate slopes (5-20% slope; Figure 6, Table 4). Mule deer were most likely to use areas with moderately high ruggedness in all seasons and for all times of day.

Mule deer were more likely to use wooded areas and shrublands than all other vegetation types during all times of day and across seasons (Figure 8). During winter, mule deer had a higher probability of selecting barren areas--nearly as high as for wooded or shrubland vegetation. Mule deer were less likely to use cropland, legumes and hayed fields, but in autumn during crepuscular hours and at night this preference was less pronounced. Relative probability of use decreased further from the nearest wooded edge, and the highest predicted probability of use was for areas within 1 km of the nearest wooded edge (Figure 9). The effect of NDVI on mule deer resource selection was not significant on its own nor with interactions.

Although natural features described most of mule deer resource selection in our study area, inclusion of anthropogenic features improved our resource selection model. Road density (km/km^2) and the number of active well pads within 2 km both had negative relationships with mule deer resource selection (Figure 10, Figure 11). Drilling rigs were too scarce across the study area to model their effect on resource selection (<0.2% of available sites had drilling rigs within 2 km).

We created a predictive map of relative probability of selection for each 30 m pixel across the study area (Figure 12). Because TPI had the strongest influence on our model (Table 4), areas with the highest probability of use corresponded highly with breaks habitats (Figure 13).

Our model predicted mule deer selection reasonably well, with 28.2% of used locations predicted to have the highest relative probability of selection and 73% of used locations ranked in the top 3 of the 6 available choices. The used locations were only predicted to be the least probable of selection out of the available choices 4.4% of the time, providing further support for the utility of our model.

Discussion

As in the North Dakota portion of this research, we found little evidence that active well pads are driving mule deer resource selection. Mule deer resource selection in response to energy-related development has been mixed across studies. In Wyoming there was avoidance of active well pads (Sawyer et al. 2017), but in Colorado and North Dakota there was little to no avoidance of well pads (Northup et al. 2015 and Kolar et al. 2017, respectively). However, in all three states there was avoidance of drilling rigs, from 600 m (Northrup et al. 2016, Kolar et al. 2017) to 3.7 km (Saywer et al. 2009). In our analysis, as in the neighboring study in North Dakota, the well pad density at 2 km was included in the top model but did not have a strong effect on the relative probability of resource selection. During migration in the Piceance Basin, Lendrum et al. (2012) did not detect mule deer avoiding areas closer to well pads; rather, deer selected areas closer to well pads in their developed sites. Lendrum et al. (2012) hypothesized that increased topography and vegetative cover might have mitigated the influence of indirect effects of drilling rigs on mule deer resource selection. Ungulates have also shown suppressed responses to anthropogenic development in areas with decreased visual distance (Webb et al. 2011, Montgomery et al. 2012). Even though parts of our study areas had very open vegetation types, the topography may help to mitigate potential effects of active well pads.

There were not enough drilling rigs in areas used by mule deer in Montana to model the effect of drilling rigs, but the presence of a drilling rig within 600m was the strongest factor affecting mule deer resource selection in North Dakota. Like Northrup et al. (2015) in the Piceance Basin of northwestern Colorado, we determined the strongest negative predictor of mule deer use to be the density of drilling rigs within 600 m across all seasons. Sawyer et al. (2009) documented avoidance of drilling rigs on winter range, but in our study, avoidance was even stronger in other seasons, particularly in summer and autumn. Although winter habitat can be crucial for mule deer and ungulate population growth in general (Forrester and Wittmer 2013), ungulates might be using areas of increased development in winter when the need for foraging outweighs the cost of vigilance. Compared to the Pinedale Anticline (Sawyer et al. 2009), both the Piceance Basin (Northrup et al. 2015) and the Little Missouri Badlands (Kolar et al. 2017) had greater topographical relief and vegetative cover.

Several studies identify road density (or traffic) as an important driver of age-related resource selection patterns. Sawyer et al. (2009) determined that high levels of traffic near well pads helped drive winter habitat selection patterns at their site, and Northrup et al. (2015) suggested that reduced vehicle traffic is likely one of the best mitigation strategies to benefit mule deer in energy landscapes. In the North Dakota study, mule deer showed stronger avoidance of areas with high road densities, particularly during the day. Mule deer in North Dakota were twice as likely to select areas with road densities of 1.4 km/km^2 or less (Kolar et al. 2017). However, only 0.4% of available locations in our study area had road densities >1.4 km/km^2, and traffic on those roads was likely lower than traffic levels in North Dakota where development levels were higher. In our eastern Montana study areas, roads did not show strong relationships with mule deer resource selection.

The principal factors driving mule deer resource selection in Montana were topographic features and vegetation. This is similar to what was found in North Dakota in areas where drilling rigs were not present (Kolar et al. 2017). We produced a predictive map that is based largely on TPI landforms, slope, and vegetation type (i.e. those predictors had the most significant odds ratios). In Montana, it will be very helpful as future development actions are proposed, to use this predictive map to help weigh the value of prospective parcels for mule deer.

Finally, it is possible that ruggedness was not as useful for predicting habitat use because it was measured at a larger scale (90 x 90 m grid cell) than slope (30 x 30 m grid cell). In North Dakota, the predictive map failed to identify high use in some areas that are known to have high mule deer densities, and it was theorized that these areas contain topographic or vegetative structure that was too small to identify with existing data resolution (e.g. small patches of buffaloberry, shallow creek beds, or sandstone outcroppings that would not have been classified by 30 m elevation data nor 30 m NASS vegetation data; Kolar et al. 2017). Thus, we must acknowledge that it is likely that some selection is occurring at scales smaller than the scale of our vegetation or elevation data.

Management Implications

The two most crucial periods for mule deer population growth and persistence are: 1) fawn recruitment (Jun - Sep) and 2) winter survival (Dec - Mar; Forrester and Wittmer 2013). Hebblewhite (2008) recommended minimizing human disturbance during the winter on mule deer winter range. In North Dakota, mule deer avoided drilling rigs and areas with increased road density in all seasons (Kolar et al. 2017), so managers should consider negative effects during the summer fawning and fawn rearing season. Although is appears that current levels of development in our study area are not driving mule deer resource selection, future development is likely based on the mineral resources in the area. We have produced a useful spatial model that could be used to identify valuable mule deer habitat in the eastern Montana ecoregions. In these areas, we would follow recommendations from Kolar et al. (2017). Specifically, well spacing that minimizes the development of new roads (and increased traffic) will have fewer negative effects on mule deer habitat. Although it is not realistic that drilling be restricted in summer and winter, it could benefit deer to consider spacing of drilling rigs during these crucial periods. Additionally, because deer selected ridges and heads of draws more than any other landform, we suggest that anthropogenic infrastructure should be placed in flatter (< 15% slope), open areas (>1.1 km from wooded edges) when possible.

We provide data that could be used to improve the primary mule deer range maps in eastern Montana. Although most of eastern Montana may be considered mule deer habitat, our models could help to identify areas that are most likely to be selected.

Table 1. Organization of variables in respective hypothesis sets used to model resource selection of mule deer in eastern Montana from 2014 to 2015.

Hypothesis	Models
Vegetation	Vegetation Class[a] Wooded edge (distance to nearest wooded edge) Interspersion Juxtaposition Index (IJI)[b] NDVI[c]
Topography	Northness (sine of aspect) Slope (%) Ruggedness (vector ruggedness measure, 0 to 1) Landform[d]
Anthropogenic Development	Distance to nearest road Road density (within 2,000 m buffer) Density of active well pads (within 900 m) Presence of drilling rig (calculated within 600 m and 2500 m)
(Interactions)	Age[e] Season[f] Time of Day[g]

[a] Vegetation Class from National Agriculture Statistics Survey data (wooded, shrubland, grassland, legume crops, row crops, fallow/planted hay, barren)

[b] IJI = a measure of landscape homogeneity

[c] NDVI = Normalized Difference Vegetation Index, a measure of vegetation greenness

[d] Landform = topographic concavity calculated using the Topographic Position Index (ridge or head of draw, mid to upper slope, lower slope, valley, flat)

[e] Age = mule deer age assuming 01 June fawning date (<1 = fawn, >1 = adult)

[f] Season: summer (01 Jun – 30 Sep), fall (01 Oct – 31 Dec), winter (01 Jan – 31 Mar), spring (01 Apr – 31 May)

[g] Time of Day = day, night or crepuscular (+/- 2 hours from sunrise or sunset).

Table 2. Summary of mule deer captured during three capture events in North Dakota and two capture events in Montana, December 2012[a] – 2014.

	North Dakota			Montana		
Year	Does	Fawns	Total	Does	Fawns	Total
2012[a]	60	30	90	-	-	-
2013[b]	16	30	46	20	20	40
2014	25	46	71	10	23	33
Total	101	106	207	**30**	**43**	**73**

[a] The initial capture in North Dakota was postponed until February 2013

[b] The initial capture in Montana was postponed until February 2014

Table 3. Number of mule deer (n) and used/random mule deer locations from 2014-2015 in eastern Montana that we used for discrete choice analyses.

Age	DayTime[a]	Season[b]	n	Used	Random
Adult	Day	Summer	51	15,340	76,700
Adult	Day	Autumn	40	3,611	18,055
Adult	Day	Spring	38	6,649	33,245
Adult	Day	Winter	42	7,517	37,585
Adult	Crepuscular	Summer	51	11,914	59,570
Adult	Crepuscular	Autumn	40	4,798	23,990
Adult	Crepuscular	Spring	39	5,287	26,435
Adult	Crepuscular	Winter	42	9,431	47,155
Adult	Night	Summer	50	8,303	41,515
Adult	Night	Autumn	40	5,779	28,895
Adult	Night	Spring	39	3,761	18,805
Adult	Night	Winter	42	11,835	59,175
Fawn	Day	Spring	29	3,161	15,805
Fawn	Day	Winter	40	3,682	18,410
Fawn	Crepuscular	Spring	29	2,519	12,595
Fawn	Crepuscular	Winter	40	4,544	22,720
Fawn	Night	Spring	29	1,763	8,815
Fawn	Night	Winter	40	5,576	27,880
Total				115,470	577,350

[a] Day = 2 hours after sunrise - 2 hours before sunset; Crepuscular = within 2 hours of sunrise or sunset; Night = 2 hours after sunset - 2 hours before sunrise

[b] Summer = Jun. 1 - Sep. 31; Autumn = Oct. 1 - Nov. 30; Winter = Dec. 1 - Mar. 31; Spring = Apr. 1 - May 31

Table 4. Estimates, robust standard errors of estimates (SE), odds ratios (OR), odds ratio 95% confidence limits (OR L95, OR U95), and significance levels (SL) for variables in the global model predicting mule deer selection in eastern Montana from 2014-2015. Colons represent interactions between variables. The reference state (variables without interactions) represents adults in summer during the day.

Variable[a]	Estimate	SE	OR	OR L95	OR U95	SL[c]
Road Density	-0.1425	0.0102	0.8672	0.658	1.1429	
Wells2000	-0.2628	0.0126	0.7689	0.5584	1.0589	
NDVI	0.4901	0.0105	1.6324	0.9843	2.7072	.
Ruggedness	0.1625	0.0115	1.1764	1.1078	1.2493	***
Ruggedness_sq	-0.1053	0.0100	0.9	0.8501	0.9529	***
Slope	0.6247	0.0143	1.8676	1.5623	2.2326	***
Slope_sq	-0.0804	0.0050	0.9228	0.8771	0.9708	**
Northness	0.0240	0.0084	1.0243	0.9582	1.0949	
TPI Ridge	1.5148	0.0369	4.5484	3.0734	6.7314	***
TPI Upper Slope	0.7435	0.0380	2.1033	1.5839	2.7929	***
TPI Lower Slope	0.6292	0.0386	1.8761	1.3056	2.6958	***
TPI Valley	0.4090	0.0384	1.5052	1.0356	2.1879	*
NASS Barren	-0.1518	0.0496	0.8591	0.6753	1.093	
NASS Crop	-1.4869	0.0882	0.2261	0.1308	0.3909	***
NASS Hay	0.0010	0.0543	1.001	0.7577	1.3223	
NASS Legume	-0.2219	0.0952	0.801	0.5291	1.2126	
NASS Shrub	0.6804	0.0354	1.9747	1.534	2.5421	***
NASS Wood	0.7929	0.0290	2.2098	1.7481	2.7935	***
IJI	0.0412	0.0124	1.0421	0.682	1.5923	
IJI_sq	-0.1262	0.0078	0.8814	0.6657	1.1671	
WoodEdge	-0.1572	0.0111	0.8546	0.5737	1.2729	
Road Density:Autumn	-0.1105	0.0161	0.8954	0.7412	1.0816	
Road Density:Spring	0.0998	0.0139	1.105	0.8928	1.3675	
Road Density:Winter	0.2064	0.0122	1.2293	0.99	1.5264	.

Road Density:Fawn	0.0798	0.0123	1.083	0.729	1.6089	
Road Density:Crepuscular	-0.0682	0.0112	0.934	0.9088	0.96	***
Road Density:Night	-0.1465	0.0115	0.8637	0.8238	0.9057	***
Wells2000:Autumn	0.0222	0.0189	1.0224	0.856	1.2212	
Wells2000:Spring	-0.2135	0.0182	0.8078	0.6751	0.9665	*
Wells2000:Winter	-0.1956	0.0153	0.8223	0.664	1.0185	.
Wells2000:Fawn	-0.0081	0.0173	0.9919	0.6482	1.5178	
Wells2000:Crepuscular	0.0434	0.0146	1.0444	1.0063	1.0839	*
Wells2000:Night	0.0801	0.0147	1.0834	1.0236	1.1466	**
NDVI:Autumn	-0.3029	0.0155	0.7387	0.4542	1.2012	
NDVI:Spring	-0.1851	0.0140	0.831	0.5095	1.3554	
NDVI:Winter	-0.3921	0.0122	0.6757	0.3902	1.1698	
NDVI:Fawn	0.3669	0.0133	1.4433	0.6325	3.2934	
NDVI:Crepuscular	0.0034	0.0113	1.0034	0.9579	1.051	
NDVI:Night	-0.0047	0.0115	0.9953	0.9285	1.067	
Ruggedness:Autumn	-0.0412	0.0162	0.9596	0.9173	1.0039	.
Ruggedness:Spring	0.0476	0.0151	1.0487	0.9954	1.1049	.
Ruggedness:Winter	0.1037	0.0134	1.1092	1.0512	1.1705	***
Ruggedness:Fawn	-0.0055	0.0146	0.9946	0.945	1.0467	
Ruggedness:Crepuscular	-0.0589	0.0128	0.9428	0.9132	0.9735	***
Ruggedness:Night	-0.1107	0.0128	0.8952	0.863	0.9285	***
Ruggedness_sq:Autumn	0.0378	0.0122	1.0385	0.9863	1.0936	
Ruggedness_sq:Spring	-0.0251	0.0126	0.9752	0.9189	1.0349	
Ruggedness_sq:Winter	-0.0381	0.0113	0.9626	0.9122	1.0159	
Ruggedness_sq:Fawn	0.0193	0.0126	1.0194	0.9712	1.0701	
Ruggedness_sq:Crepuscular	0.0429	0.0110	1.0438	1.0079	1.081	*
Ruggedness_sq:Night	0.0317	0.0108	1.0322	0.9923	1.0738	
Slope:Autumn	-0.2928	0.0207	0.7462	0.6681	0.8334	***
Slope:Spring	0.0663	0.0196	1.0685	0.9062	1.2599	
Slope:Winter	0.4719	0.0174	1.603	1.3148	1.9544	***
Slope:Fawn	0.0757	0.0197	1.0787	0.9082	1.2812	
Slope:Crepuscular	-0.2695	0.0162	0.7637	0.7221	0.8077	***
Slope:Night	-0.5171	0.0165	0.5963	0.5391	0.6594	***

Slope_sq:Autumn	0.0803	0.0075	1.0836	1.0467	1.1219	***
Slope_sq:Spring	-0.0706	0.0075	0.9318	0.8897	0.9759	**
Slope_sq:Winter	-0.1172	0.0063	0.8894	0.8447	0.9364	***
Slope_sq:Fawn	-0.0384	0.0080	0.9623	0.9166	1.0104	
Slope_sq:Crepuscular	0.0295	0.0059	1.0299	1.0136	1.0465	***
Slope_sq:Night	0.0647	0.0062	1.0668	1.0419	1.0923	***
Northness:Autumn	-0.0300	0.0125	0.9705	0.9246	1.0187	
Northness:Spring	-0.0098	0.0113	0.9903	0.9436	1.0392	
Northness:Winter	-0.0233	0.0100	0.977	0.9214	1.036	
Northness:Fawn	-0.0101	0.0106	0.99	0.9309	1.0528	
Northness:Crepuscular	-0.0236	0.0093	0.9766	0.9531	1.0007	.
Northness:Night	-0.0023	0.0094	0.9977	0.9563	1.0409	
TPI:Ridge:Autumn	0.2788	0.0461	1.3216	0.9946	1.756	.
TPI:Upper Slope:Autumn	0.0305	0.0454	1.0309	0.7428	1.4309	
TPI:Lower Slope:Autumn	-0.0933	0.0503	0.9109	0.6994	1.1864	
TPI:Valley:Autumn	0.0057	0.0484	1.0057	0.7366	1.3731	
TPI:Ridge:Spring	0.1767	0.0468	1.1933	0.8861	1.6071	
TPI:Upper Slope:Spring	0.0051	0.0481	1.0051	0.7517	1.3439	
TPI:Lower Slope:Spring	0.3051	0.0487	1.3567	1.0479	1.7566	*
TPI:Valley:Spring	0.4953	0.0478	1.641	1.2179	2.2111	**
TPI:Ridge:Winter	-0.0930	0.0425	0.9112	0.7055	1.1767	
TPI:Upper Slope:Winter	-0.0851	0.0432	0.9184	0.692	1.2188	
TPI:Lower Slope:Winter	0.4918	0.0434	1.6353	1.2651	2.1138	***
TPI:Valley:Winter	0.7868	0.0426	2.1964	1.6587	2.9083	***
TPI:Ridge:Fawn	-0.2082	0.0461	0.812	0.5476	1.2042	
TPI:Upper Slope:Fawn	-0.1331	0.0474	0.8753	0.5808	1.3192	
TPI:Lower Slope:Fawn	-0.1393	0.0462	0.8699	0.5851	1.2935	
TPI:Valley:Fawn	-0.1751	0.0453	0.8394	0.5852	1.204	
TPI:Ridge:Crepuscular	-0.5377	0.0413	0.5841	0.4927	0.6925	***
TPI:Upper Slope:Crepuscular	-0.3032	0.0427	0.7385	0.6213	0.8777	***
TPI:Lower Slope:Crepuscular	-0.1756	0.0428	0.839	0.7044	0.9993	*
TPI:Valley:Crepuscular	-0.1154	0.0422	0.891	0.7315	1.0854	
TPI:Ridge:Night	-0.8553	0.0407	0.4252	0.3331	0.5427	***

TPI:Upper Slope:Night	-0.3328	0.0414	0.7169	0.5564	0.9236	*
TPI:Lower Slope:Night	-0.2516	0.0420	0.7775	0.6147	0.9835	*
TPI:Valley:Night	-0.2728	0.0413	0.7612	0.5834	0.9932	*
NASS Barren:Autumn	-0.0761	0.0876	0.9267	0.7363	1.1665	
NASS Crop:Autumn	1.1627	0.0716	3.1985	2.1943	4.6624	***
NASS Hay:Autumn	0.2182	0.0660	1.2439	1.0263	1.5076	*
NASS Legume:Autumn	0.1604	0.0883	1.174	0.7646	1.8027	
NASS Shrub:Autumn	-0.1123	0.0587	0.8938	0.7344	1.0878	
NASS Wood:Autumn	-0.0062	0.0452	0.9938	0.7989	1.2363	
NASS Barren:Spring	-0.0875	0.0731	0.9163	0.7383	1.1371	
NASS Crop:Spring	0.2684	0.0892	1.3079	0.7818	2.1879	
NASS Hay:Spring	-0.2191	0.0703	0.8032	0.6247	1.0328	.
NASS Legume:Spring	-0.0357	0.0983	0.9649	0.5958	1.5628	
NASS Shrub:Spring	-0.1144	0.0500	0.8919	0.6996	1.1371	
NASS Wood:Spring	-0.0778	0.0412	0.9252	0.7315	1.1701	
NASS Barren:Winter	0.4593	0.0593	1.583	1.263	1.9841	***
NASS Crop:Winter	0.7856	0.0723	2.1938	1.2231	3.9348	**
NASS Hay:Winter	-0.5171	0.0654	0.5962	0.4153	0.8561	**
NASS Legume:Winter	0.0468	0.0855	1.0479	0.6139	1.7887	
NASS Shrub:Winter	-0.2781	0.0454	0.7572	0.6215	0.9226	**
NASS Wood:Winter	-0.0043	0.0363	0.9958	0.7999	1.2396	
NASS Barren:Fawn	-0.1057	0.0656	0.8997	0.6729	1.2031	
NASS Crop:Fawn	-0.5423	0.0866	0.5814	0.2776	1.2179	
NASS Hay:Fawn	-0.0698	0.0734	0.9325	0.62	1.4025	
NASS Legume:Fawn	-0.3299	0.1012	0.719	0.3831	1.3495	
NASS Shrub:Fawn	0.1816	0.0464	1.1992	0.9285	1.5488	
NASS Wood:Fawn	-0.2942	0.0460	0.7451	0.5629	0.9863	*
NASS Barren:Crepuscular	-0.3337	0.0547	0.7163	0.6341	0.8092	***
NASS Crop:Crepuscular	0.8828	0.0897	2.4176	1.9201	3.0441	***
NASS Hay:Crepuscular	0.3293	0.0615	1.39	1.1664	1.6564	***
NASS Legume:Crepuscular	0.7380	0.1019	2.0917	1.4728	2.9708	***
NASS Shrub:Crepuscular	-0.2246	0.0402	0.7988	0.7124	0.8958	***
NASS Wood:Crepuscular	-0.3205	0.0333	0.7258	0.6582	0.8003	***

NASS Barren:Night	-0.6819	0.0595	0.5056	0.419	0.6101	***
NASS Crop:Night	1.1932	0.0859	3.2978	2.4902	4.3672	***
NASS Hay:Night	0.4647	0.0608	1.5916	1.3088	1.9354	***
NASS Legume:Night	1.1102	0.0978	3.0349	2.0378	4.5199	***
NASS Shrub:Night	-0.4570	0.0428	0.6332	0.5364	0.7475	***
NASS Wood:Night	-0.7168	0.0356	0.4883	0.4257	0.5601	***
IJI:Autumn	0.0780	0.0187	1.0811	0.8948	1.3062	
IJI:Spring	0.0024	0.0166	1.0024	0.7913	1.2698	
IJI:Winter	0.0342	0.0146	1.0348	0.7999	1.3385	
IJI:Fawn	0.0375	0.0155	1.0382	0.6851	1.5734	
IJI:Crepuscular	0.0821	0.0137	1.0855	1.0275	1.1468	**
IJI:Night	0.1196	0.0138	1.1271	1.036	1.2262	**
IJI_sq:Autumn	-0.1159	0.0122	0.8905	0.7945	0.9982	*
IJI_sq:Spring	0.0042	0.0105	1.0042	0.8669	1.1633	
IJI_sq:Winter	0.0322	0.0092	1.0327	0.8818	1.2094	
IJI_sq:Fawn	-0.0304	0.0100	0.97	0.7611	1.2363	
IJI_sq:Crepuscular	-0.0008	0.0087	0.9992	0.9688	1.0305	
IJI_sq:Night	-0.0032	0.0088	0.9968	0.9526	1.043	
WoodEdge:Autumn	-0.1923	0.0182	0.825	0.658	1.0344	.
WoodEdge:Spring	-0.2305	0.0162	0.7941	0.5877	1.073	
WoodEdge:Winter	-0.0631	0.0138	0.9389	0.6865	1.2839	
WoodEdge:Fawn	0.3626	0.0131	1.4371	1.0108	2.0431	
WoodEdge:Crepuscular	-0.1140	0.0124	0.8923	0.8516	0.9349	
WoodEdge:Night	-0.2071	0.0127	0.8129	0.7564	0.8736	

[a] Road Density = road density (km/km^2) of primary and secondary roads; NDVI = normalized difference vegetation index; Rugged = ruggedness index; Slope = percent slope; Northness = quantity describing how north-facing the slope is; TPI = landform topographic position index; NASS = national agricultural statistics service vegetation; IJI = interspersion and juxtaposition index; WoodEdge = distance to wooded edge; Well900 = number of well pads within 900 m; Rig600/2500 = presence/absence of drilling rigs within 600/2500 m.

