MOVEMENT PATTERNS, RESOURCE SELECTION, SURVIVAL AND DEVELOPMENT OF A MONITORING PROGRAM FOR ELK POPULATIONS IN WESTERN NORTH DAKOTA

by

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Executive Summary

In western North Dakota, oil and gas extraction has become a predominant sector of the economy and landscape and, given abundant oil reserves, will continue to impact the region into the future. The infrastructure built to access these natural resources has created a highly disturbed landscape with the potential to negatively impact wildlife in the region. Recent studies have evaluated the effects of energy development on white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), but they have not been assessed for elk (*Cervus canadensis*), despite being a highly valued species for both hunting and viewing. Additionally, elk in western North Dakota recently expanded beyond the boundary of the South Unit Theodore Roosevelt National Park (SUTRNP), and there are many knowledge gaps regarding their population dynamics, movements, and habitat use. Furthermore, there is a need for robust, cost effective, monitoring methods to help biologists better manage this valuable population of elk. To address these concerns, we investigated elk survival, movement patterns, and resource selection, while simultaneously developing a long-term monitoring program for elk in western North Dakota from 2019 – 2023.

We captured and fitted GPS collars on 149 elk (97 adult female, 8 yearling female, 6 adult male, 38 yearling male) in 9 herds between 2019 and 2021. We programmed collars to collect locations every 2 hours, and emit a signal if collars were stationary for > 8 hours so we could investigate cause-specific mortality. We collected 1,094,003 locations between February 16, 2019, and August 31, 2023. Between February 2019 and January 2023, we observed 27 mortalities: 22 legal harvest (16 female, 6 male), 2 wounding loss (1 female, 1 male), 1 probable epizootic hemorrhagic disease (EHD), 1 malnutrition due to a tongue abscess, and 1 unknown.

We used Migration Mapper v 3.1 to visually examine each elk's movements to determine migration patterns, dispersal, and whether they moved to Montana. We then used the dynamic Brownian bridge movement model (dBBMM) to estimate a 99% utilization distribution (UD) of the annual and seasonal home ranges for each elk and combined these individual home ranges to create herd level ranges. We estimated the size of each UD and assessed the amount of space use overlap between individuals and herds. Finally, we created maps of all migrations, dispersals, movements to Montana, movements in/out of SUTRNP, and herd level ranges.

We observed 6 yearling males disperse (2 to Montana), 3 females disperse (1 to Montana), 5 other females move between North Dakota and Montana, and 1 female migrate. Out of the 23 elk collared within SUTRNP, 14 made at least one movement outside the park, with most of these movements occurring in April – August and the least between November – February. The average annual home range size was 129.11 km^2 for females (SD = 59.97) and 181.62 km^2 for males (SD = 108.95). Seasonally, males had the largest home range size in the fall (average = 124.07 km^2; SD = 100.16) and the smallest home range size in the winter (mean = 43.78 km^2; SD = 35.73). Females had the largest home range size in the fall (107.30 km^2; SD = 65.76) and the smallest home range size in the summer (51.18 km^2; SD = 27.58). Overall, elk had high space use overlap with other elk within their herd, and there was little space use overlap between adjacent herds. Herds with the largest amount of overlap were 1) Reservation and Mormon Butte, 2) Belle Lake/Tommy O and Elkhorn, and 3) SUTRNP and Elkhorn.

We evaluated male and female elk resource selection at two distinct spatial scales, 1) within home range (resource selection function [RSF]) and 2) at the individual step level (step selection function [SSF]) and in 5 seasons: early fall, late fall, winter, spring, and summer. We predicted terrain, land ownership, vegetation type, oil/gas well pads, and roads would impact elk resource selection in all seasons, so we included covariates that described these attributes in our models. We grouped oil and gas wells by their activity status (active, drilling, inactive) and roads by their surface type (paved, improved, unimproved). We conducted model selection using Akaike's Information Criterion for both the RSF and SSF analyses and the global model was the top model for male and female SSFs and RSFs in all seasons.

Overall, we found elk generally selected for similar resources by scale and season. At both the home range and step level, woodlands and crops ranked highest for males and females as the top vegetation categories and selected sites farther away from all road types and active wells. Additionally, females selected areas farther away from paved roads in all seasons, had no response to inactive wells in the spring and summer, and selected private land over public land in all seasons. Finally, males in the summer selected sites closer to inactive wells and selected private land over public land in all seasons except winter and spring. These strategies highlight the consistent negative influence of roads and the more nuanced impacts of oil and gas wells on elk selection, in addition to the importance of crops as high value food resources, and the effects of winter weather conditions.