[b] "_sq" = quadratic form of the variable.

[c] Significance Level: "***" = p-value < 0.001; "**" = p-value < 0.01; "*" = p-value < 0.05; "." = p-value < 0.1

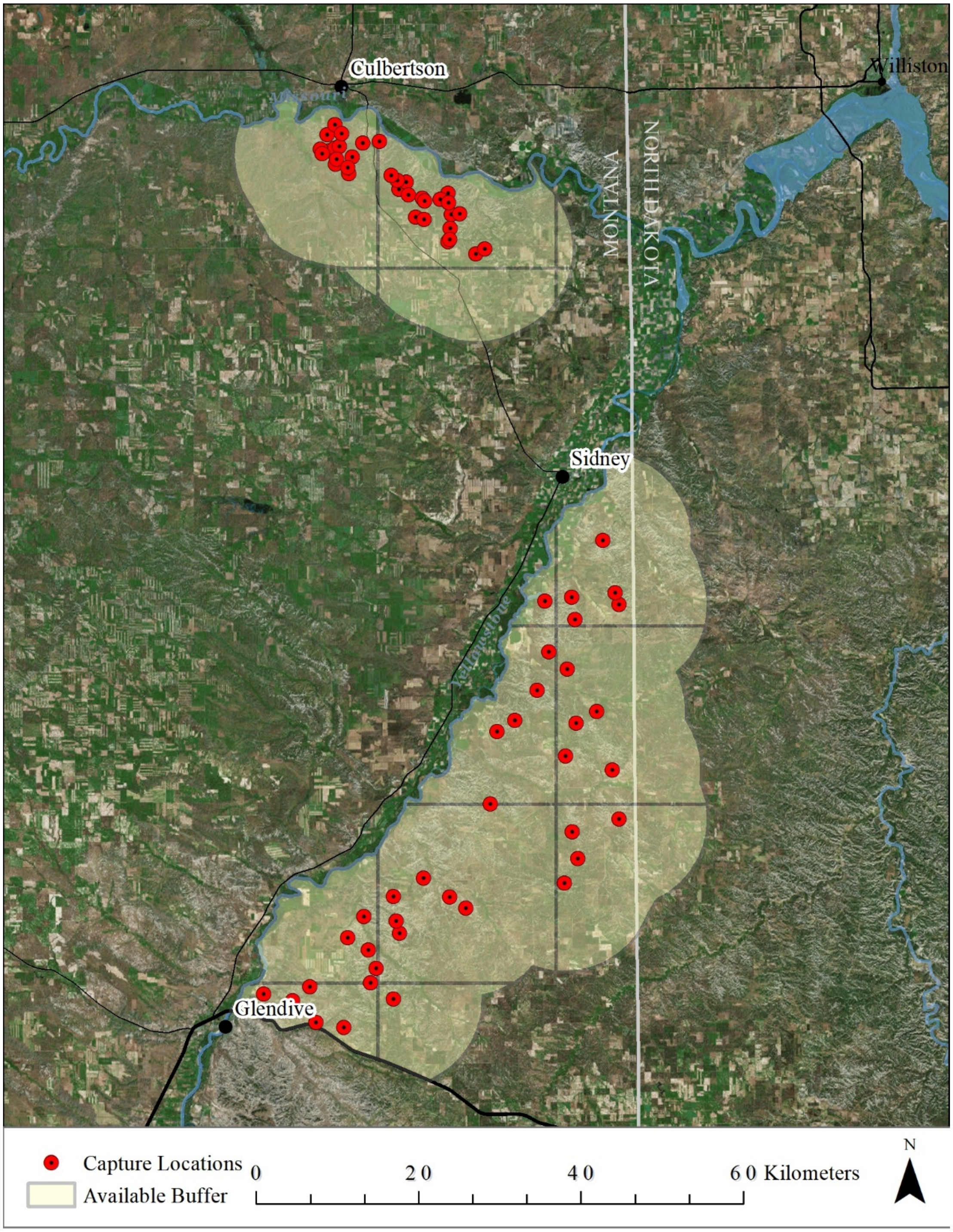


Figure 4. Mule deer capture locations in eastern Montana from 2014 –2015 and extent "available" habitat, defined as the composite area of each capture location buffered by the mean of maximum distances mule deer moved from capture sites (11 km). We randomly placed 5 "available" locations per used location within each grid cell shown.

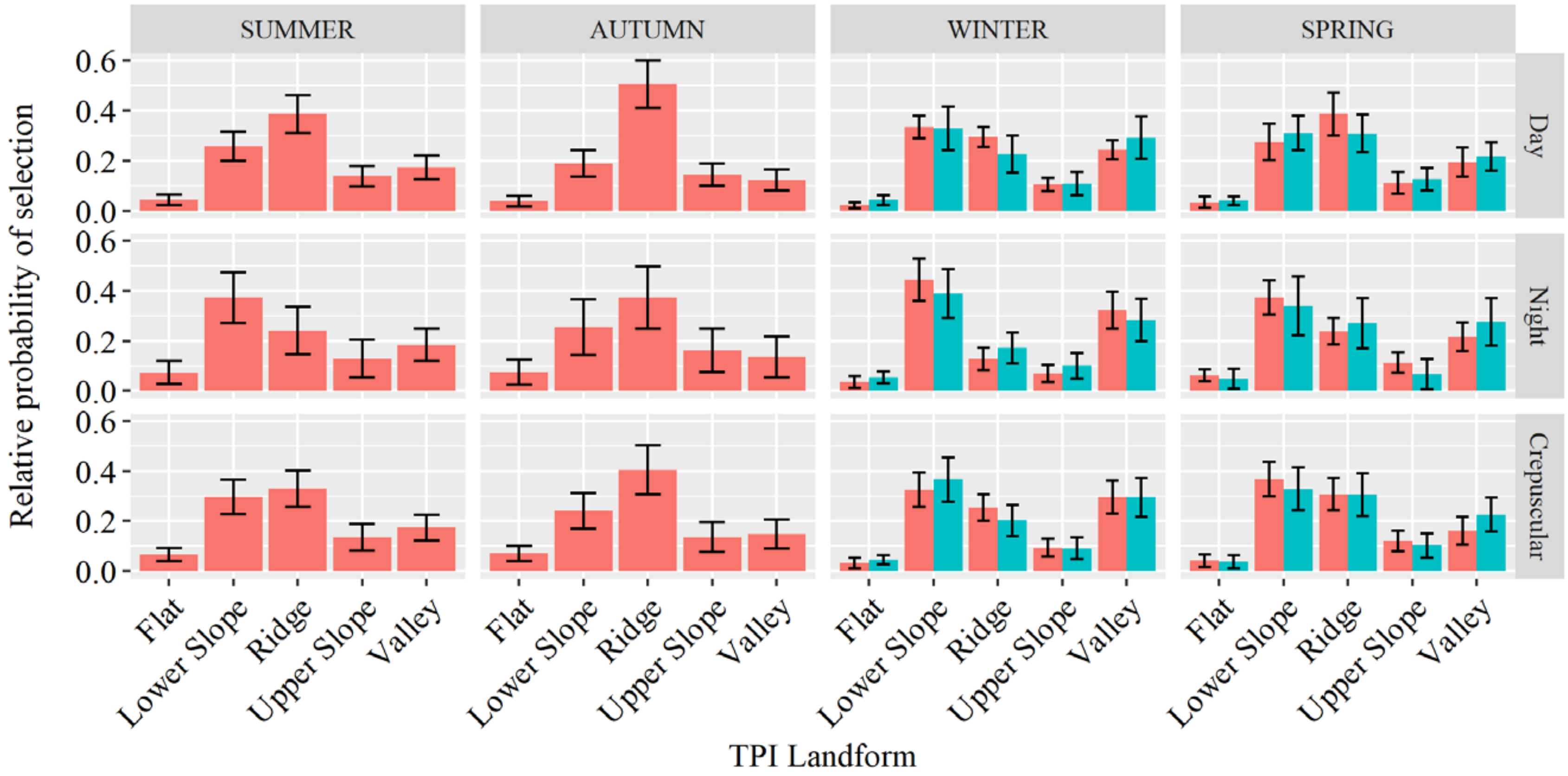


Figure 5. Effect of TPI Landform on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red represents adults, blue represents fawns (no fawns were tagged during summer and autumn seasons), and error bars represent 95% confidence intervals. Probabilities shown are relative, not absolute.

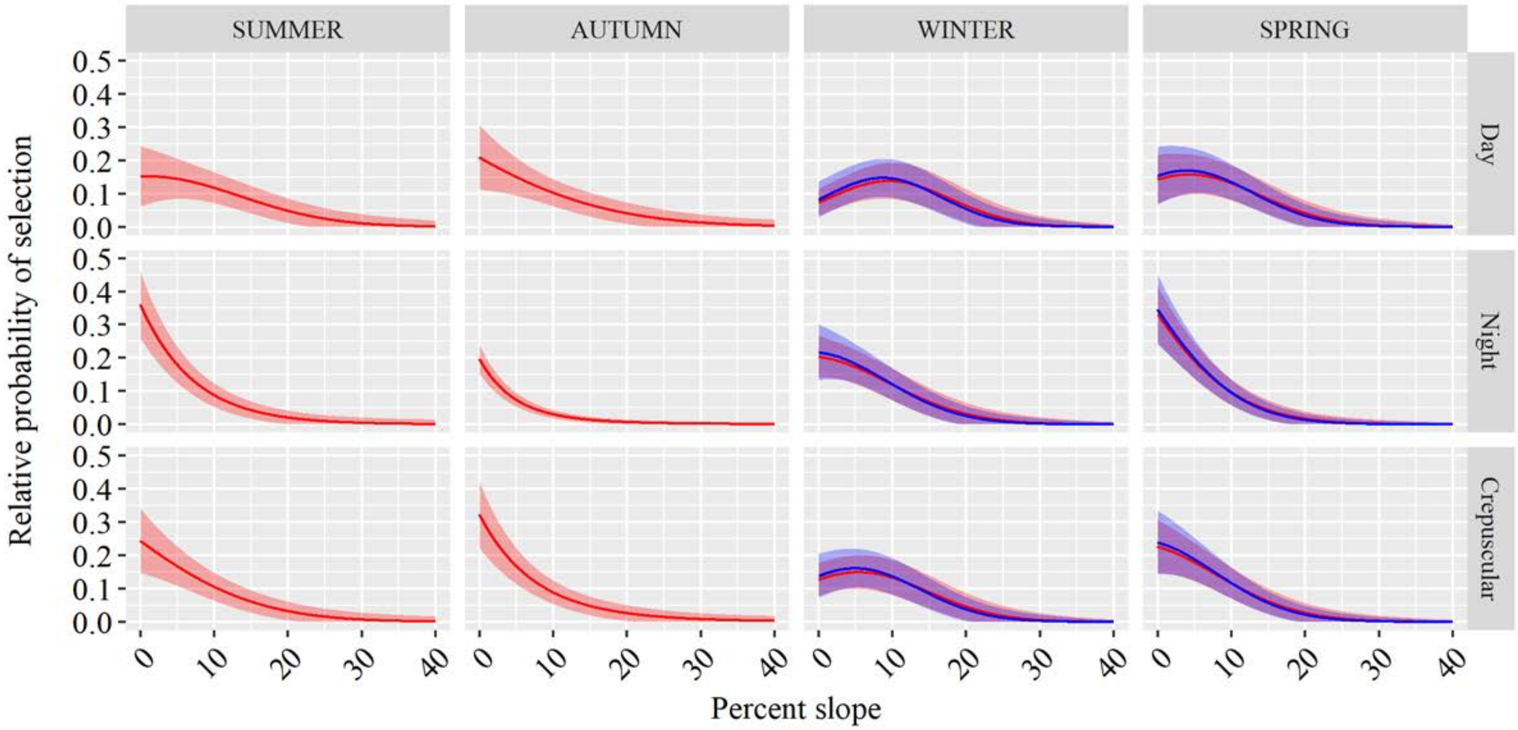


Figure 6. Effect of percent slope on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red represents adults, blue represents fawns (no fawns were tagged during summer and autumn seasons), and ribbons represent 95% confidence intervals. Probabilities shown are relative, not absolute.

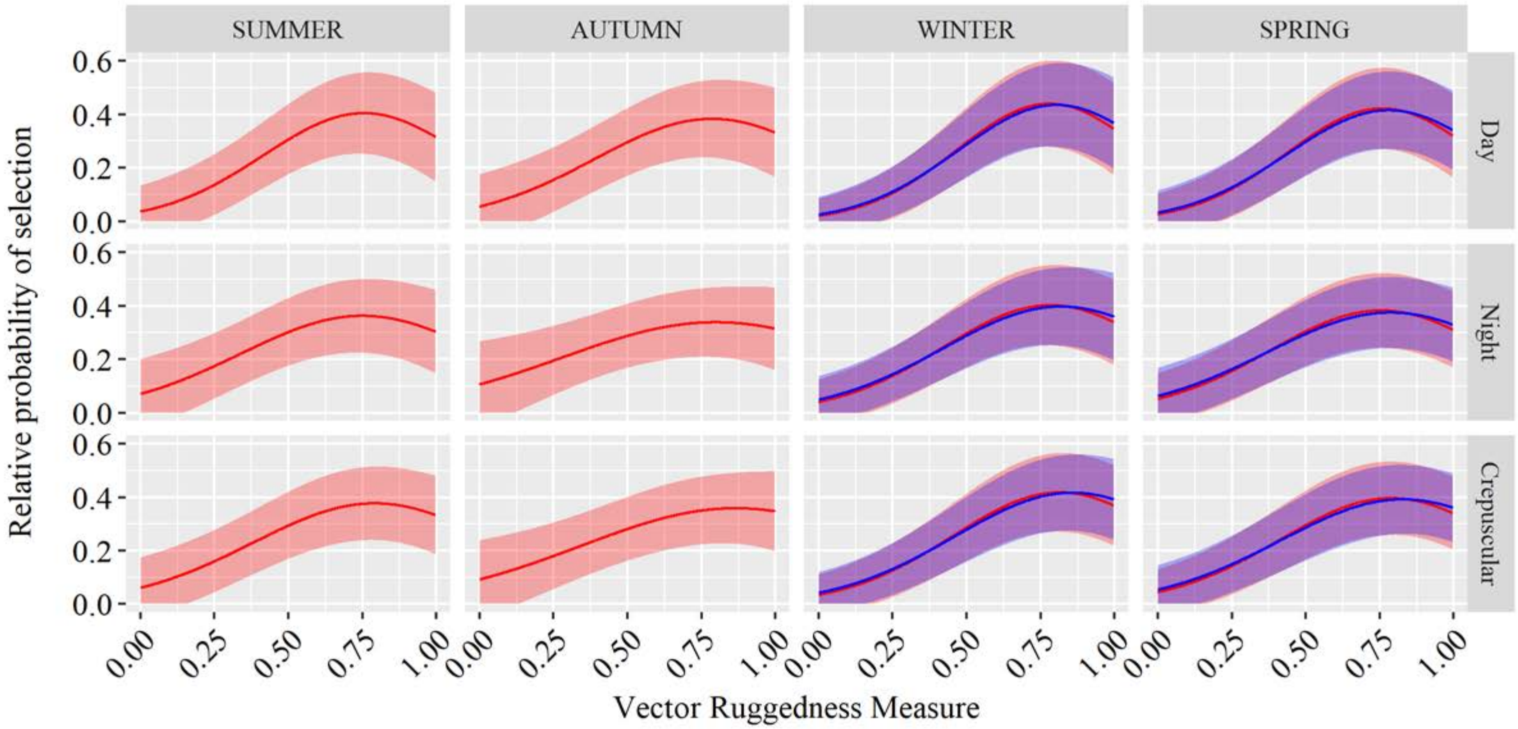


Figure 7. Effect of ruggedness on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Higher ruggedness index values represent more rugged terrain. Red represents adults, blue represents fawns, and ribbons represent 95% confidence intervals; no fawns were tagged during summer and autumn seasons. Probabilities shown are relative, not absolute.

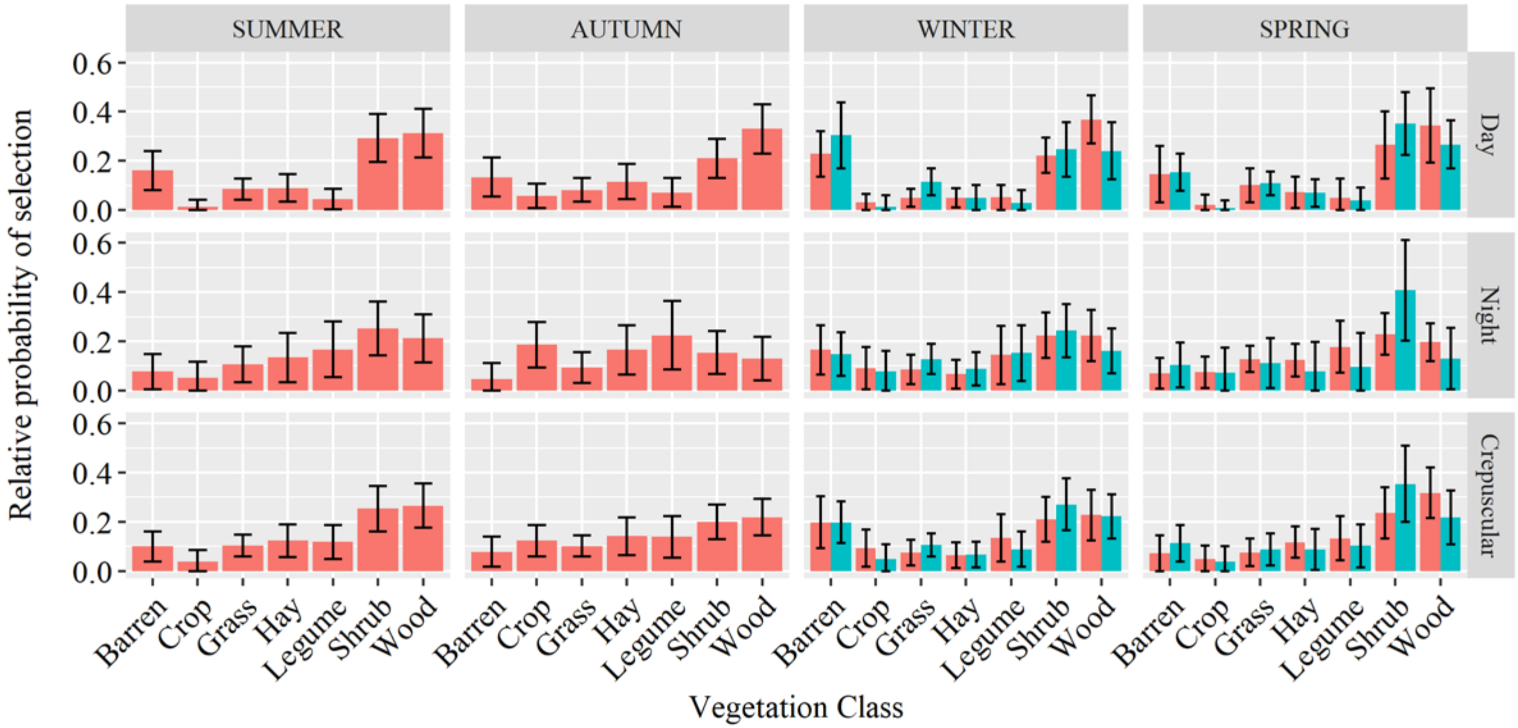


Figure 8. Effect of vegetation type on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red bars represent adults and blue bars represent fawns; no fawns were tagged during summer and autumn seasons. Error bars represent 95% confidence intervals. Probabilities shown are relative, not absolute.

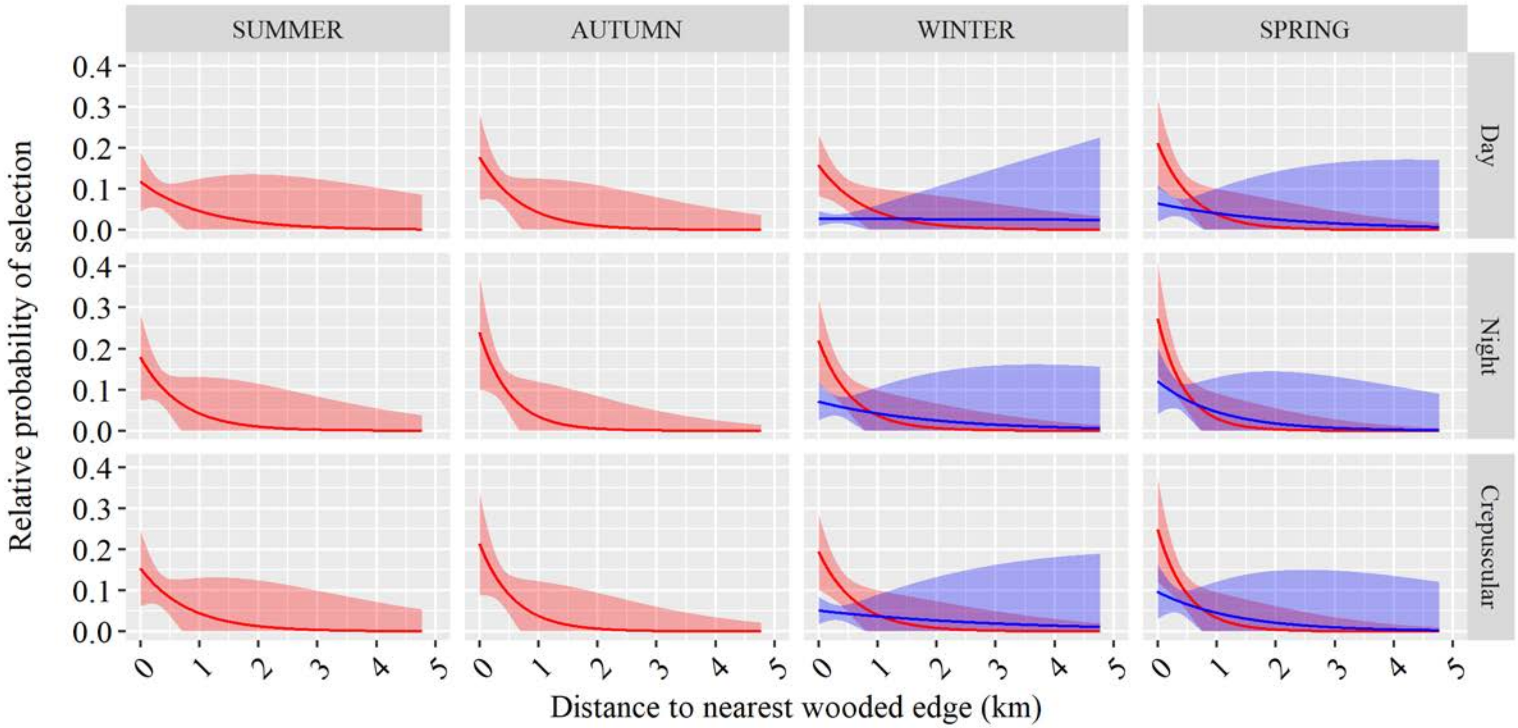


Figure 9. Effect of distance to wooded edge on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red represents adults, blue represents fawns, and ribbons represent 95% confidence intervals; no fawns were tagged during summer and autumn seasons. Probabilities shown are relative, not absolute.

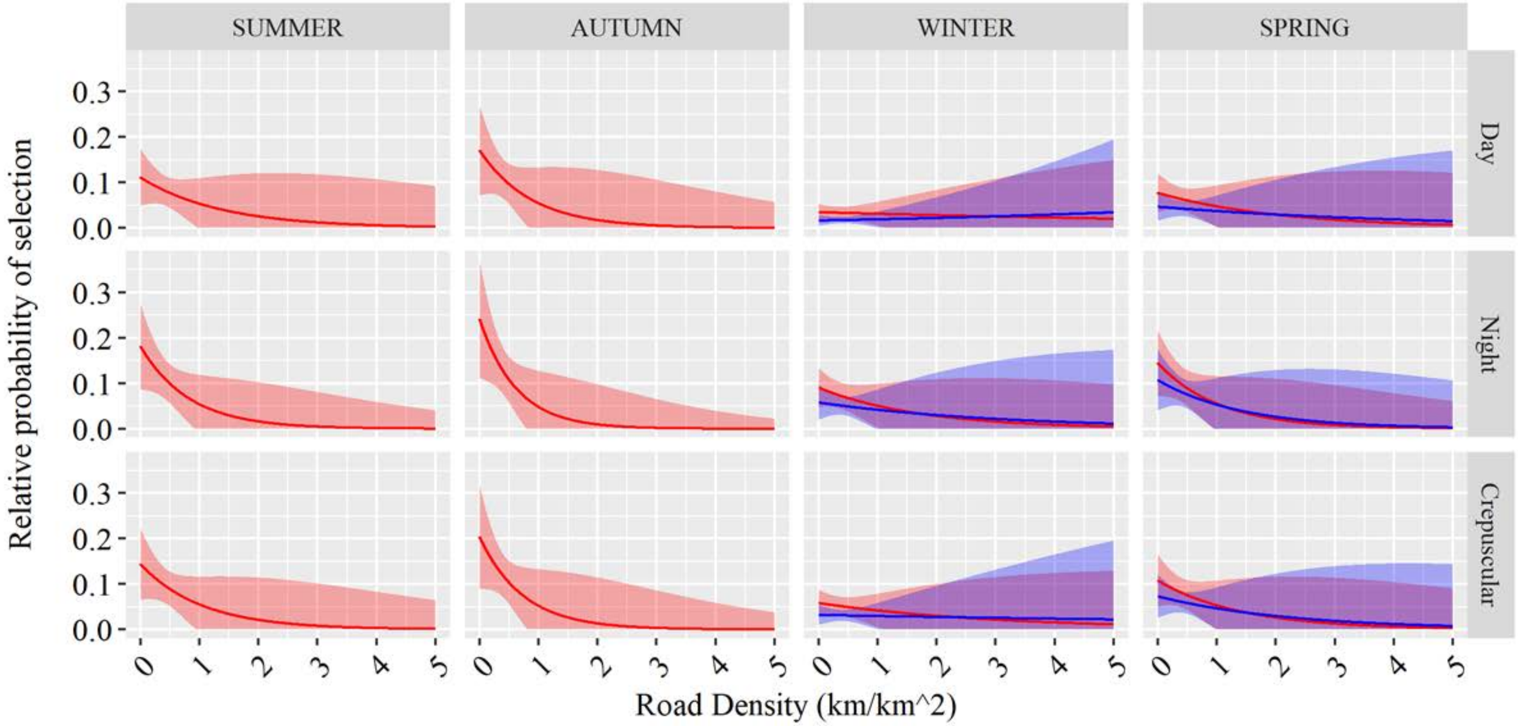


Figure 10. Effect of primary and secondary road density on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red bars represent adults and blue bars represent fawns; no fawns were tagged during summer and autumn seasons. Error bars represent 95% confidence intervals. Probabilities shown are relative, not absolute.

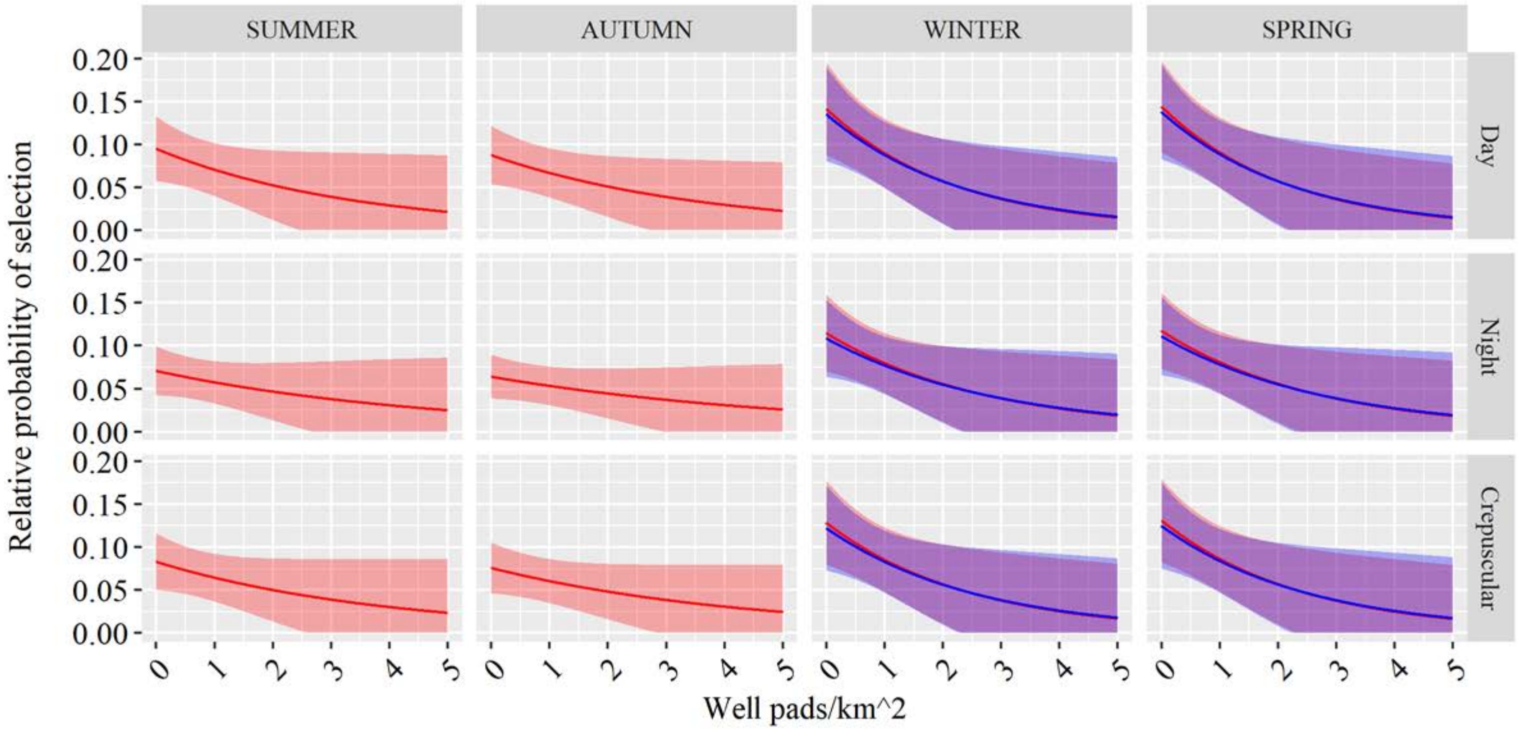


Figure 11. Effect of active well pad density on the relative probability of mule deer selecting locations in eastern Montana from 2014-2015. Red represents adults, blue represents fawns, and ribbons represent 95% confidence intervals; no fawns were tagged during summer and autumn seasons. Probabilities shown are relative, not absolute.

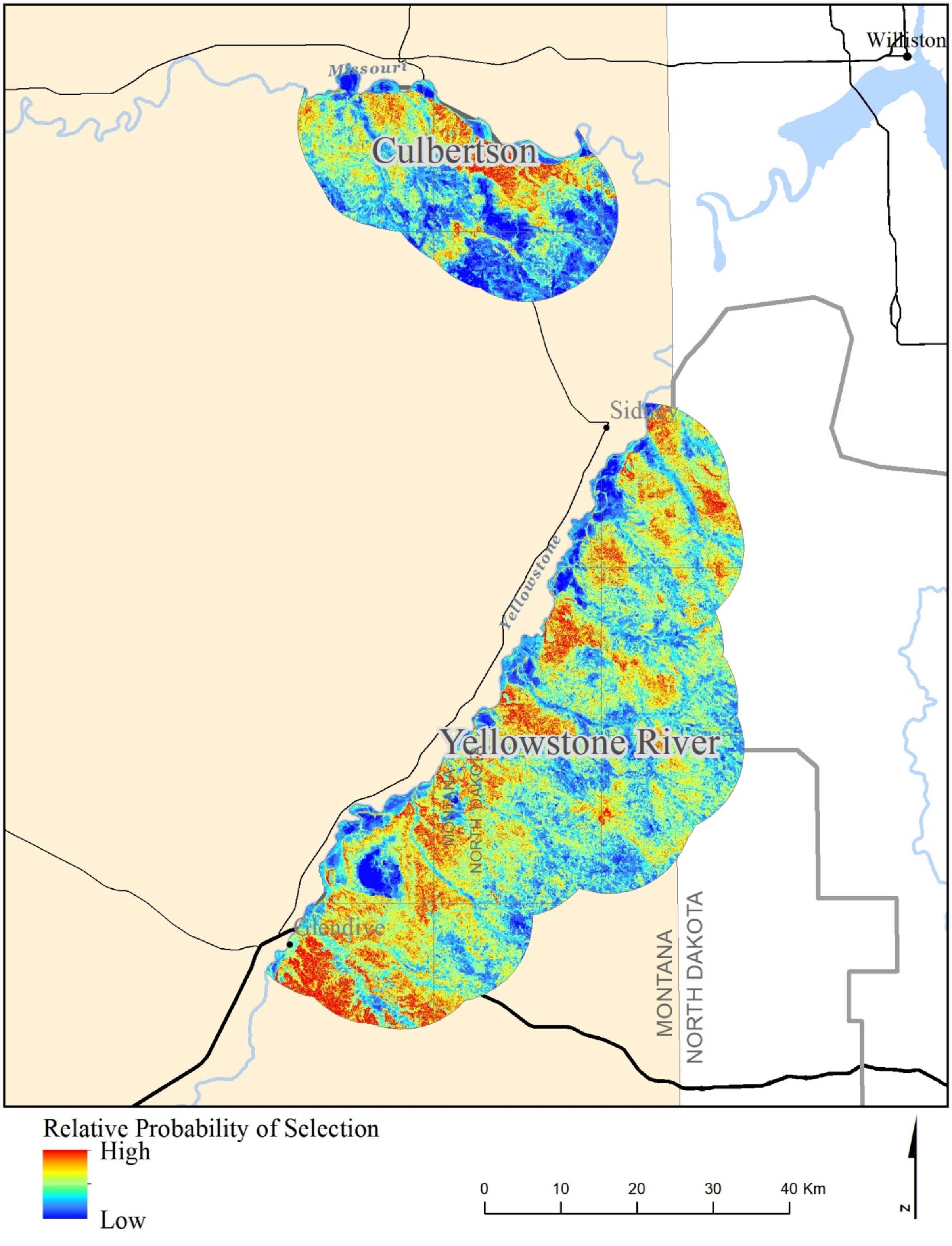


Figure 12. Predictive map of adult mule deer selection during the day in winter across the study area in eastern Montana. Warmer colors represent higher relative probabilities of selection.

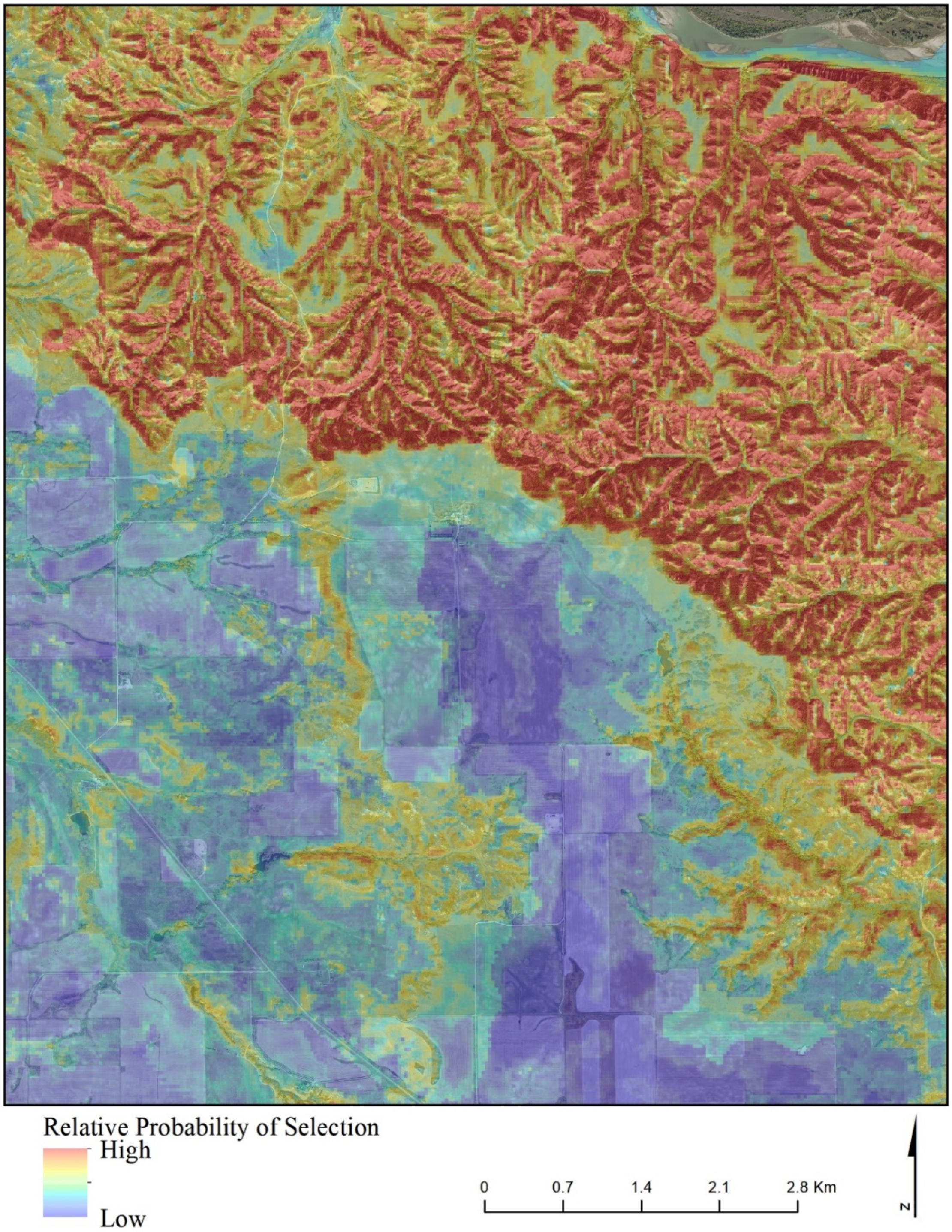


Figure 13. Detailed predictive map of adult mule deer selection during the day in winter across the study area in eastern Montana. Warmer colors represent higher relative probabilities of selection.

Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest, Hungary.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620-623.

Borowik, T., N. Pettorelli, L. Sönnichsen, and B. Jedrzejewska. 2013. European Journal of Wildlife Research 59:675-682.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi model inference: a practical information theoretic approach. Second edition. Springer Verlag, New York, USA.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2017. Setting an evolutionary trap: could the hider strategy be maladaptive for white-tailed deer? Journal of Ethology: DOI 10.1007/s10164-017-0514-z.

Cooper, A. B. and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80:566-575.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Dilts, T. 2015. Topography Toolbox for ArcGIS 10.1 and Earlier. Great Basin Landscape Ecology Lab, University of Nevada, Reno, NV.

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

Fox, R. A. 1989. Mule deer (Odocoileus hemionus) home range and habitat use in an energy-impacted area of the North Dakota Badlands. Master's Thesis. University of North Dakota. Grand Forks, North Dakota, USA. 88 pp.

Franklin, A. B., D. R. Anderson, R. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Fretwell, S. D. and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Frid, A. and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Ecology and Society 6:11.

Hebblewhite, M. 2008. A literature review of the effects of energy development on ungulates: Implications for central and eastern Montana. Report prepared for Montana Fish, Wildlife and Parks, Miles City, MT.

Hebblewhite, M. and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834-844.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345-354.

Horncastle, V. J., R. Fenner Yarborough, B. G. Dickson, and S. S. Rosenstock. 2013. Summer habitat use by adult female mule deer in a restoration-treated ponderosa pine forest: mule deer and forest restoration. Wildlife Society Bulletin 37:707–713.

Jenkerson, C. B., T. Maiersperger, and G. Schmidt. 2010. eMODIS: A user-friendly data source: U.S. Geological Survey Open-File Report 2010–1055, 10 p.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen-Gill model to Yellowstone Grizzly Bears. Journal of Wildlife Management 68:966-978.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530-566.

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

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

Lutz, D. W., J. R. Heffelfinger, S. A. Tessmann, R. S. Gamo, and S. Siegel. 2011. Energy development guidelines for mule deer. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2012. Variation in elk response to roads by season, sex and road type. Journal of Wildlife Management 77:313-325.

National Oceanic and Atmospheric Administration. 2017. 2012-2016 Daily Summaries. https://www.ncdc.noaa.gov/cdo-web/datasets/. Accessed 1 Feb 2017.

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

Northrup, J. M., G. B. Stenhouse, and M. S. Boyce. 2012. Agricultural lands as ecological traps for grizzly bears. Animal Conservation 15:369-377.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

Pulliam, H. R. and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137:S50-S66.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/.

Rice, W. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. Evolutionary Ecology 1:301-314.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419-1426.

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

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

Shafer, B. A., J. M. Northrup, K. White, M. S. Boyce, S. D. Côté, and D. Coltman. 2012. Habitat selection predicts genetic relatedness in an alpine ungulate. Ecology 93:1317-1329.

Switzer, P. V. 1997. Past reproductive success affects future habitat selection. Behavioral Ecology and Sociobiology 40:307-312.

Therneau, T. 2015. A Package for Survival Analysis in S. Version 2.38. http://CRAN.R-project.org/package=survival>.

U.S. Census Bureau. 2016. TIGER/Line Shapefiles (machine-readable data files). <https://www.census.gov/geo/maps-data/data/tiger-line.html>.

United States Department of Agriculture National Agricultural Statistics Service. 2013-2016. USDA, National Agricultural Statistics Service, Cropland Data Layer for the United States. USDA, NASS Marketing and Information Services Office, Washington, D.C.

U.S. Energy Information Administration [USEIA]. 2012. Energy explained: your guide to understanding energy. U.S. Department of Energy, Energy Information Administration, Washington, DC. <http://www.eia.gov/energyexplained/index.cfm> Accessed 04 Aug 2017.

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

Webb, S. L., M. R. Dzialak, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011. Effects of human activity on space use and movement patterns of female elk. Wildlife Society Bulletin 35:261-269.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

CHAPTER II. MOVEMENTS OF MULE DEER IN EASTERN MONTANA

Introduction

“Movement is the glue that connects local population dynamics in space” (Turchin 1996, p. 2086), and increased movement distances to meet daily requirements requires more energy (Parker et al. 1984, Morales et al. 2010). Anthropogenic development has the potential to affect wildlife movements by fragmenting landscapes or by increasing risk aversion. Recent research in the Piceance Basin of Colorado documented longer step lengths for migrating mule deer in areas with high well pad densities (Lendrum et al. 2012). Additional studies have found differences in resource use around development features such as: roads, well pads, and drilling rigs (Sawyer et al. 2006, Northrup et al. 2015; Kolar et al. 2017). It is also possible that ungulates can acclimate to predictable disturbances (Stankowich 2008), and in some instances, show less responsiveness to risk in areas with increased traffic (Brown et al. 2012). In the North Dakota portion of this study, we examined the relationship between movement distances (step lengths; Lendrum et al. 2012) and natural and anthropogenic development features. However, five-hour step lengths of mule deer were too variable to be useful for modelling. To provide meaningful information on movements for the Montana portion of this study, this chapter focuses on migration distances, seasonal site fidelity and home range sizes.

In Montana, mule deer are surveyed in survey blocks, and when results deviate from expectations, it is often assumed that the population has made minor shifts due to snow cover or attraction to higher quality forage (e.g. verdant crops or alfalfa). The mule deer population in eastern Montana is mostly non-migratory (Hamlin and Mackie 1989, Carnes 2009), but managers still observe seasonal population shifts. Additional information on movement distances between seasons would be helpful in interpreting survey results and understanding appropriate scales for addressing depredation complaints. Biologists can use migration information to identify appropriate mitigation for potential barriers to movement, define populations and sub-populations, and better predict disease transmission rates.

Many ungulates show high fidelity to summer home ranges such as: pronghorn (Kolar 2009), white-tailed deer (Campbell 2003), elk (Adams1982), and mule deer (Thomas and Irby 1990, Brown 1992, Sawyer et al. 2005, Polfus 2012). Few studies document dispersals of female adult mule deer, although it is not uncommon for yearlings, especially in May-June when adult females show territoriality prior to fawning (Eberhardt 1984, Hamlin and Mackie 1989, Hygnstrom et al. 2008). Research on pronghorn in South Dakota suggests that yearling dispersals may be the main mechanism to recolonize vacated ranges (Jacques and Jenks 2007). Hamlin and Mackie (1989) reported that 16% of yearling does in an undeveloped area of badlands along the Missouri River in Montana dispersed. Because eastern Montana mule deer populations fluctuate with winter severity and summer precipitation, knowledge of fidelity and dispersal tendencies of mule deer can help managers to better predict recolonization rates after areas have experienced population declines. We will assess home range overlap of yearling and adult (non-yearling) mule deer to determine the level of fidelity to summer home ranges.