Part of current elk monitoring includes annual flights to count elk. Until now, those flights have been conducted using similar flight transects as are used for mule deer counts. We used 99% UDs of winter home ranges (January - March) for each herd to create new transects for aerial elk surveys. Transects are oriented North/South, spaced 1 mile apart, and extend 3 miles to the north, south, east, and west of each UD to account for future elk expansion outside of the existing home range. Surveys require clear skies to improve detectability of elk, since surveys during overcast skies make it harder to observe elk in the broken landscape of the Badlands.

Elk surveys begin at sunrise and take 2-4 hours to complete. Aerial elk count data will be used as auxiliary data for the population monitoring model.

We used the program PopRecon v3 to produce a Statistical Population Reconstruction (SPR) model for elk within the study unit. The program is an integrated population model that pairs age-at-harvest and hunter-effort data, which has been collected by NDGF since elk harvest began, with auxiliary information to estimate annual age-specific abundance, survival, and harvest rates, and their associated variances. SPR has numerous advantages over other methods in that maximum likelihood methods are used to estimate annual hunter-harvest probabilities that, in turn, are used to estimate age-class and annual abundance. This approach provides better optimization and more realistic estimates of SEs and confidence intervals. It also allows age structures to change annually with yearly variation in recruitment. The age-at-harvest data we used for our model were provided by NDGF for years ranging from 2014 through 2023. Ages of elk harvested over that period ranged from 0.5 to 15 years old for both males and females. GPS collar data provided the number of elk at risk at the beginning of each year and if those elk were harvested, died of other causes, or survived until the next year and was input into the model as an auxiliary data source.

Total annual abundance estimates from the SPR model indicate the Badlands elk population has grown from approximately 900 to 1900 individuals since 2014. The geometric mean ($\bar{\lambda}$) for all years in the SPR model is $\bar{\lambda}$ =1.08, indicating the population is increasing. Further, if we isolate the average growth rate from the last 4 years ($\bar{\lambda}$ =1.02), we see that recent growth is comparable to what has been observed in Montana elk herds ($\bar{\lambda}$=1.01). If greater elk abundance is desirable, the current harvest allowances are sufficient. However, if landowner tolerance of elk is surpassed, managers may need to increase harvest. Harvesting females will have the greatest effect on abundance.

We estimated annual adult survival rates using the Kaplan-Meier estimator with collar data and within the SPR model. For the Kaplan-Meier estimator, we started the year on June 1 which is the average birth date for elk in northern regions. Setting the start date on June 1 means we left-truncated the dataset between February and May 2019, but no mortalities occurred within this time frame, so it did not bias our results. We stratified estimates by sex, year, and herd, then used log-rank tests to test for significant differences in survival among these groups. We summarized cause specific mortality sources by sex, age, herd, and year. We included all mortalities that occurred between the start of the study and January 7, 2023.

The annual Kaplan-Meier survival estimate for all elk was 0.88. Annual Kaplan-Meier survival estimates were 0.90 for females and 0.80 for males. Survival was significantly lower in 2020 (survival = 0.76) compared to 2019 (survival = 0.93), 2021 (survival = 0.94), and 2022 (survival = 0.91). There weren't enough mortalities within each herd to assess differences in survival between herds. All elk caught as yearlings aged up to adults (2-year-old) in June of the year they were caught, and no yearlings died within this period. Therefore, we were not able to distinguish survival differences between yearlings and adults for male or female elk. Survival estimates calculated from the SPR model were 0.91 for females and 0.77 for males, similar to estimates from the Kaplan-Meier estimator. The estimated survival rates are normal compared to other elk populations that have high survival. However, natural survival of elk in North Dakota is higher than most other elk populations. North Dakota elk mortalities are almost exclusively a result of harvest and none are caused by predation, while other elk populations' mortalities result from a combination of harvest and predation.

Introduction

Energy development is one of the largest sources of human disturbance in the western United States and Canada and has been expanding since the late 1990s (Naugle and Copeland 2011). Extraction of oil and natural gas creates a large network of roads, pipelines, transmission lines, and well pads used to access these resources (Copeland et al. 2011, Pickell et al. 2015). Allred et al. (2015) estimated that well pads, roads, and storage facilities built between 2000 and 2012 occupied approximately 3 million ha of land in North America. The scale and distribution of this development creates a highly fragmented landscape with increased disturbance risk that may disrupt migration corridors, alter wildlife behavior, and affect population demographics (Northrup and Wittemyer 2013, Sawyer et al. 2013, Johnson et al. 2017).