Mule deer home ranges across the species distribution are variable in size. Even within populations, mule deer home ranges can range from 87 to 3001 ha (Nicholson et al. 1997). Summer home ranges for yearling and adult female mule deer in North Dakota averaged 236 ha (minimum convex polygon; MCP) in an area with rugged terrain and a great interspersion of vegetation types (Jensen 1988) and 346 ha (range: 110 – 690 ha; MCP) in more open terrain with less variation in vegetation types (Fox 1989). Our movements and fidelity results include summaries of home range sizes for mule deer in our study area. Home range estimates are useful for identifying appropriate scales for management and research.

Methods

We calculated geometric centroids (mean X and Y of coordinates) for individual deer for each season. We calculated Euclidean distances moved between winter and summer seasons to evaluate migration distances. Likewise, Euclidean distances between successive winter and successive summer locations was used to assess seasonal site fidelity. We censored any movements for deer that had fewer than 60 locations for the given season. We summarized site fidelity and movement distances by age using 4 age classes: fawn to yearling, yearling (12-18 months old), and yearling to adult (> 18 months old) and adult. We classified all deer ≥ 18 months as adults because adults captured in December included yearlings, and we could not confidently discern yearlings from adults during capture. Because movement patterns were more varied than “migratory,” “non-migratory,” “disperser,” etc… we also calculated the proportion of deer that were making longer movements between summer and winter. We calculate this proportion for deer that moved > 3.2 km and >16 km. We chose 3.2 km based on an approximated distance it would take for two seasonal ranges to be non-overlapping, and 16 km because it was near the maximum movement distance (excluding extreme outliers) from our preliminary analyses.

We analyzed seasonal and annual home ranges for fawns, yearlings and adults. Fawns were captured in December and graduated to yearlings in June, so we only calculated winter and spring home ranges for fawns. For fawns that survived their first year after capture, we classified them as fawn/yearling. We could only classify yearlings with certainty if we captured them as a fawn; however, some adults may have been captured as 18-month old yearlings. We used 95%

minimum convex polygons (MCP's) to measure home range size. When calculating annual home range, we censored deer that survived less than 330 days post-capture. Although MCP's may over-estimate home range sizes (Franzreb 2006), we were interested in the extent that a mule deer travelled during a year. Further, because MCP's have been used in previous studies in Montana (Carnes 2009), our results are comparable to prior studies.

For movements, home range and fidelity summaries we calculated weighted medians by first averaging data for repeat individuals (i.e. individuals that survived > 2 consecutive seasons or years). Weighted medians ensure that estimates are not biased by individuals that were tracked for multiple seasons.

Results

We analyzed seasonal mule deer movements of 73 mule deer (30 does and 43 fawns) in eastern Montana from February 2014 to June 2016. Movement data were strongly skewed toward lower movement distances, so we summarized distances using medians of movement distances (Figure 14). We removed one outlier, a fawn that left the study area (Figure 15). Movement distances varied by age. Movement distances by fawns ranged from 236 m to 140 km (median = 1.2 km), and 25% moved >3.2 km (2 miles), and 8.3% moved >16.1 km (10 miles; Table 5). Yearling mule deer movements ranged from 236 m to 21 km (median = 1.3 km, and 15.4% moved > 3.2 km (Table 5). Adult doe movements ranged from 41 m to 17 km (median = 608 m), and only 6.1% moved > 3.2 km (Table 5).

We seasonal site fidelity for 30 mule deer (19 does and 11 fawns). Median distances between successive seasonal centroids was similar for each age class, but maximum distances during spring and summer were greater for fawns and yearlings (Table 6). Mule deer does showed strongest fidelity to spring and summer ranges.

We summarized seasonal home ranges (95% MCPs) of 67 deer (29 does and 38 fawns). We removed one fawn that dispersed >160 km and left the study area (Figure 16). We also removed the summer home range for one yearling that made long exploratory movements during the summer and had a summer home range of >98,620 ha. Median seasonal home range sizes ranged from 417 ha to 842 ha, and the smallest ranges were observed in mule deer does during the summer (Table 7). Maximum seasonal home range sizes were large (i.e. >3,000 ha for most seasons and ages, and up to 17, 645 ha for yearling summer home ranges).

Finally, we summarized annual home ranges (95% MCP's) for 30 mule deer (19 does and 11 fawn/yearlings—deer captured as fawns for the first year after capture). We removed one fawn home range that was an outlier, 30,784 ha (Figure 16). Median annual home ranges were larger for fawns/yearlings (median = 1,698 ha) than does (median = 952 ha; Table 8).

Discussion

Although we observed deer making movements of up to 140 km, the mule deer in our study area were nonmigratory (only 6.1% of adults made movements > 3.2 km). Large mule deer migrations are more common in the Rocky Mountain West where snowpack in the higher elevations forces mule deer to migrate to lower elevations in the winter (Hygnstrom et al. 2008). Our data confirms findings from other studies that describe mule deer in this region as nonmigratory (Fox 1989, Hamlin and Mackie 1989, Carnes 2009). We observed higher seasonal movement distances for fawns and yearlings; however, only one fawn made an obvious dispersal without returning to its natal range (i.e. a "spring dispersal" [Hygnstrom et al. 2008]).

Mule deer home ranges are typically small with much variation (Wallmo 1981, Nicholson et al. 1997). Although we found a large range in home range sizes in our study, the maximum home range sizes may be exaggerated due to using 95% MCP to measure home ranges for deer that used multiple home range cores. Previous studies in Montana report larger average home range sizes (Hamlin and Mackie 1989, Carnes 2009), but Carnes (2009) admits that means were larger than medians and that outliers were affecting estimates. We observed summer home ranges that are similar to those reported in western North Dakota (Jensen 1988, Fox 1989). Although it is typically thought that ungulates migrate between seasonal ranges, deer in our study that had larger home ranges were those that made movements between multiple ranges, within a season. For these deer, there were core areas that were nearer to the median home range sizes we documented (e.g. Figure 16).

We observed high fidelity to seasonal ranges, especially for adults which is consistent with previous mule deer research (Hamlin and Mackie 1989, Thomas and Irby 1990, Brown 1992, Sawyer et al. 2005, Polfus 2012). However, unlike previous findings (Hygnstrom et al. 2008), we found that mule deer with multiple seasonal ranges moved between summer and winter ranges during the summer. Hygnstrom et al. (2008) concluded that mule deer movements are influenced most by social pressures and seasonal changes. Since we observed multiple mid-season movements, it is possible that mule deer that made movements between multiple ranges were being forced out by more dominant individuals.

We only observed one dispersal of a fawn emigrating from our study area, but six mule deer fawns and yearlings made exploratory movements > 10 km from their home range. Five of these movements occurred during June when it is likely that does are forcing them from an area prior to fawning (Eberhardt 1984, Hamlin and Mackie 1989). Our finding that 20% of yearling mule deer moved >4.2 km from their first summer home range is consistent with the 16% yearling dispersal rate reported by Hamlin and Mackie (1989) and 11% reported by Carnes (2009).

Management Implications

Mule deer populations in northern latitudes are subjected to sudden and sharp population declines during severe winters. After significant population declines, it is common for localized areas to be devoid of deer. There is little information about how these areas are recolonized but judging by the high rates of site fidelity by adults, it appears that recolonization depends largely upon dispersals of fawns. This might explain the time lag that often occurs between population crashes and rebounds in periphery habitat areas, and could help managers better project populations using trend data.

Mule deer appear quite sedentary in this region, and depredation problems might be directly addressed by local harvest efforts. Likewise, after localize population decreases (e.g. following severe winter), it might take multiple years of yearling dispersals to recolonize, even when neighboring areas have higher deer densities.

Natural disease transmission appears less likely with a sedentary wildlife population. With recent documentation of the first cases of chronic wasting disease in the state, it may be a relief that most of the mule deer in our Yellowstone River and Missouri River breaks study areas we were sedentary. However, some mule deer made regular migrations and fawns made dispersals and erratic movements of up to 114 miles. Moreover, deer in our study traversed state boundaries as well as major geographic boundaries: Yellowstone River, Missouri River and Interstate 94. It is important that disease monitoring and responses consider the interconnectedness of the mule deer population in eastern Montana and western North Dakota.

Table 5. Summary of seasonal movement distances (distance between winter and summer centroids), by age, for mule deer in two study areas in eastern Montana. Age was based on the deer's age at the beginning of the movement period, so we only had fawn movement data from winter to summer, and yearling movement data from summer to winter. All deer ≥ 18 months were considered adults. If individuals were alive for winter to summer and summer to winter, we averaged distances among individual deer prior to summarizing to provide a weighted median. We used median movement distances because movement distance data were not normally distributed.

			Movement Distance m (mi)			Proportion that moved	
Age	Ind.	n	Median	Min	Max	>2 miles	>10 miles
Fawn	23	23	1,223 (0.76)	236 (0.15)	27,883 (17.33)	21.7%	4.4%
Yearling	12	22	1,121 (0.70)	236 (0.15)	13,949 (8.67)	8.3%	0.0%
Adult	66	84	608 (0.38)	41 (0.03)	17,004 (10.57)	6.1%	3.0%

Table 6. Distances moved between successive seasonal centroids (i.e. site fidelity), summarized by age, for mule deer in two study areas in eastern Montana, 2014-2015. Age indicates the age of the deer at the first of two successive seasonal centroids.

Seasonal Site Fidelity Distances							
			m (mi)			Proportion that moved	
Age	Season	n	Median	Min	Max	>2 miles	>10 miles
Fawn	Winter	11	752 (0.47)	108 (0.07)	4,092 (2.54)	9.1%	0.0%
	Spring	11	358 (0.22)	66 (0.04)	4,059 (2.52)	9.1%	0.0%
Yearling	Summer	10	691 (0.43)	233 (0.14)	5,040 (3.13)	20.0%	0.0%
Adult	Winter	36	607 (0.38)	48 (0.03)	4,610 (2.86)	11.1%	0.0%
	Spring	19	487 (0.30)	70 (0.04)	1,345 (0.84)	0.0%	0.0%
	Summer	18	458 (0.28)	109 (0.07)	3,232 (2.01)	5.6%	0.0%
	Autumn	14	558 (0.35)	94 (0.06)	3,104 (1.93)	0.0%	0.0%

Table 7. Summary of seasonal home range sizes (95% MCPs) by age. Some individuals were on air for >1 year; we averaged home range sizes among individuals prior to summarizing to provide unbiased weighted medians. We removed data from one fawn that dispersed from the study area and one yearling that had a large summer home range due to exploratory movements. [1]We did not age mule deer does during winter captures, so some adults may have been yearlings their first winter and spring on air.

				Home Range Size ha (mi)		
Age	Season	Ind.	n	Median	Min	Max
Fawn	Winter	37	37	635.2 (2.45)	132 (0.51)	9,942.8 (38.39)
	Spring	27	27	628 (2.42)	219.6 (0.85)	5,363.3 (20.71)
Yearling	Summer	22	22	483.4 (1.87)	136.2 (0.53)	17,644.7 (68.13)
	Autumn	14	14	654.3 (2.53)	338.4 (1.31)	3,259.3 (12.58)
	Winter	12	12	842.8 (3.25)	353.8 (1.37)	5,252.9 (20.28)
	Spring	11	11	650.1 (2.51)	394.6 (1.52)	1,290 (4.98)
Adult	Winter[1]	29	68	484.8 (1.87)	112.3 (0.43)	3,119.1 (12.04)
	Spring[1]	27	46	428.9 (1.66)	150.3 (0.58)	4,881.3 (18.85)
	Summer	37	55	417.3 (1.61)	27.1 (0.10)	4,441.6 (17.15)
	Autumn	26	40	540.6 (2.09)	205.9 (0.80)	4,446.4 (17.17)

Table 8. Summary of annual home ranges (95% minimum convex polygon) for 30 mule deer in two study areas in eastern Montana, 2014-2015. The Fawn/Yearling age category represents deer that were captured as a fawn but transitioned to yearlings prior to the end of their first year on air.

		Annual Home Range Size ha. (mi^2)		
Age	n	Median	Min	Max
Fawn/Yearling	11	1,697.7 (6.55)	639.6 (2.47)	6,659.1 (25.71)
Adult	19	952.1 (3.68)	378.6 (1.46)	6,111.9 (23.60)

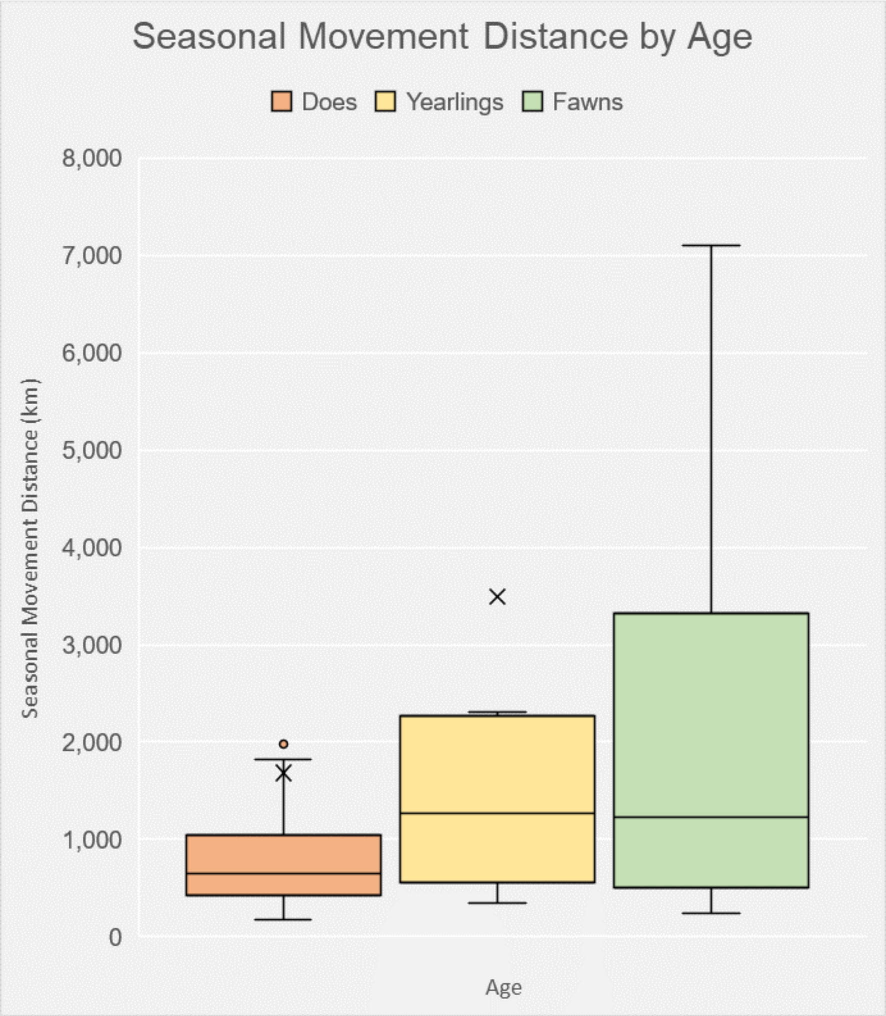


Figure 14. Box and whisker plot of seasonal movement distances between winter and summer centroids by age. Boxes show interquartile range and median (horizontal line). Whiskers show minimum and maximum values with outliers removed. The means, including outliers, are denoted with x's (notice the mean for fawns is beyond the scale of this plot and the mean for yearlings is outside of the quartile range, due to extreme outliers). Migration distances were not normally distributed (highly skewed toward shorter distances), so use of mean distances is misleading.

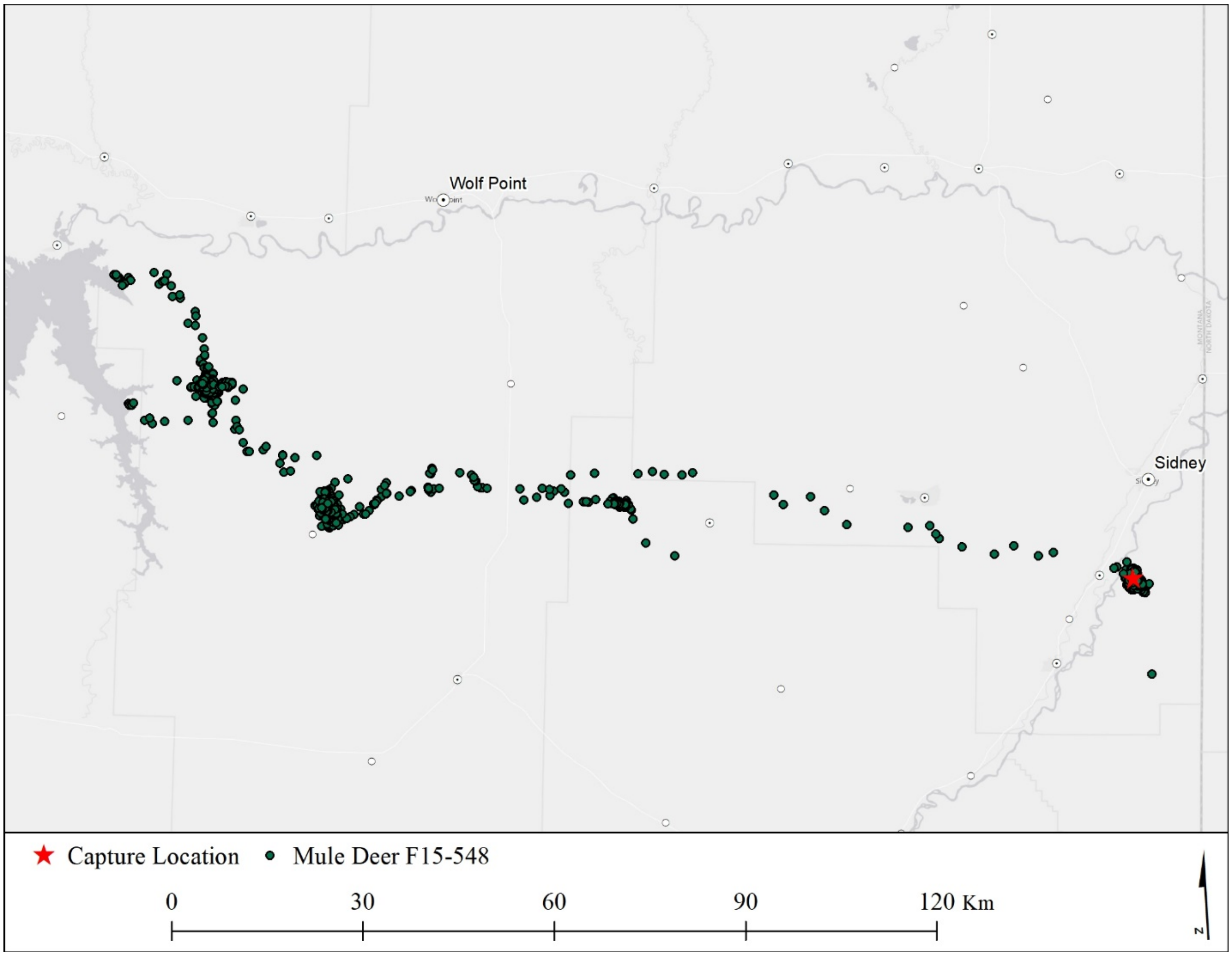


Figure 15. Map of mule deer F15-548, which was captured as a fawn and dispersed >160 km, out of the study area.

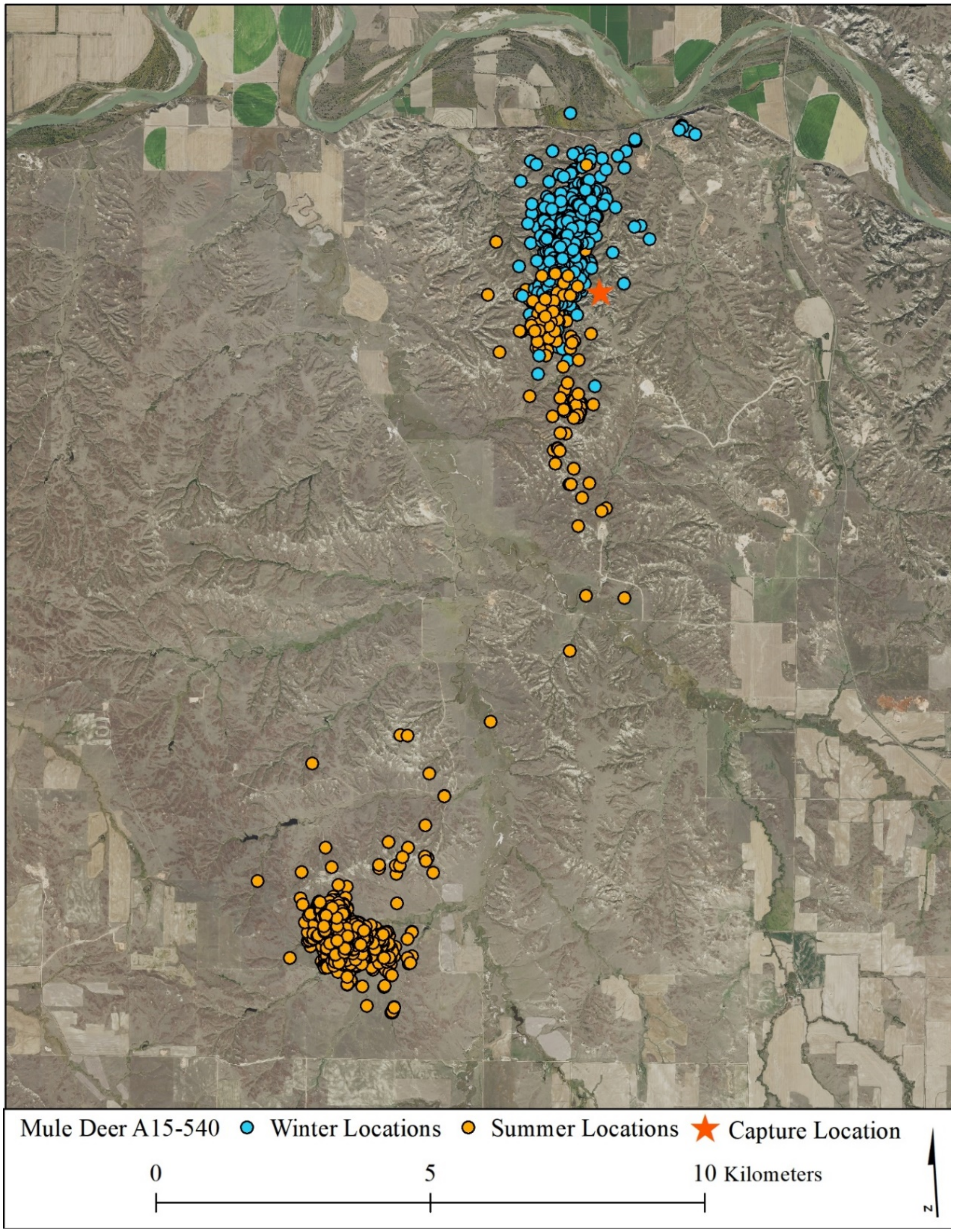


Figure 16. Map of mule deer doe A15-540 locations for winter (Dec-Mar) and summer (Jun-Sep) showing a migratory pattern but use of both winter and summer range during summer. Note: multiple trips between summer and winter ranges occurred during the summer season, so this was not a traditional migration pattern.

Literature Cited

Adams, A. W. 1982. Migration. Pages 301-321 in Potential influence of coyote predation on mule deer populations. Pages 111-118 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: Ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. PLos ONE 7:e40505.

Byrne, M. E., J. C. McCoy, J. W. Hinton, M. J. Chamberlain, and B. A. Collier. 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83:1234-1243.

Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2003. Movements of female white-tailed deer (Odocoileus virginianus) in relation to timber harvests in the central Appalachians. Forest Ecology and Management 199:371-378.

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

Eberhardt, L. E., E. E. Hanson, L. L. Cadwell. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. Journal of Mammalogy 65:404-409.

Fox, R. A. 1989. Mule deer (Odocoileus hemionus) home range and habitat use in an energy-impacted area of the North Dakota Badlands. Master’s Thesis. University of North Dakota. Grand Forks, North Dakota, USA. 88 pp.

Franzreb K. E. 2006. Implications of home-range estimation in the management of red-cockaded woodpeckers in South Carolina. Forest Ecology and Management 288:274-284.

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

Hygnstrom, S. E., S. R. Groepper, K. C. VerCauteren, C. J. Frost, and J. R. Boner. 2008. Literature review of mule deer and white-tailed deer movements in western and midwestern landscapes. Great Plains Research: A Journal of Natural and Social Sciences 18:219-231.

Jacques, C. N. and J. A. Jenks. 2007. Dispersal of yearling pronghorns in western South Dakota. Journal of Wildlife Management 71:177-182.

Jensen, W.F. 1988. Summer and fall ecology of mule deer in the North Dakota badlands. Dissertation. University of North Dakota. Grand Forks, USA. 220 pp.

Kolar, J. L., J. J. Millspaugh, and B. S. Stillings. 2011. Migration patterns of pronghorn in southwestern North Dakota. Journal of Wildlife Management 75:198-203.

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

Lendrum, P. E., C. R. Anderson, Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3(9):82. http://dx.doi.org/10.1890/ES12-00165.1

Morales, J.M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2289–23201.

Nicholson, M. C. R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

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

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

Polfus, J. L. and P. R. Krausman. 2012. Impacts of residential development on ungulates in the Rocky Mountain West. Wildlife Society Bulletin 36:647-657.

Sawyer, H. M., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266-1273.

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

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159-2173.

Thomas, T. R. and L. R. Irby. 1990. Habitat use and movement patterns by migrating mule deer in southeastern Idaho. Northwest Science 64: 19-27.

Turchin, P. 1996. Fractal analyses of animal movement: a critique. Ecology 77:2086-2090.

Wallmo, O. C. Editor. 1981. Mule and black-tailed deer of North America. Univ., Nebraska Press, Lincoln, USA.

CHAPTER III. SURVIVAL OF MULE DEER IN EASTERN MONTANA

Introduction

Reproduction and survival are the principal elements of wildlife population growth. For mule deer, female adult survival and fawn recruitment are the most significant demographic parameters affecting population growth rates (Wallmo 1981, White and Bartmann 1998, Bishop et al. 2009, Forrester and Wittmer 2013). Managers currently use age-structure information from hunter-harvested deer to make indirect assumptions about mule deer survival, and hence have little information on survival and cause-specific mortality for mule deer in Montana. Mule deer doe survival rates across their distribution tend to be high and stable (Forrester and Wittmer 2013). Currently, Montana Fish, Wildlife and Parks (FWP) biologists collect information on fawn production (fawn-to-doe ratios) during post-harvest aerial surveys and recruitment (fawn-to-adult ratios) during spring green-up (in April), but little else is known about the survival of fawns during winter and spring. Fawn overwinter survival rates tend to vary in mule deer (Pac et al. 1991, Gaillard et al. 1998, Unsworth et al. 1999, Forrester and Wittmer 2013), so high fecundity rates and high, steady survival rates in adults may be necessary to account for low fawn survival (Pac et al. 1991, Forrester and Wittmer 2013).

Although there are few published studies linking oil and gas energy development metrics with mule deer survival, Sawyer et al. (2002) concluded that long-term avoidance of energy development could result in decreased fitness, including decreased survival. Sawyer et al. (2017) documented decreases in abundance of mule deer in an oil and gas developed area, but the demographic parameter causing declines was unknown. Decreases in abundance may be due to emigration, reduced fecundity, or reduced survival, but additional research is needed to identify the mechanisms that could link mule deer abundance to oil and gas energy development.

Several ungulate studies suggest that human developments and disturbance could indirectly affect survival via decreased foraging time (Freddy et al. 1986) or increased energy expenditure (Parker and Robbins 1984). However, Freddy et al. (1986) found that despite increased energetic costs near snowmobile trails, disturbances did not affect survival. The leading causes of mortality in unhunted mule deer populations are predation and malnutrition/disease (Forrester and Wittmer 2013), and oil and gas developments could increase survival by reducing predation rates (Hebblewhite et al. 2005, Hebblewhite et al. 2009) or improving forage quality by disturbing senescent vegetation (Lutz et al. 2011). In Colorado and New Mexico, Webb et al. (2011) documented no strong associations between the survival of Rocky Mountain elk and anthropogenic development, but there was a weak negative relationship noted for elk that used a core gas field. Additional information on the relationship between ungulate survival and oil and gas energy development is needed to understand how energy development could affect ungulate populations.

Methods

Survival Analysis

We evaluated mule deer survival with GPS collar data. We programmed the GPS collars to activate a ‘mortality mode’ if the onboard activity sensor did not detect movement for > 6 hours; in mortality mode, collars would transmit a real-time mortality notification and hourly coordinates until activity was detected or the collar was retrieved. We attempted to retrieve all mortalities promptly after receiving mortality notifications to investigate carcasses prior to rotting or scavenging. We examined evidence in the field (tracks, weather conditions, risks) and transported carcasses or remains to the NDGF veterinary lab to conduct formal necropsies. We used information from the field investigation and GPS location data to determine actual mortality times. We determined proximate causes of mortality, but in some instances multiple sources may have contributed to the ultimate fate (e.g. if malnutrition led to increased vulnerability to predation, the ultimate cause was likely poor forage quality).

We evaluated survival status using a biweekly temporal scale to aid in determining the environmental conditions the deer encountered before a mortality event occurred. We coded survival as either 1 (alive) or 0 (dead). We coded rows after collar failures or after a mortality event as ‘NA’ until the end of the study period. We evaluated survival probability using logistic regression with the glm function in program R (R Core Team 2016), which is equivalent to known-fate analysis in program MARK.

We used survival covariate data that corresponded with the survival status time periods. We organized covariates into 3 major categories: background (e.g. temperature, season, etc.), gas and oil development metrics, and road metrics (Table 9). We standardized covariate collected by calculating presence/ absence, count, and density values within a pre-defined buffered area. We determined the buffered area by first calculating home ranges using a 99% kernel density estimator (KDE) using all locations collected over the biweekly time interval. The median home range area was determined as the area to buffer a ‘central point’. A ‘central point’ was calculated from the median of all Easting and Northing locations used in home range construction.

We aged deer as either adults (> 6 months) or fawns (< 6 months) at capture. We graduated all fawns to the adult cohort if they survived to the next biological year (01 June; thus we only have data for fawns from December captures through 01 June). We used the following seasons: spring (1 April - 31 May), summer (1 June - 30 September), autumn (1 October - 30 November), and winter (1 December - 31 March). Collars were equipped with an onboard thermometer, and temperature was recorded with each successful GPS fix. We averaged the onboard temperature data over the biweekly temporal interval.

We used the Normalized Difference Vegetation Index (NDVI) as a proxy for mule deer forage quality (Hurley et al. 2014). We calculated NDVI for each GPS location using Movebank's Env-DATA interface (Dodge et al. 2013). Band 1 (red) and band 2 (near infrared) are collected daily at a 250-meter resolution (https://lpdaac.usgs.gov/). We calculated NDVI with the formula: $NDVI = (band2 - band1)/(band2 + band1)$ (Jackson and Huete 1991). We averaged NDVI values for each location used in home range construction.

We assigned surface snow depth values for each GPS location using Movebank's Env-DATA interface. Env-DATA uses daily, 250-meter resolution snow depth data interpolated from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) model (http://rda.ucar.edu/datasets/ds608.0/index.html#sfol-wl-/data/ds608.0?g=3). We averaged snow depth values for each location used for home range construction.

We collected gas and oil development covariates using the ArcIMS viewer (https://www.dmr.nd.gov/OaGIMS/viewer.htm). We first obtained locations of oil and gas extraction, which we further categorized temporally into drilling rigs and well pads. We classified a well pad as a drilling rig for any period when a well was being drilled on the well pad. We re-categorized well pads as active well pads after the drilling infrastructure had been removed from the site, if there was at least one producing well on the well pad. We calculated the distance to nearest drilling rig and active well pad (hereafter, well pad) from the central point. We determined the number of drilling rigs and well pads by counting the number of drilling rigs and well pads that occurred within the buffered area during the same time period. We calculated drilling rig and well pad density by dividing the count of drilling rigs and well pads by the buffered area (km^2).

We used line shapefiles for roads from the North Dakota Department of Transportation and manually digitized missing roads from 2015 aerial imagery at a 1:5,000 scale. We calculated Euclidean distance to nearest primary or?? secondary road (hereafter road) using the central point as the starting point. We calculated road length as the total length of road within the buffered area. We then calculated road density within the buffered area by dividing road length by the area within the buffer. We centered all continuous variables and scaled them using the scale() function in R.

Model Selection

We determined the covariates that best described mule deer survival probabilities by first finding parsimonious "background", "oil and gas", and "road" models. First, we fit models that contained all covariates (full models) within each covariate group (Table 9). After fitting full models, we removed slope coefficients with a Wald Test *p*-value > 0.1 from the model (reduced model). We then conducted a likelihood ratio test to compare the full and reduced model. We used covariates from the three covariate groups with the most support from the likelihood ratio test in the next step, where we fit 8 models with different combinations of background, gas and oil, and road covariates (Table 9). We used Akaike information criteria (AIC; Akaike 1973) to compare the 8 different model combinations. Any model within 2 AIC units of the top model were considered for predicting mule deer survival probabilities.

Results

From 2014-2016, we collared and collected GPS locations on 73 mule deer in Montana and observed 18 mortality events over the course of the study period. Annual adult survival probability was 82.6 % (upper 95% CI = 96.0%, lower 95% CI = 51.1%, Table 10). Overwinter (01 December – 01 June) fawn survival probability was 77.0% (95% CI = 47.1 - 93.3%, Table 10). Adult survival was greater than fawn survival, however it was not significantly higher (Test Statistic = 1.284, *p*-value = 0.199). Fawns and adults had similar seasonal survival rates (spring, test Statistic = 0.070, *p*-value = 0.944, summer, test statistic = 0.502, *p*-value = 0.616, winter, test statistic = -1.141, *p*-value = 0.254). Winter survival was lower than all other seasons for both adults and fawns (Figure 17).

Most of the mortalities we detected were due to unknown causes (that is, scavenging precluded the ability to determine cause of mortality). For known causes, malnutrition was the leading cause of mortality for does and fawns (Figure 18). We only confirmed predation by 1 mountain lion and 1 coyote; however, since many of the unknown mortalities were scavenged by coyotes, it is likely we underestimate coyote predation rates. Only one deer was harvested by a hunter during our study.

Our top reduced model for background covariates contained age, spring, summer, winter, autumn, spring and snow depth interaction, spring and NDVI interaction, spring and temperature interaction, and summer and temperature interaction (likelihood ratio test statistic = 14.134, degrees of freedom = 9, *p*-value = 0.3645; Table 11). In the oil and gas covariate group, the reduced model containing a state and distance to nearest rig (pseudo-threshold) interaction and state covariate was selected over the full model (likelihood ratio test statistic = 3.7277, degrees of freedom = 3, *p*-value = 0.4441; Table 11). The top model in the road and gravel pit covariate group was the reduced model, which contained distance to nearest road (quadratic) (likelihood ratio test statistic = 3.413, degrees of freedom = 3, *p*-value = 0.1815; Table 11).

Our AIC model selection results demonstrated that 4 models adequately described mule deer survival (Table 11). All models contained the set of background covariates, while the top model contained covariates from all three covariate groups, the next 2 competitive models both contained background and roads and gas and oil development. No other covariate grouping was competitive (i.e, ΔAIC > 88 for all other models), thus we used the top 4 models for inference.

There was a quadratic relationship between mule deer survival and distance to nearest road (*p*-value = 0.022). When deer were close to a road (< 2km) survival was lower than at intermediate distances (2-3 km). Deer at further distances (> 3km) had lower survival probabilities, but the confidence intervals were wide at further distances due to few locations >4 km from the nearest road (Figure 19).

The most influential environmental covariates for mule deer survival was an interaction between spring and three separate covariates: (1) NDVI, (2) snow depth, and (3) temperature (Figure 21). As spring NDVI values increased mule deer survival decreased (*p*-value = 0.006). When there was any snow accumulation in spring mule survival probabilities significantly decreased (*p*-value = 0.000). As spring temperatures increased mule deer survival probabilities also significantly increased (*p*-value = 0.003).

Discussion

Mule deer survival was best described by background covariates and distance to nearest road. We observed a quadratic relationship between mule deer survival and distance to nearest road. When a deer was close to a road (< 2km) and far from a road (> 3km) survival decreased, however when a deer was at intermediate distances (2-3km) survival was at its highest. However, at far distances there is large uncertainty due to a small sample size compared to our relatively tight confidence intervals at close and intermediate road distances (Figure 20). No mortality was attributed to vehicle collisions. Deer located closer to roads could be experiencing decreased survival related to increased vigilance and perceived predation risk leading to increased flight energy expenditures. While deer at intermediate distances are not experiencing as much perceived predation risk from vehicle traffic leading to less flight energy expenditures and decreased interruption in foraging time (Sawyer et al. 2009 and Northrup et al. 2015). Research that occurred simultaneously to ours in the North Dakota badlands, found that mountain lions selected areas further from anthropogenic developments (Johnson 2017). Increased predator density is one possible theory to explain why survival would be lower further from roads. However, our one instance of mountain lion predation occurred at ~740 m from the nearest road—a high grade gravel road (this area is rugged and wooded, so the perceived distance from the road may have been greater). In the North Dakota portion of this study, there was no evidence that mule deer were finding refugia nearer to developments.

We documented annual female adult mule deer survival probability (0.82) which is in line with survival rates found in literature reviews of multiple survival studies (0.85, Unsworth et al. 1999; 0.84, Forrester and Wittmer 2013). The literature reviews did not describe whether survival rates were affected by hunter harvest; during our study there was a moratorium on doe harvest in 2014, and a minimal number of does harvested in 2015 by hunters with either-sex licenses (e.g. only 34 in HD 651). Adult survival was greater with less variation than fawn survival, however this was not a significant relationship. White et al. (1987), Bishop et al. (2005), and Lukcas et al. (2009) found that doe mule deer survival was higher and less variable than fawn survival.

We observed overwinter female fawn survival probability of 77%. This is higher than 63% and 57% observed in two study areas in southeast Montana (Carnes 2009), but not statistically different (e.g. our 95% CI 41 - 93% overlapped previously documented survival rates). Nonetheless, female fawn survival was relatively high in our study, which reflected that our study was conducted during years of rebounding mule deer population following a series of harsh winter events that caused the Region 7 mule deer population to bottom out at 43% below the long-term average in spring 2012 (FWP, unpublished data). By spring 2016, the Region 7 population had recovered to 47% above the long-term average. The mule deer population in hunting district (HD) 651 in Region 6 was not as severely impacted by winters of 2008-2011, and population estimates have been more static (FWP, unpublished data). Both a rebounding or static population show that the mule deer in our study area were finding adequate resources to sustain the population at the 2014-2015 densities and habitat condition.

Despite the population likely below carrying capacity, the leading cause of mortality in our study was malnutrition. Mule deer survival was lower in winter compared to all other months, however this relationship was not significant. This result is similar to other studies on mule deer survival in northern latitudes (White et al. 1987, Bishop et al 2005, Lomas and Bender 2007, Carnes 2009, Hurley et al. 2011, Brodie et al. 2013, Monteith et al. 2013) as well as previous population models on mule deer in North Dakota (Ciuti et al. 2015, Kolar et al. 2017). Periods of cold weather and deep snow have attributed to malnutrition, increased competition, and decreased ability to flee predators (Bishop et al. 2005, Brinkman et al. 2005, Ciuti et al. 2015). During this time deer are typically in a negative energy balance and relying on fat storages built up during the summer and fall months (Wallmo 1981).

We observed a strong relationship between mule deer survival and spring interactions with environmental covariates. We detected a strong relationship between mule deer survival and snow depth in spring. When snow was absent from the landscape in spring mule deer survival remained high. Once snow accumulated on the landscape in spring (even small accumulations totaling 2 - 4 cm) survival probabilities significantly decreased. This could be attributed to deer coming out of a severe winter already in a negative energy balance not being able to restore fat reserve quickly enough due to the added stress and energy of traversing a snowy landscape. Increased snow depth also limits the amount of available forage and makes digging for grasses and forbs more difficult. During the spring of 2014 there was a lot of ice on the landscape and deer were unable to reach forage below and it made traversing the landscape more difficult. This icy spring could be driving the trend of low snow pack significantly decreasing mule deer survival probabilities.

Cold springs significantly lowered mule deer survival probabilities. Cold temperatures increase the demand for maintaining body heat thus increasing energy needs (Ciuti et al. 2015 and Beckmann et al. 2016). Deer coming out of winter are typically in a negative energy balance and the added stress and energy demand to regulate body temperature could be driving the trend we are seeing in lower survival probabilities.

Mule deer survival probability was negatively related to NDVI in the spring. This relationship was significant, however not an intuitive result (i.e. as spring NDVI values increased mule deer survival decreased). This result could be being driven by a harsh winter and early spring that depleted fat reserves too low that deer were unable to recover regardless the amount of forage on the landscape. Thus, high NDVI values might correspond with areas that had more snow cover. Alternatively, NDVI data may not have directly captured the amount of available forage on the landscape. For example, areas with more residual would have lower NDVI values earlier in the spring than areas with little residual cover. The quality and quantity of forage is typically better in areas with good residual cover, because residual cover is indicative of good range management practices and healthier vegetation than overgrazed areas which are the first to "green up" visually.

We did not detect oil and gas energy development influences on survival in Montana. However, due to low development levels in eastern Montana, we did not have locations in proximity to active drilling rigs, nor in areas with medium to high well pad densities. In the simultaneous research conducted in North Dakota, there was a significant negative relationship between survival and well pad density (Kolar et al. 2017).

NOTE: *Results from meta-analyses of the North Dakota and Montana studies will be documented in thesis by Brett Skelly, thesis research at the West Virginia University.*

Management Implications

The principle driver of mule deer population fluctuations in northern latitudes is winter severity. Our results confirm the negative relationship between mule deer survival and snow depth and temperature. This finding confirms the importance of high-quality winter habitat for persistent mule deer populations. Maintaining high-quality wintering habitats are important to wildlife managers, especially in highly developed landscapes found throughout eastern Montana. Because those habitats are often limiting, maintaining a mule deer population below carrying capacity is often the management goal for several reasons. Mule deer densities will increase in these areas during harsh winter months potentially increase human/wildlife conflicts issues with landowners, development and urban areas. While maintaining those lower populations to reduce potential conflicts, lower deer numbers will likely reduce competition and stress throughout those tough winter months.

Further, we observed average doe survival rates from 2014-2015 despite low levels of antlerless hunter harvest. Population growth was steady to rebounding during our study, and mule deer in Region 7 were below long-term average densities (Figure 23 B). Nonetheless, malnutrition during or immediately following winter was the leading cause of mortality. This suggest that winter habitat may be limiting in some portions of the study area. Eastern Montana is a heavily manipulated landscape so maintaining and conserving high quality wintering habitats is an important goal for wildlife managers. Areas near wooded draws with moderate slopes and ruggedness should be prioritized for mule deer wintering habitat (see Chapter 1).

Although energy development levels were relatively low in our study area, future development is likely. Developers should follow specific timing and sighting guidelines to reduce negative impacts on wintering herds and to help minimize negative influences on mule deer winter survival. Reducing human activity during winter months may help increase winter survival (Kolar et al. 2017).

Table 9. Major groupings of mule deer survival covariates with parameters in each group. Background covariates are any covariate not directly related to oil and gas development. Gas and oil development are related only to drilling rig and well pad development on the landscape. Road and gravel pit covariates are related to primary and secondary roads and gravel pits located within the study area.

Covariate Group	**Parameter**	**Retained**
Background	Age	Yes
	Biological year	No
	Season	Yes
	Spring * NDVI	Yes
	Summer * NDVI	No
	Autumn * NDVI	No
	Spring * Snow depth	Yes
	Winter * Snow depth	No
	Autumn * Snow depth	No
	Spring * Temperature	Yes
	Summer * Temperature	Yes
	Autumn * Temperature	No
	Winter * Temperature	No
	Home range area	No
	Geographic location	No
Gas and Oil Development	State	Yes
	Distance to nearest rig	Yes
	Distance to nearest well pad	No
	Well pad presence/ absence	No
Road and Gravel Pit	Distance to nearest road	Yes
	Road density	No
	Distance to nearest gravel pit	No

Table 10. Season survival rates with 95% upper and lower confidence intervals. Estimates obtained by bootstrapping (n = 1000) results from a model containing age, season, and biological year. Each season and age were estimated with all seasons multiplied together for annual adult survival, and winter and spring were multiplied together for post-winter fawn and adult survival.

	Survival Rate	**Upper 95% CI**	**Lower 95% CI**
Adult			
Annual	82.6%	96.0%	51.1%
Overwinter (Dec – May)	87.3%	97.1%	62.5%
Winter	88.8%	97.6%	68.5%
Spring	98.1%	99.8%	92.9%
Summer	97.1%	99.9%	84.7%
Autumn	97.1%	99.9	84.0
Fawn			
Overwinter (Dec – May)	77.0%	93.3%	47.1%
Winter	79.7%	94.5%	53.4%
Spring	96.3%	99.6%	86.3%

Table 11. Top mule deer survival models ranked by lowest AIC. Background covariates are age, spring, summer, winter, spring and snow depth interaction, spring and NDVI interaction, spring and temperature interaction, and summer and temperature interaction. Oil and gas development covariates are state and distance to nearest drilling rig (pseudo-threshold) interaction and state. Road and gravel pit covariates is distance to nearest primary/ secondary road (quadratic).

Model Parameters	**K**	**ΔAIC**	**AIC**
Global	13	0.00	1014.45
Background + Road and Gravel Pit	11	0.98	1015.43
Background + Oil/Gas Development	11	1.11	1015.56
Background	9	1.41	1015.86
Oil/Gas Development + Road and Gravel Pit	5	88.59	1103.04
Road and Gravel Pit	3	89.12	1103.57
Oil/Gas Development	3	93.08	1107.53
Intercept	1	93.19	1107.64

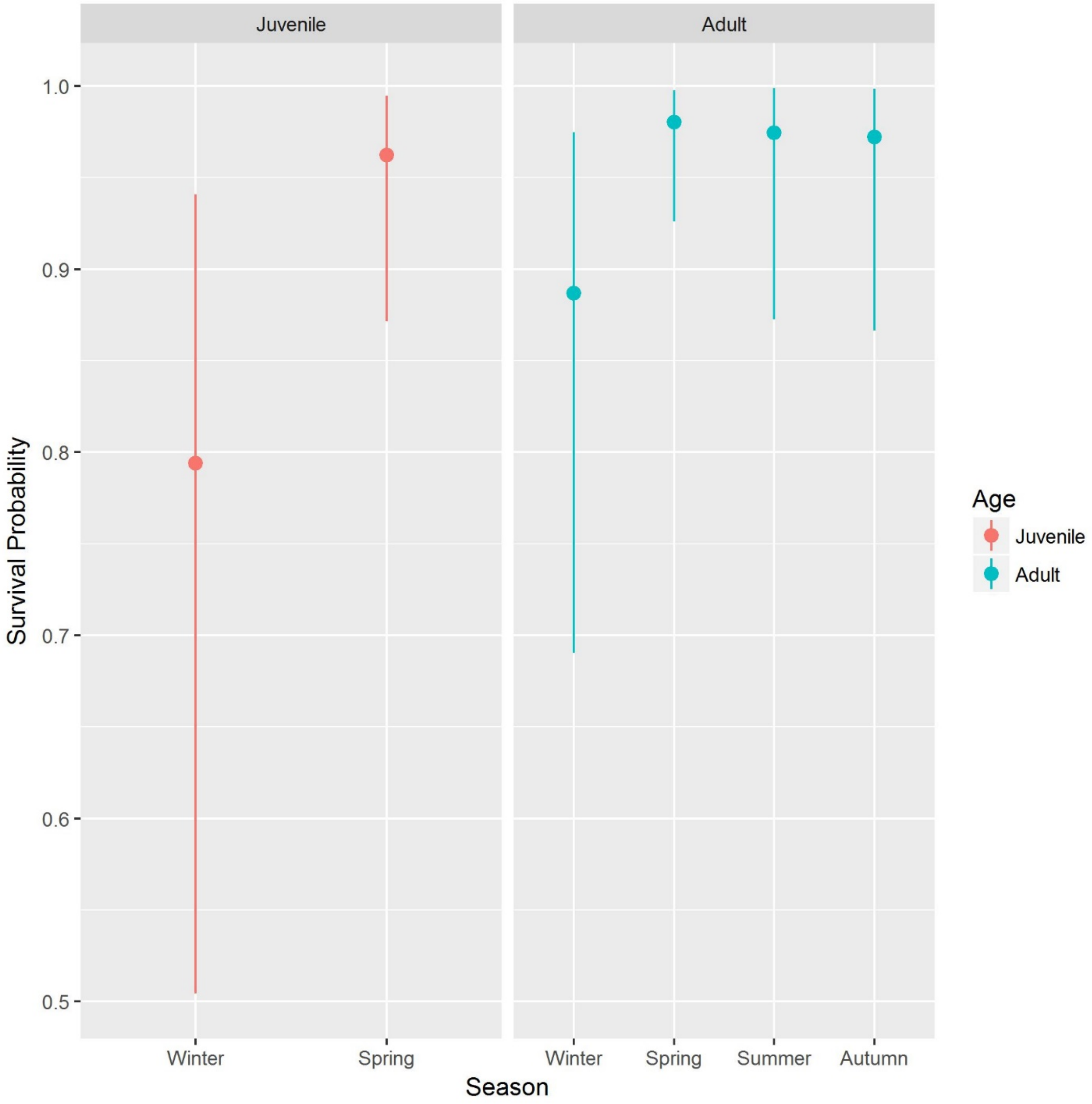


Figure 17. Seasonal survival probabilities and 95% confidence intervals for fawn (< 1 year) and adult (> 1 year) mule deer in eastern Montana. The seasonal survival probabilities for fawns shows only winter and spring, because we captured fawns in winter. The seasons varied in length: summer 8.7 biweekly intervals, winter = 8.6 biweekly intervals, autumn = 4.4 biweekly intervals, and spring = 4.3 biweekly intervals.

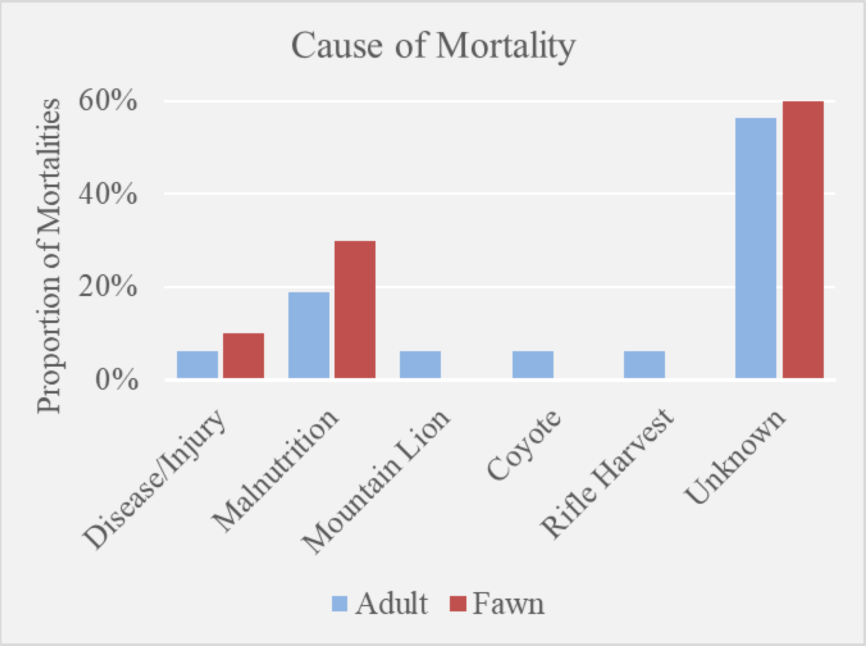


Figure 18. Plot of mortalities by cause (n=18). Note: all unknown causes were too heavily scavenged (by coyotes) to determine cause of mortality. Thus, coyote predation may have accounted for a higher proportion of the mortalities.

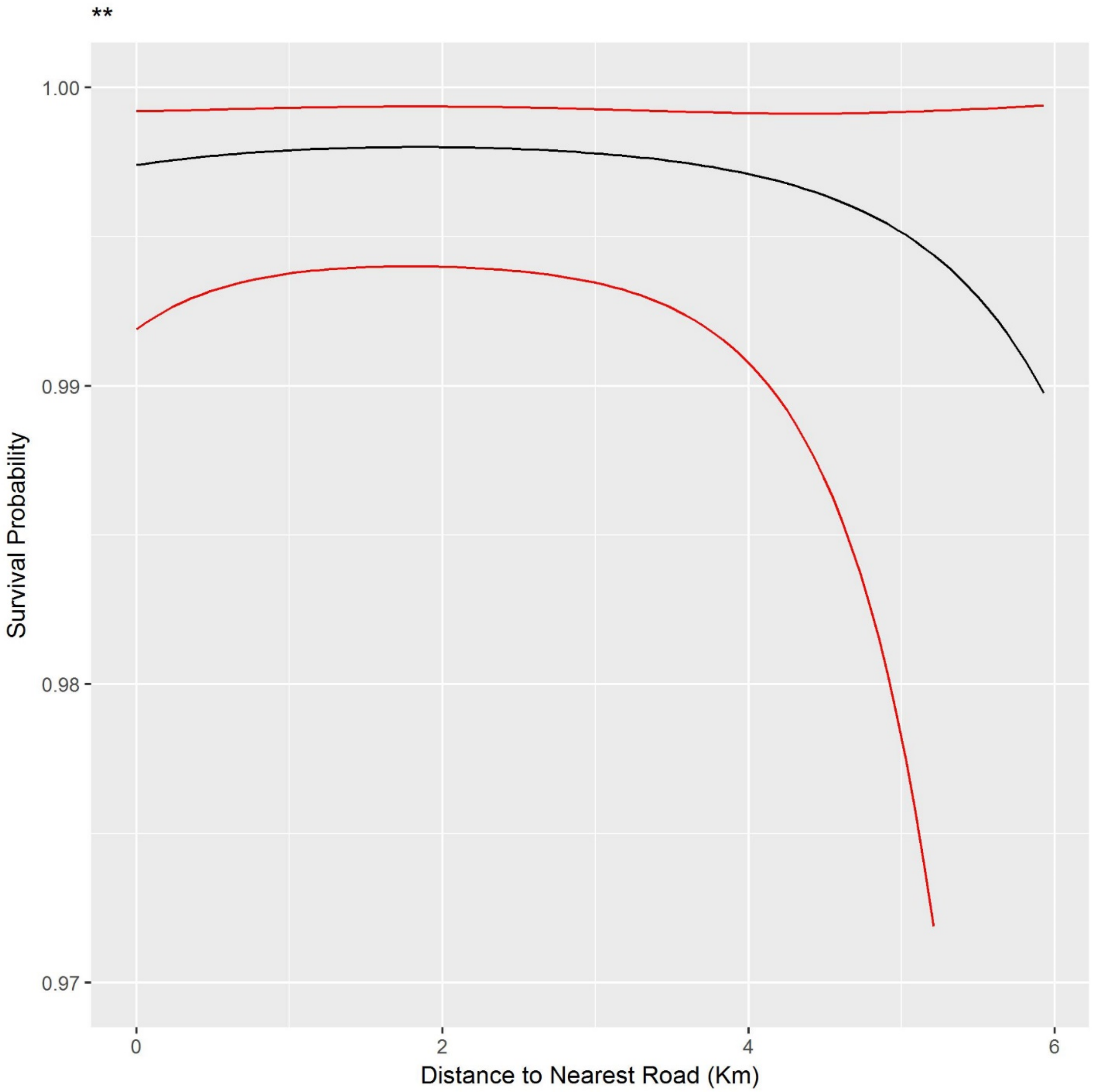


Figure 19. Mule deer survival probability in eastern Montana related to distance to nearest primary or secondary road. Mule deer survival was slightly lower closer to roads (< 2km) and was highest at intermediate distances (2-3 km). Beyond 3 km the confidence intervals were too wide to make inferences (due to very few used or available locations beyond 4 km from the nearest road).

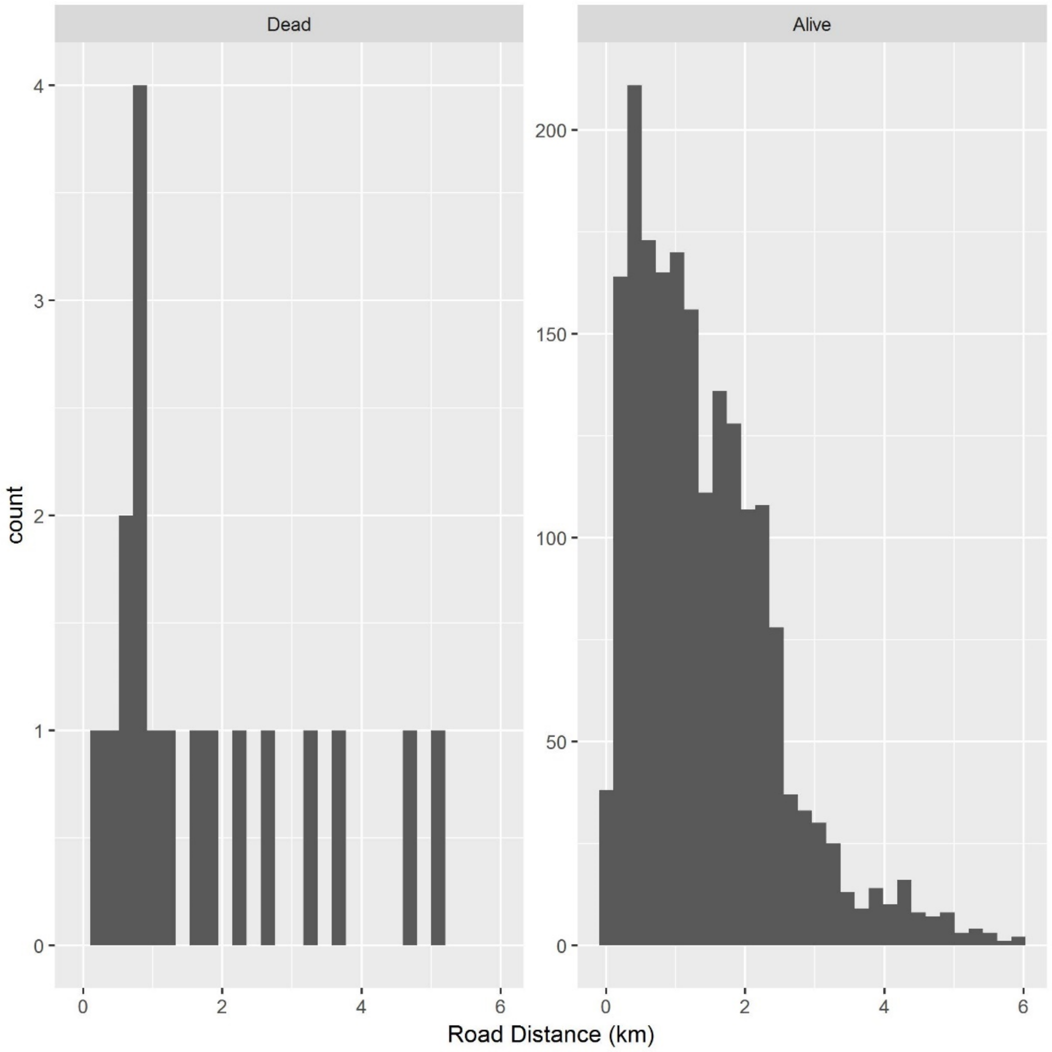


Figure 20. Distribution plots of bi-weekly periods where deer survived “Alive” or died, “Dead” plotted against distance to nearest road. The two mortalities that occurred >4 km from the nearest road likely drew the survival probability estimates lower at distances further from roads, but the sample size is very small.

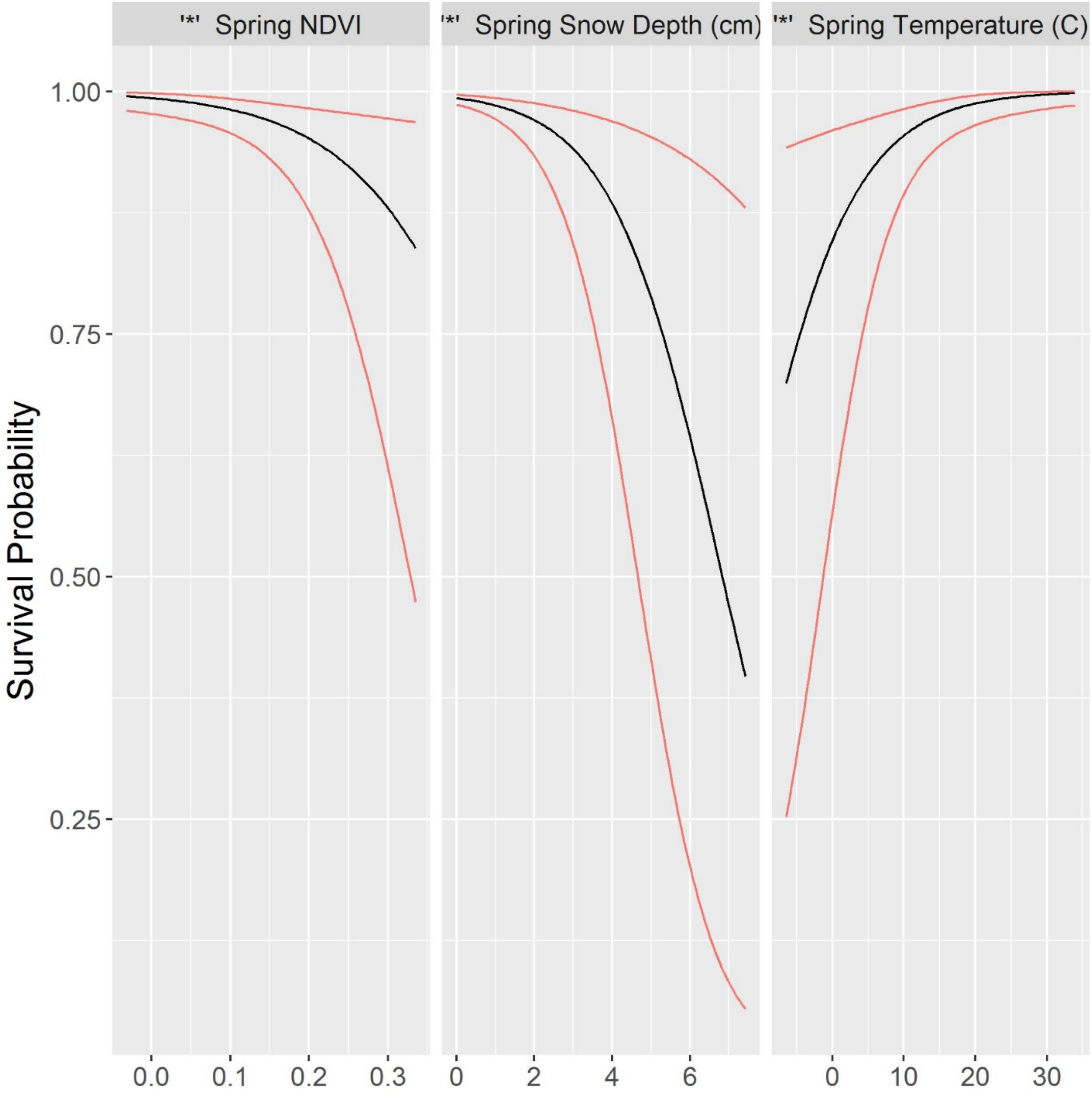


Figure 21. Mule deer survival probability in eastern Montana related to significant background covariates. Survival probability decreased as NDVI values increased in spring. In spring as snow depth increased mule deer survival probability decreased. Survival probability was inversely related to spring temperature, as temperature increased survival also increased.

Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest, Hungary.

Anderson, D. R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer. New York, New York, USA.

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

Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172.

Brinkman, T. J., C. S. Deperno, J. A. Jenks, B. S. Haroldson, and R. G. Osborn. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. Journal of Wildlife Management 69:1099-1111.

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K. Hersey, M. Hurly, P.M. Lukacs, S. McCorquodale, E. Mclntire, J. Nowak, H. Sawyer, D. Smith, and P. J. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology. 50:295-305.

Brown, C.G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management 56:246-53.

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

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

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D., and Wikelski, M. 2013. The Environmental-Data Automated Track Annotation (Env-DATA) System: Linking animal tracks with environmental data: Movement Ecology 3:1-14.

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

Freddy, D. J., M. B. Whitcomb, and M. C. Fowler. 1986. Responses of mule deer to disturbances by persons afoot and snowmobiles. Wildlife Society Bulletin 14:65-68.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58-63.

Hebblewhite, M. and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445-3454.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

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

Philosophical Transactions of the Royal Society B 369:20130196. http://dx.doi.org/10.1098/rstb.2013.0196

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

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

Johnson, R. D. 2017. Mountain Lion (*Puma* concolor) population characteristics and resource selection in the North Dakota badlands. Thesis. South Dakota State University, Brookings, USA. 132pp.

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

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

Lukacs, P. M., G. C. White, B. E. Watkins, R. H. Kahn, B. A. Banulis, D. J. Finley, A. A. Holland, J. A. Martens, and J. Vayhinger. 2008. Separating components of variation in survival of mule deer in Colorado. The Journal of Wildlife Management. 73:817-826.

Lutz, D. W., J. R. Heffelfinger, S. A. Tessmann, R. S. Gamo, and S. Siegel. 2011. Energy development guidelines for mule deer. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology 82:377-388.

North Dakota Game and Fish Department & North Dakota Petroleum Council. 2013. Recommended management practices for reducing oil/gas impacts to wildlife. <https://gf.nd.gov/sites/default/files/publications/mgmt-practices-reducing-oil-gas-impacts-to-wildlife.pdf> Accessed 28 Aug 2017.

North Dakota GIS. 2017. GIS hub data portal. URL: https://apps.nd.gov/hubdataportal/srv/en/main.home

North Dakota Industrial Commission. 2017. Oil and Gas: ArcIMS Viewer. https://www.dmr.nd.gov/OaGIMS/viewer.htm

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

Pac, D. F., R. J. Mackie, and H. E. Jorgensen. 1991. Mule deer population organization, behavior and dynamics in a northern Rocky Mountain Environment. Final Report, Montana Fish Wildlife & Parks, Helena, Montana, USA.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/.

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

Sawyer H, N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer and energy development—long-term trends of habituation and abundance. Global Change Biology 00:1–9.

Sawyer, H. M., F. Lindzey, D. McWhirter, and K. Andrews. 2002. Potential effects of oil and gas development on mule deer and pronghorn populations in western Wyoming. Transactions of the 67th North American Wildlife and Natural Resources Conference. 67:350-355.

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

Wallmo, O. C. Editor. 1981. Mule and black-tailed deer of North America. Univ., Nebraska Press, Lincoln, USA.

Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. HaydenWing, and J. B. Winstead. 2011. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. Population Ecology 53:483–493.

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

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. Journal of Wildlife Management 62:214-225.

CHAPTER IV. ABUNDANCE AND COMPOSITION OF MULE DEER IN EASTERN MONTANA

Introduction

The management objectives for mule deer in Montana are typically based on long-term averages (LTA's) of population survey counts and proportions of fawns and bucks to does in the population. FWP uses large aerial survey blocks for mule deer trend data with the goal of obtaining trend information on densities and herd compositions; however, FWP does not attempt to attain a complete census within survey blocks.

Despite the utility of trend data for management, actual population densities are helpful for comparing habitats, assessing productivity of habitat, and assessing effects of external factors on populations. Numerous researchers have made attempts to develop correction factors based on probability of detection and occupancy models (Griffin et al. 2013). We attempted to develop sightability models from actual detection rates of mule deer with known locations (i.e. GPS-collared mule deer) to develop a correction factor complete coverage (i.e. census) aerial survey blocks (Kolar et al. 2017). These models would provide estimates of population density. However, despite having time-stamped GPS locations of radio collared deer and observations recorded during surveys, we were unable to determine whether collared deer were detected. In areas with high deer densities, there were too many GPS locations of observed deer to confidently declare any radio-collared mule deer was not detected. Further, to develop sightability models, it is necessary to estimate group size for missed deer. Even with a second observer using radio telemetry to locate marked deer, we were unable to get accurate counts of deer in wooded habitats--the deer that were most likely to be missed during aerial surveys.

Therefore, in this chapter we summarized density and herd composition observed in aerial survey blocks. We reported uncorrected mule deer densities and compositions. With any ungulate research, it is important to understand the context of the population density and herd composition. Our survey methods were consistent with survey methods used by the NDGF, so results are comparable to NDGF trend data.

Methods

We developed 6 aerial survey blocks in our two study areas: 4 in the Yellowstone area and 2 in the Culbertson area (Figure 22). These survey blocks were established around drainages and ranged from 8.8 to 17 miles^2. Biologists surveyed blocks from fixed-wing aircraft (Piper Supercub or Aviat Husky) and attempted complete coverage of survey areas. Pilots primarily followed drainages, and GPS tracks were used to ensure complete coverage of survey blocks. Surveys were started 30 minutes prior to sunrise and completed before 2 hours after sunrise.

During spring green-up surveys (mid-April to early May) biologists recorded deer counts of survey areas to census deer without regard to age or sex. During fall composition surveys (October) biologists recorded counts of all deer observed and classified each deer as: fawn, buck or doe.

Results

We flew complete coverage aerial surveys of 6 survey blocks set up in the two study areas twice annually 2014-2015. The two survey blocks in Culbertson totaled 19.5 mi^2, and four survey blocks in Yellowstone covered 57 miles^2.

During our abundance surveys we counted an average of 1.56 deer/mi^2 (range = 0.82 – 2.26; Table 1). The average density in 2015 (1.63 deer/mi^2) was slightly higher than the average density in 2014 (1.43 deer/mi^2), and the mule deer density in Culbertson (2.16 deer/mi^2) was higher than the mule deer density in the Yellowstone River study area (1.26 deer/mi^2).

We classified 340 mule deer in 2014 and 299 in 2015 (Table 2). Our cumulative fawn-to-doe ratio was 0.76, and buck-to-doe ratio was 0.58. Fawn-to-doe ratios and buck-to-doe ratios were higher in 2014 than 2015 (0.87 vs. 0.66, and 0.68 vs. 0.49, respectively). Deer density was more than double in October (4.17 deer/mi^2) compared to April counts (1.56 deer/mi^2).

Discussion

High fawn-to-doe ratios in 2014 revealed good reproduction that year. Although fawn-to-doe ratios were lower in 2015, that may have been due to a high proportion of yearlings in the population and little to no doe harvest in 2014; yearling does rarely have fawns, so they inflate the denominator portion of the ratio. Typically, fawn-to-doe ratios above 0.60 indicate a stable to growing population (Forrester and Wittmer 2013), so the fawn-to-doe ratios we observed were indicative of a positive population growth rate. High mule deer reproduction is often linked to higher precipitation from the previous summer, good forage conditions the year prior to fawning, mild winters, and/or low predator densities. We documented malnutrition as a leading cause of mortality for mule deer during our study, which Carnes (2009) suggested might indicate that mule deer are near carrying capacity of the habitat in his study area in southeast Montana. Based on increases in population density (albeit limited to two years) and high fawn-to-doe ratios, it appears that mortalities due to malnutrition during winter do not necessarily indicate that the population is near carrying capacity.

High buck-to-doe ratios (other than the Three Buttes area) are suggestive of a high proportion of younger deer in the population or low hunting pressure. Much of the area surveyed was on private lands, so hunting access may have been limiting. However, based on trend data from elsewhere in eastern Montana, it is more likely that high buck-to-doe ratios were a result of a high proportion of younger deer in the population. Anecdotally, we observed very high rates of buck fawns during captures. Capture crews could not reliably identify male vs. female fawns until they were captured, and in our December 2014 capture, capture crews captured over 50 fawns to obtain the objective of 20 female fawns. Although there was notable variation between survey units, herd compositions and counts may be variable when looking at smaller areas, so we emphasize total numbers from multiple survey units.

NDGF surveyed similar-sized blocks in the Little Missouri Badlands, 2013-2015, and spring densities ranged from 2.27 deer/km^2 in the northern badlands to 3.41 deer/km^2 in the southern badlands (NDGF unpublished data). No survey blocks flown in the Montana portion of this study had average densities this high, possibly due to more general season hunting structure and rebounding populations.

Management Implications

Biologists typically estimate herd composition with counts of ≥ 100 deer. In our study area biologists had to survey 20-30 square miles to classify 100 mule deer. Biologists completed most survey blocks in less than 2 hours, so larger, complete coverage survey blocks should be completed in the region and habitat type of our study area. (Trend areas that the FWP currently surveys are much larger and contain more deer than the survey blocks used during this project.) Results from this project further emphasize the importance of surveying larger areas over a variety habitats and access opportunity for a higher confidence in mule deer compositions across the landscape.

High fawn-to-doe ratios and buck-to-doe ratios lend support to current management strategies that allow unlimited buck harvest and liberal doe harvest. Limited access due to low road densities and mixed private and public land ownership appear to be protecting mule deer from over-harvest despite liberal license allocations.

Table 12. Mule deer abundance results from 6 aerial block surveys flown in April 2014 and 2015.

Study Area	Survey Area	Year	Mule Deer Observed	Area (miles^2)	Mule Deer Density
Yellowstone River	Belle Prairie	2014	20	12.15	1.65
		2015	25	12.15	2.06
		Average	22.5	12.15	1.85
	Boxelder Creek	2014	12	11.92	1.01
		2015	14	11.92	1.17
		Average	13	11.92	1.09
	Sagebrush Creek	2014	14	17.09	0.82
		2015	23	17.09	1.35
		Average	18.5	17.09	1.08
	Shadwell Creek	2015	16	15.88	1.01
	Cumulative				1.26
Culbertson	Boulder Mine	2015	23	10.62	2.17
	Three Buttes	2014	20	8.84	2.26
		2015	18	8.84	2.04
		Average	19	8.84	2.15
	Cumulative				2.16
2014		2014		50	1.43
2015		2015		76.5	1.63
Total				**76.5**	**1.56**

Table 13. Mule deer composition results from 6 block survey areas flown in October 2014 and 2015.

Study Area	Survey Area	Sq. Miles	Year	Bucks	Does	Fawns	Total	f:d ratio	b:d ratio	Deer/mi^2
Culbertson	Three Buttes	8.84	2014	1	15	12	28	0.80	0.07	3.17
			2015	7	23	10	40	0.43	0.30	4.52
			Avg.					0.62	0.19	3.85
	Boulder Mine	10.62	2014	14	23	21	58	0.91	0.61	5.46
			2015	5	21	17	43	0.81	0.24	4.05
			Avg.					0.86	0.42	4.76
	Average	19.46	2014	7.5	19	16.5	43	0.86	0.34	4.31
			2015	6	22	13.5	41.5	0.62	0.27	4.29
			Total					0.74	0.30	4.30
Yellowstone River	Sagebrush Creek	17.09	2014	10	16	13	39	0.81	0.63	2.28
			2015	13	19	17	49	0.89	0.68	2.87
			Avg.					0.85	0.65	2.57
	Shadwell Creek	15.88	2014	23	13	13	49	1.00	1.77	3.09
			2015	6	12	12	30	1.00	0.50	1.89
			Avg.					1.00	1.13	2.49
	Boxelder Creek	11.92	2014	21	24	21	66	0.88	0.88	5.54
			2015	31	18	14	63	0.78	1.72	5.29
			Avg.					0.83	1.30	5.41
	Belle Prairie	12.15	2014	31	39	33	103	0.85	0.79	8.48
			2015	20	30	24	74	0.80	0.67	6.09
			Avg.					0.82	0.73	7.28
	Average	57.04	2014	21.25	23	20	64.25	0.88	1.02	4.85
			2015	14	15.8	13.4	43.2	0.69	0.71	3.23
			Total					0.88	0.95	4.44
Totals		76.5	2014					0.87	0.68	4.58
			2015					0.66	0.49	3.76
			Total					**0.76**	**0.58**	**4.17**

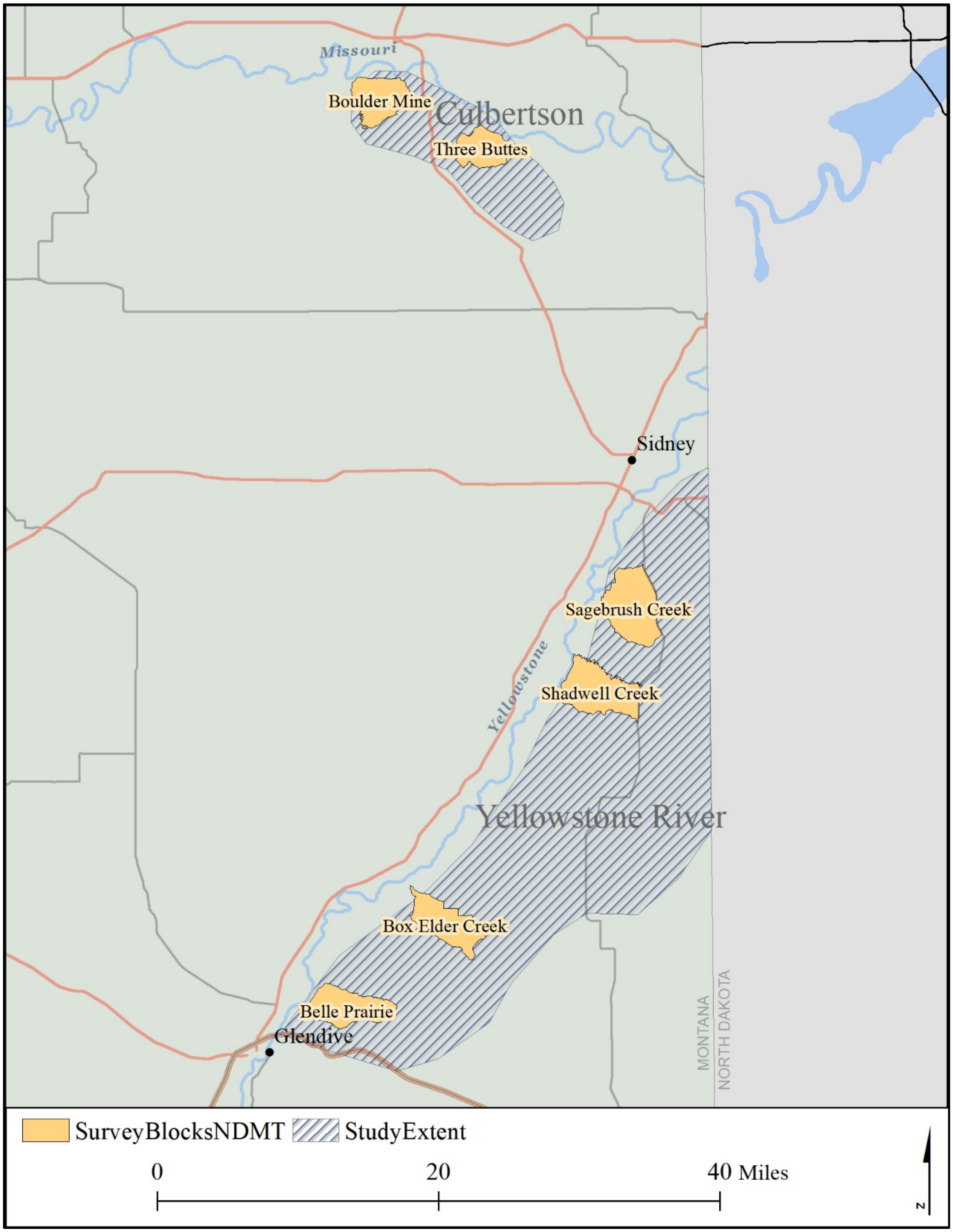
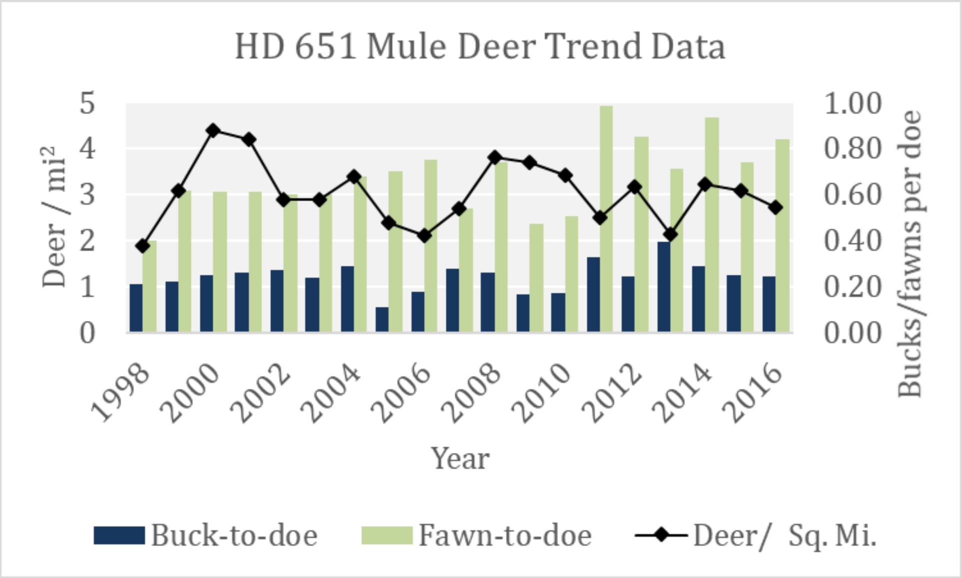


Figure 22. Map of six aerial survey blocks flown in April and October 2014 and 2015 to monitor abundance and composition of mule deer in the Culbertson and Yellowstone River study areas.

A.



B.

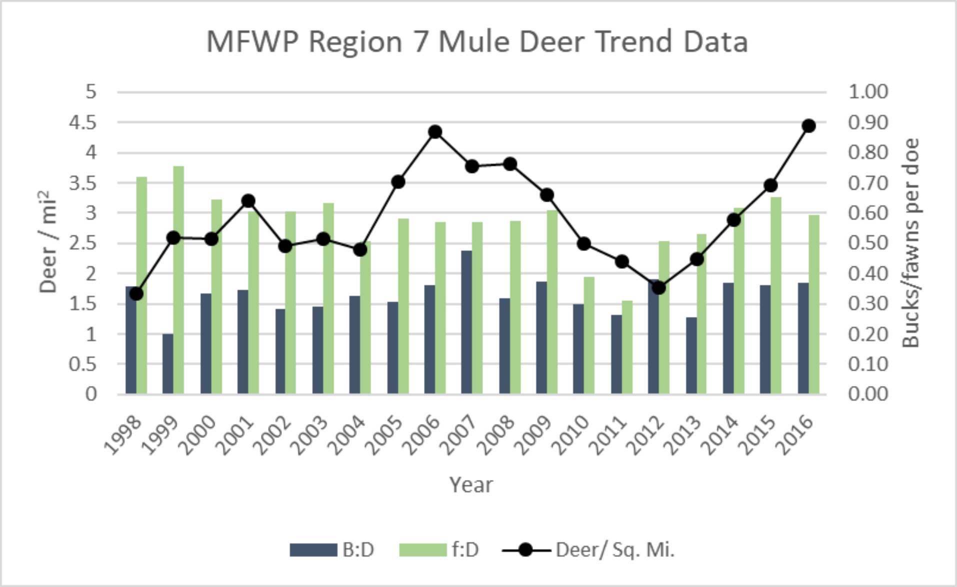


Figure 23 A & B. Mule deer trend data for hunting district 651 (A) and Region 7 (B), from Montana Fish, Wildlife and Parks, showing summarized results of deer density, buck-to-doe ratios and fawn-to-doe ratios. FWP collected trend data from two aerial block surveys in HD 651 14 trend areas in Region 7.

Literature Cited

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

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

Griffin, P. C., B. C. Lubow, K. J. Jenkins, D. J. Vales, B. J. Moeller, M. Reid, P. J. Happe, S. M. Mccorquodale, M. J. Tirhi, J. P. Schaberl, and K. Beirne. 2013. A hybrid double-observer sightability model for aerial surveys. The Journal of Wildlife Management 77:1532-1544.

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

CHAPTER V. PHYSIOLOGICAL STRESS RESPONSE OF MULE DEER TO OIL AND GAS ENERGY DEVELOPMENT AND ENVIRONMENTAL CONDITIONS IN WESTERN NORTH DAKOTA AND EASTERN MONTANA

Note: *this chapter is taken directly from the report of the North Dakota portion of the study (Kolar et al. 2017).*

Introduction

Animals respond to external stimuli behaviorally and physiologically and stress hormones are commonly used to measure adrenocortical activity (Millspaugh et al. 2001, Sheriff et al. 2011). Stress hormones can be detected in blood, urine, and feces (Harvey et al. 1984, Wingfield et al. 1994, Wasser et al. 2000). However, with free-ranging animals the response to capture, handling, and blood collection might induce a physiological stress response and complicate data interpretation (Le Maho et al. 1992). Procedures have been developed to quantify adrenal activity non-invasively, through measurement of fecal glucocorticoid metabolite (FGM) levels (Graham and Brown 1996, Wasser et al. 2000, Millspaugh et al. 2002, Keay et al. 2006, Rothschild et al. 2008, Sheriff et al. 2011). In many studies use of fecal material has the added benefit of showing cumulative effects of stressors as they contain metabolites of stress hormones produced over a period of time (Harper and Austad 2000, Wasser et al. 2000, Millspaugh and Washburn 2004).

Physiological stress has many potentially deleterious effects (Sapolsky et al. 2000). Wildlife managers care about physiological stress in wildlife because it is a sensitive measure of wildlife response and can often foreworn of population level effects such as reduced survival (Millspaugh and Washburn 2004). Further, managers might use such information about the physiological stress response of wildlife to help mitigate human-induced disturbances. Ungulates in particular are sensitive to such disturbances, which can affect their behavior, physiology, and demographics (Cassirer et al. 1992, Phillips and Alldredge 2000, Creel et al. 2002, Stankowich 2008). Thus, measurements of the wildlife physiological stress measurements can offer additional insight into wildlife response to human activities, particularly when partnered with other metrics such as behavior and demographics. Many researchers use physiological stress measures as an indicator of general animal well-being (Sheriff et al. 2011). We used fecal hormone assays to evaluate mule deer (*Odocoileus hemionus*) response to human disturbance (i.e., energy development) and biological factors such as age and environmental conditions.

Methods

Field Methods

We collected fecal samples opportunistically from doe and fawn mule deer, after they were captured to be fit with radio collars for a research project in western North Dakota and eastern Montana. Captures occurred during the winter from 2013-2015. We homogenized and froze all fecal samples until assays were completed; fresh samples avoided complications of microbial breakdown of hormone metabolites (Millspaugh and Washburn 2004). We confirmed information about the animal such as sex and age which provides useful context for hormone measurements.

Laboratory Methods

We placed frozen fecal samples in a lyophilizer (Freeze-dry Specialties, Inc., Osseo, Minnesota) for 24 hr. Once freeze-dried, we ground samples, sifted them through a stainless steel mesh to remove large particles, and mixed them thoroughly. We placed dried feces (~0.2 g) in a test tube with 2.0 mL of 90% methanol and vortexed at high speed in a multi-tube vortexer for 30 min. Samples were then centrifuged at ~1900*g* for 20 min, and the supernatant was saved and stored at –20 °C until assayed.

We measured corticosterone metabolites in deer feces (FGM) using a commercially available corticosterone I^{125} double-antibody RIA kit (Cat. #07120103, MP Biomedicals, Solon, Ohio). We followed the manufacturer's method for the corticosterone I^{125} RIA, except that we halved the volume of all reagents (Wasser et al. 2000). These procedures were previously validated by Millspaugh et al. (2002) for white-tailed deer. We conducted a standard assay validation including assessment of parallelism, recovery of exogenous analyte, intra- and interassay precision, and assay sensitivity (Jeffcoate 1981, Grotjan and Keel 1996, O'Fegan 2000) to confirm the assay accurately and precisely measured testosterone metabolites in white-tailed deer feces. We conducted parallelism and recovery of exogenous testosterone validation assays on two pooled fecal extract samples (expected low and high levels; each pool consisted of feces from three samples). Parallelism ensures the assay maintains linearity under dilution, and recovery of exogenous corticosterone verifies accurate measurement throughout the working range of the assay (Jeffcoate 1981). We added exogenous corticosterone to the low and high pooled fecal extracts to obtain testosterone values under higher dilution levels. We used tests for equal slopes (parallelism) to determine if log-transformed curves of serially diluted pooled fecal extracts were parallel to log-transformed corticosterone standard curves. We selected two mule deer fecal samples and analyzed them in the two assays; interassay variation was calculated from these two samples. We calculated intra-assay variation by averaging the coefficient of variation (CVs) of replicate tubes from 20 randomly chosen samples. Inter-assay variation 4.1% and average intra-assay variation for 20 random samples was 1.6%.

Data Analysis

We evaluated the association of FGM levels in mule deer with natural and anthropogenic factors using a multi-stage (e.g., Washburn et al. 2004) information-theoretic modeling approach

(Burnham and Anderson 2002). We divided potentially influential variables into 4 hypothesis sets, including biological, temperature, landscape, and anthropogenic disturbance (Table 14). In biological models we included biological year of capture (01 June – 31 May: 2012-13, 2013-14, 2014-15); season of capture (fall or winter) because cortisol levels vary seasonally in white-tailed deer (Bubenik et al. 1977); and mule deer age (adult, >1.5 years old; and fawns, < 1 year old) because FGM levels were affected by age in elk (Creel et al. 2002). We included minimum temperature from the nearest weather station (Amidon, Watford City, Grassy Butte, Medora, Culbertson, Sidney, Glendive; National Oceanic and Atmospheric Administration, 2013-2015) within the previous 24 and 48 hours of mule deer capture in temperature models. FGM levels are an index of plasma corticosteroid levels 12-24 hours prior to sampling (Millspaugh et al. 2002), and a physiological stress response may occur up to 36 hours after a significant drop in temperature (Moll et al. 2009), thus we considered this potential lag effect.

To determine the potential effects of landscape features on FGM levels in mule deer, we included a ruggedness index and proportion of forest/shrub cover in landscape models, both of which might mitigate the effects of anthropogenic disturbance on physiological stress (Easterly et al. 1991, Lendrum et al. 2012; in elk, Montgomery et al. 2012). We used the 30-m 2011 National Land Cover Database (NLCD; Homer et al. 2015) in ArcInfo 10.5 (Environmental Research Systems Institute, Redlands, CA) to calculate the proportion of forest or shrub cover by dividing the number of pixels identified as forest or shrub cover by the total number of pixels within 2 km of the capture site (scale based on Kie et al. 2002). We used a 30-m Digital Elevation Model layer to calculate the ruggedness index (Sappington et al. 2007) for each pixel using a 3 x 3 pixel neighborhood (8,100 m^2), which captures the complexity of the landscape without over-smoothing it (Sappington et al. 2007). We then calculated the mean ruggedness index within 2 km of the capture site.

Anthropogenic disturbance may decrease time spent foraging by ungulates (in white-tailed deer, Lagory 1986; elk, Laundre et al. 2001) and has been correlated with increased FGM levels in elk (Millspaugh et al. 2001, Creel et al. 2002), thus we included the following variables in our anthropogenic disturbance models: road density and number of active well pads, drilling rigs, and gravel pits. We used a combination of available and digitized line shapefiles for roads. We used ND Department of Transportation State and Federal Highways and County and City Roads (ND GIS Hub 2016, online), and digitized missing roads at a 1:5,000 scale. We estimated road densities by dividing the total length of roads by the area within 1.91 km of the capture site. We determined the number of active well pads within 1.91 km, drilling rigs within 2.91 km, and gravel pits within 2.91 km of mule deer capture locations using spatial data from the ND Oil and Gas Division (ND Department of Mineral Resources). We used 1.91 km and 2.91 km buffers to quantify anthropogenic disturbance variables because 0.91 km is the approximate radius of a 2.4 km^2 winter home range, which was the upper range of home ranges for non-migratory, female, adult mule deer in the Missouri River Breaks of Montana (Hamlin and Mackie 1990), and indirect impacts on mule deer have been identified up to 1 km and beyond 2 km by well pads and drilling rigs, respectively (Fox et al. 2009, Sawyer et al. 2009).

Next, we determined which form of each continuous vegetation variable, including linear, quadratic, and pseudo-threshold (e.g., Franklin et al. 2000) was most supported at each scale by comparing Akaike's information criterion (Akaike 1973) adjusted for small sample size (AICc) values across variable forms. We used the non-linear form of the variable if it was >2 AICc units better than the linear form; otherwise, we used the linear form. We checked for multicollinearity between variables by calculating Pearson's correlation coefficient (*r*) using the cor() function in R (R Core Team 2016). If $r > 0.65$, we removed the correlated variable with the highest AICc value. Finally, we established which biological, temperature, landscape, and anthropogenic disturbance model was most supported and combined top models to determine which hypothesis or combination of hypotheses explained the most variation in mule deer FGM levels. For all model stages, we used the glm() linear regression function with a Gaussian family and Identity link in R (R Core Team 2016) to estimate AICc values and model parameters

Results

We collected 190 fecal samples from 62 adults and 128 fawns (Table 15). FGM levels ranged from 40.24 – 247.29 (mean = 118.47, SD = 44.83). The global model was most supported (Table 16). The winter of 2014-15 had higher FGM levels than the previous two winters (Figure 27). When temperatures were below 0^{o}C, FGM values were higher than when the temperature was above 0^{o}C (Figure 27C), but the effect was marginal. Contrary to our hypothesis that ruggedness might mitigate the impacts of development, FGM increased with increasing ruggedness (Figure 27D), although the result was not significant.

Beyond annual differences, the most significant effect we observed related to energy development. FGM increased with increasing density of gravel pits, but not until the density of gravel pits was above 3 within 2.91 km of the capture location (Figure 27A). The trend was observed in all years of study. Similarly, FGM values doubled when there were >1 drilling rigs within 2.91 km of the capture location (Figure 27B).

Discussion

Disturbance in the form of density of gravel pits and drilling rigs were the most important factor correlated with mule deer FGMs in this study, while road density and active well pad density were not significantly correlated with mule deer FGMs. This result supports previous research indicating that ungulates might grow accustomed to consistent, low levels of predictable traffic and disturbance (Stankowich 2008, Malo et al. 2011, Brown et al. 2012, Shannon et al. 2014). Gravel pits and drilling rigs have higher levels of traffic, and because drilling rigs are on the landscape for a short time, the traffic is less predictable. This result is also supported by other stress physiology research (Millspaugh et al. 2001, Creel et al. 2002, Crino et al. 2011, Hayward et al. 2011) which indicates that unpredictable disturbances can elicit a physiological stress response in a diversity of wildlife species. For example, Millspaugh et al. (2001) noted higher FGMs of elk in the Black Hills, South Dakota as human activity levels increased in the summer. Similarly, Creel et al. (2002) noted increased FGMs as snowmobile activity increased in Yellowstone National Park. The lack of mule deer specific data, and our results, indicate that physiological stress metrics might be similarly sensitive and useful indicator of animal response to environmental and human-induced disturbances.

These results also indicate that human disturbance was correlated with elevated physiological stress and overrode climate factors, such as temperature. Temperature was a factor affecting mule deer physiological response. Numerous studies have documented a correlation between ungulate FGMs and temperature. For example, Moll et al. (2009) observed an inverse relationship between temperature and FGM in white-tailed deer (Moll et al. 2009). FGM was positively correlated with temperature in elk in Custer State Park, South Dakota (Millspaugh et al. 2001). In many other ungulates, the pattern of FGM secretion throughout the year is not consistent (e.g., caribou, Bubenik et al. 1998; moose, Franzman et al. 1975). We suspect that the FGM secretion we observed is owed to the predominant stressors of the environment at the time of capture. In studies such as ours, it is difficult to tease out the factors affecting FGMs because it is possible human activities and temperature exhibit similar seasonal trends. However, each of these factors explained a different portion of the variation in FGMs, so both might offer insight into how mule deer response to human-induced and environmental disturbances.

These findings are consistent with recent resource selection studies that have shown stronger avoidance of actively drilling rigs than roads or well pads (Sawyer et al. 2009, Northrup et al. 2015) and Chapter I of this study, which indicates mule deer respond spatially to energy development. Thus, we hypothesize that several metrics of response by mule deer point a similar direction and indicate that mule deer are responsive to energy development and the associated activity. It is possible that other potential stressors, many of which could co-vary with human development and temperature, such as food shortages or drought could affect the patterns we observed. However, there is no evidence that deer were malnourished or that other unmeasured environmental conditions overrode what we considered as covariates. We suspect that the degree of human activity in this environment is perceived to be stressful. The elevated FGMs that we observed are not necessarily bad, rather they indicated that the animal has initiated a coping mechanism, through the physiological stress response. In fact, elevated FGMs are an important part of the vertebrate stress response which is stimulated in response to a diversity of stressors, whether they are real or perceived (Selye 1937). Secretion of FGMs helps the animal deal with a stressor and redirects behavior and other coping mechanisms to avoid the stressor. It only becomes deleterious to the animal when these coping mechanisms fail and the animal is unable to eliminate the stressor in the environment. This inability to cope leads to chronic stress which can have multiple negative effects (Sapolsky et al. 2000). We are unable to determine whether these FGM levels were chronic for several reasons including the one-time nature of our sample collection in winter only, the lack of repeated sample collection from the same individuals, and the lack of an experimental design that allows us to assign cause and effect responses.

Age was not a significant predictor of physiological stress levels in our study, but we noted year effects. We detected higher physiological stress levels in 2014-2015 which could be owed to drier environmental conditions that summer, which could have affected forage quality and potentially mule deer condition before winter. For ungulates, seasonal availability of water and forage abundance and quality can vary greatly by year, resulting in seasonal differences in basal fecal glucocorticoid metabolite concentrations (Huber et al. 2003, Dalmou et al. 2007, Chinnadurai et al. 2009, Corlatti et al. 2011). For a number of reasons we might expect age to be influential. For example, fawns might have less body fat and more likely to be stressed by nutritional limitations in winter. Further, fawns might be less accustomed to human activities than adults. However, age was not important indicating that deer of all ages responded similarly from a physiological stress perspective to human-induced and environmental disturbances.

Management Implications

Although we observed increased physiological stress, as measured by FGMs, correlated with energy development metrics including the density of gravel pits and number of drilling rigs, it is important to keep these results in context. We did not correlate physiological stress with demographic parameters, thus we are unable to ascertain whether these observed increased values in FGMs have any deleterious effects on demographics. These findings could be causal, or they could be surrogates for another stressor that we did not include in our analysis. Our study is correlative and it is difficult to tease apart the implications of these results. However, we do hypothesize that mule deer are initiating a physiological stress response, a coping mechanism, in response to these metrics of energy development. Instead of relying solely on FGMs, we encourage managers to use these results in conjunction with other metrics of mule deer response, such as survival, movements, and resource selection to more fully assess whether energy development has a negative impact on mule deer populations. Experimental manipulations, in conjunction with year-round sampling, particularly of the same individuals would more fully allow cause and effect relationships to be determined.

There has been a great deal of research investigating the response of wildlife to energy development. We believe that FGMs could be one important measure, when combined with traditional metrics of spatial ecology and population demographics to elucidate the potential impacts. Our results indicate that FGMs could be a useful method for passively examining physiological stress levels of wildlife in areas with anthropogenic development. We advocate for the application of this technique to complement other measurements of disturbance and to partner multiple metrics.

Table 14. Models included in broad hypotheses related to the influence of natural and anthropogenic factors on FGM levels in mule deer in North Dakota and Montana in 2013 and 2014.

Hypothesis	Models[a]
Biological	
	Null
	Age
	Year
	Season
	Year + Season
	Age + Year
	Age + Season
	Age + Year + Season
Landscape	
	Null
	Wood/Shrub
	Rugged
	Wood/Shrub + Rugged
Temperature	
	Null
	Temp<24h
	Temp<48h
Anthropogenic Disturbance	
	Null
	Active well pads
	Drilling rigs
	Gravel
	Roads
	Active well pads + Drilling rigs + Gravel
	Active well pads + Drilling rigs + Gravel + Roads

[a] Null = intercept-only model; Age = mule deer age (adult or fawn); Year = biological year (2012-13, 2013-14, 2014-15); Season = fall or winter; Wood/Shrub = proportion of area dominated by forest or shrub cover within 2 km of mule deer capture site; Rugged = mean ruggedness index within 2 km of capture site; Temp<24 = minimum temperature in the 24 hours leading up to mule deer capture; Temp<48 = minimum temperature in the 48 hours leading up to mule deer capture; Active well pads = number of active well pads within 1.91 km of capture site; Drilling rigs = number of active drilling rigs within 2.91 km of capture site; Gravel = number of active gravel pits within 2.91 km of capture site; Roads = road density (km/km^2) within 1.91 km of capture site.

Table 15. Summary of mule deer fecal samples collected during 3 consecutive winters in western North Dakota, summarized by age and state.

	2012-13		2013-14		2014-15		Total		
	Adult	Fawn	Adult	Fawn	Adult	Fawn	Adult	Fawn	Total
ND	7	12	25	27	0	46	32	85	117
MT	NA	NA	20	20	10	23	30	43	73
Total	7	12	45	47	10	69	62	128	190

Table 16. Summary of top model results for physiological stress response of mule deer. Those marked with "*" are significant at the P < 0.05 level and those marked with "." are between P 0.05 and 0.10.

Parameter	Estimate	SE	t value	Pr(>|t|)	Significance
(Intercept)	30.2859	50.18557	0.603	0.547	
BioYear13-14	3.2077	15.23614	0.211	0.8335	
BioYear14-15	23.22126	10.94491	2.122	0.0352	*
rugged	121.7659	74.18563	1.641	0.1025	
temp24	-0.62561	0.33753	-1.854	0.0654	.
temp24_sq	-0.0263	0.01981	-1.327	0.1861	
rig	-75.2101	46.65048	-1.612	0.1087	
rig_sq	66.30546	29.37873	2.257	0.0252	*
gravel	-7.08733	5.05097	-1.403	0.1623	
gravel_sq	1.69643	0.65265	2.599	0.0101	*

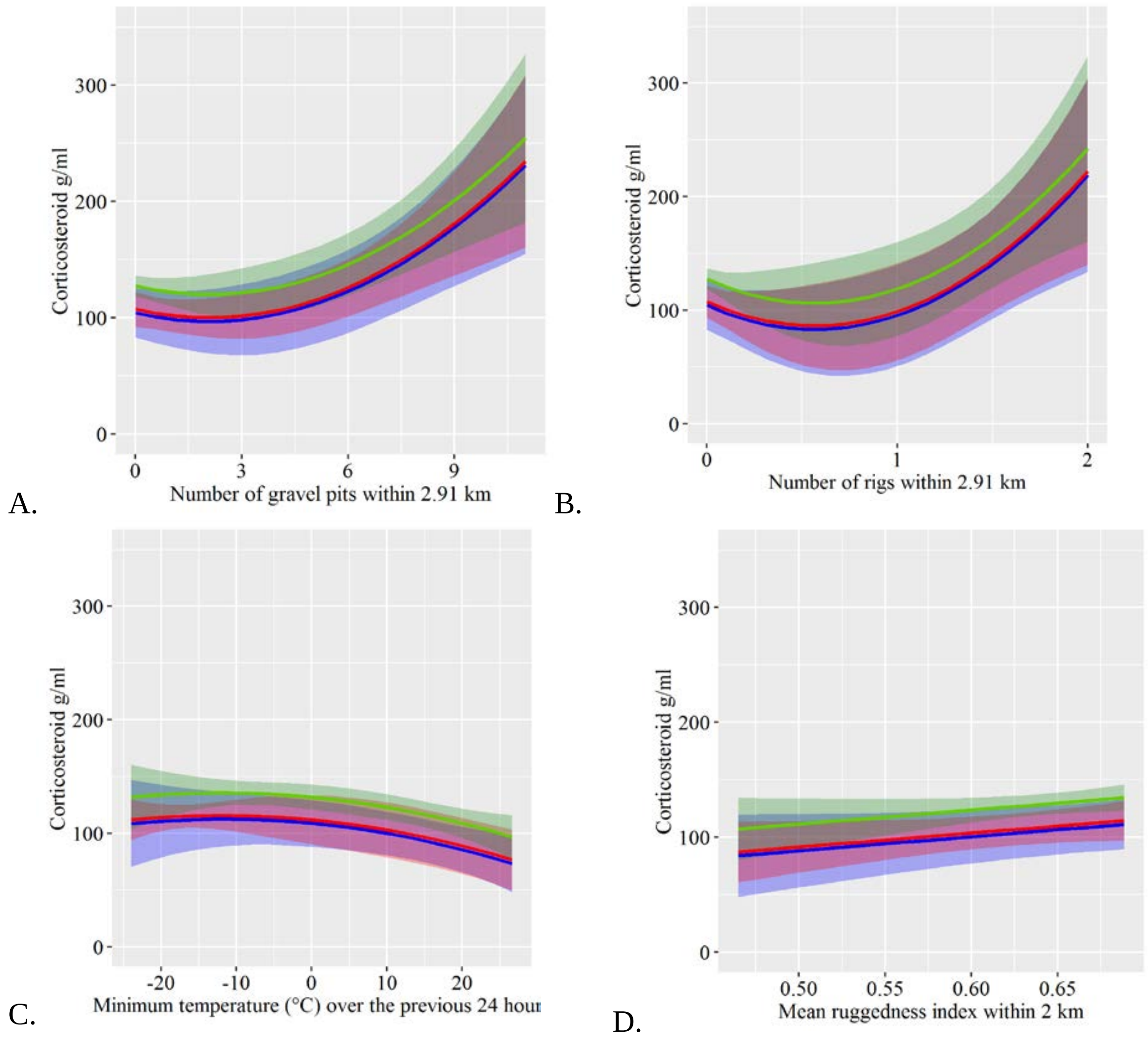


Figure 24 (A-D). Physiological stress response of mule deer to disturbance and environmental conditions in eastern Montana and western North Dakota. Blue = 2012-2013, Red = 2013-2014, and Green = 2014-2015. Ribbons represent 95% confidence intervals.

Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest, Hungary.

Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. PLos ONE 7:e40505.

Bubenik, G. A, A. B. Bubenik, A. Trenkle, A. Sirek, D. A. Wilson, and G. M. Brown. 1977. Short-term changes in plasma concentration of cortisol, growth hormone and insulin durin gthe annual cycle of a male white-tailed deer (*Odocoileus virginianus*). Comparative Biochemistry and Physiology 58:387-391.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi model inference: a practical information theoretic approach. Second edition. Springer Verlag, New York, USA.

Cassirer, E. F., D. J. Freddy, and E. D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375-381.

Chinnadurai, S. K., Millspaugh, J. J., Matthews, W. S., Canter, K., Slotow, R., Washburn, B. E., and Woods, R. J. 2009. Validation of fecal glucocorticoid metabolite assays for South African herbivores. J Wildlife Manage 73:1014-1020.

Corlatti, L., R. Palme, F. Frey-Roos, and K. Hackländer. 2011. Climatic cues and glucocorticoids in free-ranging riparian population of red deer (*Cervus elaphus*). Folia Zoologica 60:176-180.

Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814.

Crino, O.L., B. K. Van Oorschot, E. E. Johnson, J. L. Malisch and C. W. Breuner. 2011. Proximity to a high traffic road: glucocorticoid and life history consequences for nestling white-crowned sparrows. General and Comparative Endocrinology 173:323-332.

Dalmou, A., A. Ferret, B. Chacon, and X. Manteca. 2007. Seasonal changes in fecal cortisol metabolites in *Pyrenean chamois*. Journal of Wildlife Management 71:190-194.

Easterly, T. E., A.W. Wood, and T. Litchfield. 1991. Responses of Pronghorn and Mule Deer to Petroleum Development on Crucial Winter Range in the Rattlesnake Hills. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Fox, L. B., A.A. Arsenault, C.E. Brewer, L.H. Carpenter, Jellison, J.A. Jenks, W.F. Jensen, T.W. Keegan, D.J. Kraft, D.W. Lutz, C.L. Richardson, B.D. Trindle, A.P. Schmidt, and T.S. Stivers. 2009. Habitat Guidelines for Mule Deer: Great Plains Ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies. 60 pp.

Franklin, A. B., D. R. Anderson, R. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Franzman, A. W., A. Flynn, and P. D. Arneson. 1975. Serum corticoid levels relative to handling stress in Alaskan moose. Canadian Journal of Zoology 53:1424-1426.

Graham, L.H. and J. L. Brown. 1996. Cortisol metabolism in the domestic cat and implications for non-invasive monitoring of adrenocortical function in endangered felids. Zoo Biology 15:71-82.

Grotjan, H. E., and B. A. Keel. 1996. Data interpretation and quality control, p. 51–93. i*n* E. P. Diamandis and T. K. Christopoulos, eds. Immunoassay. Academic Press, New York, New York, USA.

Hamlin, Kenneth L.; Mackie, Richard J. 1989. Mule deer in the Missouri River Breaks, Montana: A study of population dynamics in a fluctuating environment. Final Report. Helena, MT: Montana Department of Fish, Wildlife, and Parks. 401 p.

Harper, J. M., S. N. Austad. 2000. Fecal glucocorticoids: a noninvasive method of measuring adrenal activity in wild and captive rodents. Physiological and Biochemical Zoology 73:12-22.

Harvey, J. N., I. F. Casson, A. D. Clayden, G. F. Cope, C. M. Perkins, and M. R. Lee. 1984. A paradoxical fall in urine dopamine output when patients with essential hypertension are given added dietary salt. Clinical Science 67:83-88.

Hayward, L.S., Bowles, A.E., Ha, J.C., & Wasser, S.K. 2011. Impacts of acute and long-term vehicle exposure on physiology and reproductive success of the northern spotted owl. Ecosphere 2:art65.

Homer, C.G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N.D. Herold, J.D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345-354.

Huber, S., R. Palme and W. Arnold. 2003. Effects of season, sex and sample collection on concentrations of fecal cortisol metabolites in red deer (*Cervus elaphus*). General and Comparative Endocrinology 130:48-54.

Jeffcoate, S. L. 1981. Efficiency and effectiveness in the endocrinology laboratory. Academic Press, San Diego, California, USA.

Keay, J. M., J. Singh, M. C. Gaunt, and T. Kaur. 2006. Fecal glucocorticoids and their metabolites as indicators of stress in various mammalian species: A literature review. Journal of Zoo and Wildlife Medicine 37:234-244.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530-566.

LaGory, K. E. 1986. Habitat, group size, and the behavior of white-tailed deer. Behavior 98:168-179.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401-1409.Moll, R. J., J. J. Millspaugh, J. Beringer, J. Sartwell, R. J. Woods, and K. C. Vercauteren. 2009. Physiological stress response of captive white-tailed deer to video collars. Journal of Wildlife Management 73:609-614.

Le Maho Y., H. Karmann, D. Briot, Y. Handrich, J.-P. Robin, E. Mioskowski, Y. Cherel, J. Farni. 1992. Stress in birds due to routine handling and how to avoid it. American Journal of Physiology 263:R775–R781.

Lendrum, P. E., C. R. Anderson, Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere 3(9):82. http://dx.doi.org/10.1890/ES12-00165.1

Malo, J. E., P. Acebes, and J. Traba. 2011. Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? Biodiversity Conservation 20:3477-3488.

Millspaugh, J. J. and B. E. Washburn. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. General and Comparative Endocrinology 138:189-199.

Millspaugh, J. J., B. E. Washburn, M. A. Milanick, J. Beringer, L. P. Hansen, and T. M. Meyer. 2002. Non-invasive techniques for stress assessment in white-tailed deer. Wildlife Society Bulletin 30:899–907.

Millspaugh, J. J., R. J. Woods, K. E. Hunt, K. J. Raedeke, G. C. Brundige, B. E. Washburn, and S. K. Wasser. 2001. Fecal glucocorticoid assays and the physiological stress response in elk. Wildlife Society Bulletin 29:899-907.

Moll, R. J., J. J. Millspaugh, J. Beringer, J. Sartwell, R. J. Woods, and K. C. Vercauteren. 2009. Physiological stress response of captive white-tailed deer to video collars. Journal of Wildlife Management 73:609-614.

Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2012. Variation in elk response to roads by season, sex and road type. Journal of Wildlife Management 77:313-325.

National Oceanic and Atmospheric Administration. 2017. 2012-2016 Daily Summaries. https://www.ncdc.noaa.gov/cdo-web/datasets/. Accessed 1 Jan 2017.

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

O’Fegan, P. O. 2000. Validation, p. 211–238. *in* J. P. Gosling [ed.], Immunoassays. Oxford University Press, New York.

Phillips, G. E., and A. W. Alldredge. 2000. Reproductive success of elk following disturbance by humans during calving season. Journal of Wildlife Management 64:521-530.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/.

Rothschild, D. M., T. L. Serfass, W. L. Seddon, L. Hegde, and R. S. Fritz. 2008. Using fecal glucocorticoids to assess stress levels in captive river otters. Journal of Wildlife Management 72:138-142.

Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress–responses? Integrating permissive, suppressive, stimulatory, and adaptive actions. Endocrine Reviews 21:55–89.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419-1426.

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

Selye, H. 1937. Studies on adaptation. Endocrinology 21:169-188.

Shannon, G., L. S. Cordes, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2014. Behavioral responses associated with a human-mediated predator shelter. PLos ONE 9:e94630.

Sheriff, M. J., B. Dantzer, B. Delehanty, R. Palme, R. Boonstra. 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecologia 166:869–887

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159-2173.

U.S. Census Bureau. 2016. TIGER/Line Shapefiles (machine-readable data files). <https://www.census.gov/geo/maps-data/data/tiger-line.html>.

Washburn, B. E., D. J. Tempel, J. J. Millspaugh, R. J. Gutiérrez, and M. E. Seamans. 2004. Factors related to fecal estrogens and fecal testosterone in California spotted owls. The Condor 106:567-579.

Wasser, S. K., K. E. Hunt, J. L. Brown, K. Cooper, C. M. Crockett, U. Bechert, J. J. Millspaugh, S. Larson and S. L. Monfort. 2000. Generalized fecal glucocorticoid assay for use in a diverse array of non-domestic mammalian and avian species. General and Comparative Endocrinology 120:260-275.

Wingfield, J. C., P. Deviche, S. Sharbaugh, L. B. Astheimer, R. Holberton, R. Suydam, and K. Hunt. 1994. Seasonal changes of the adrenocortical responses to stress in redpolls, *Acanlhis flammea*, in Alaska. Journal of Experimental Zoology 270: 372-380.