Perhaps most crucially, oil and gas development has the potential to affect species' survival (Sawyer et al. 2017). This outcome is particularly true for game species such as ungulates, who face predation risks from both natural predators and humans, because the infrastructure built to access these wells can increase their mortality risk from both sources (Hurley and Sargeant 1991, Unsworth et al. 1991, Whittington et al. 2011). Certain predators, such as wolves (*Canis lupus*), use linear features (e.g., roads) to increase their hunting efficiency and encounter rate with prey (Whittington et al. 2011) and a similar relationship likely exists between ungulates and human hunters (Cooper et al. 2002, Hayes et al. 2002, McCorquodale et al. 2011). Indeed, Hayes et al. (2002) found that bull elk (*Cervus canadensis*) mortality risk in Idaho increased as road density increased. Similarly, McCorquodale et al. (2011) found that distance-to-road and road density variables were useful predictors of elk harvest mortality risk in Washington. Therefore, it is imperative that management agencies understand the effects of oil and gas development on ungulate harvest vulnerability. If oil and gas infrastructure significantly increase hunter success, harvest may exceed desirable levels.

Additionally, while direct habitat loss resulting from energy extraction is a major concern, indirect impacts of energy development on ungulates, such as functional habitat loss, may be of greater concern (Van Dyke and Klein 1996, Sawyer et al. 2006, Hebblewhite 2008, Festa-Bianchet et al. 2011). Functional habitat loss occurs when species abandon areas in response to human disturbances even though there is no physical change to the area. Negative effects of oil and gas development on ungulate resource selection have been documented in caribou (*Rangifer tarandus*; Dyer et al. 2001, 2002), elk (Sawyer et al. 2007), and mule deer (*Odocoileus hemionus*; Sawyer et al. 2006). For example, Buchanan et al. (2014) found that elk selected areas with greater juniper cover, increased terrain ruggedness, and farther from roads when natural gas well development began in northeastern Wyoming. Additionally, elk shifts in resource selection due to development resulted in functional habitat loss of high-use areas by 43.1% and 50.2% in summer and winter, respectively. Results from other studies reported elk avoid roads and active wells during the summer and, to a lesser extent, during the fall and winter (Powell 2003, Sawyer et al. 2007). These studies observed elk continuing to avoid oil and gas development long after exploration and development was completed.

In North Dakota, oil and gas production has become an important part of the economy and landscape, with more than 17,500 wells drilled into the Bakken and Three Forks Formations in the western part of the state since the 1950s (Marra et al. 2021). Energy development will continue to alter western North Dakota landscapes as an estimated 4.3 billion barrels of oil and 4.9 trillion cubic feet of natural gas are still potentially recoverable from this area (Marra et al. 2021). The average size of a well pad is 3.7 acres and includes an average of 1.5 acres of access road development, but 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). During the first year of development, roughly 2,000 vehicles travel to/from each well pad (NDIC Energy Presentation, Bismarck State College, 29 January 2014). In January 2019, 925 oil rigs were actively drilling in western North Dakota, a significant increase over the 78 active wells in January 2010 (Kolar et al. 2017). This scale of development clearly has the potential to impact local ungulate populations.

Ungulate species in western North Dakota include bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), mule deer, white-tailed deer (*Odocoileus virginianus*), and elk. The bighorn sheep and bison populations are small, with bighorn sheep license numbers ranging from 3 – 7 depending on the year, and no current bison harvest. Mule deer and white-tailed deer are more abundant, and the effects of oil and gas development on their populations in western North Dakota have been recently studied (Moratz 2016, Kolar et al. 2017, Skelly et al. 2024). Elk are highly valued for viewing inside the South Unit Theodore Roosevelt National Park (SUTRNP) and the demand for hunting licenses far exceeds supply, with 23,618 applications for 829 any elk licenses in 2024. Despite being one of the most valued large game animals in the state, the effects of oil and gas development on elk populations in this area remain unstudied.

Additionally, there are many knowledge gaps regarding elk population dynamics and movements in western North Dakota. Elk were extirpated from the state by the late 19th century, and the current population in western North Dakota is the result of translocations to SUTRNP in 1985 and escape of elk from Fort Berthold Indian Reservation in 1977. Without natural adult predators within the region, the population size quickly exceeded acceptable levels within the park, leading to periodic culls. Most elk remained within the park until a culling event in 2010, when herds began establishing outside SUTRNP. Biologists estimate population trends for these elk using annual aerial surveys and manage the harvest by regulating hunting permits within specific hunting units. However, as the population continues to grow and expand throughout the Badlands there is a great need for information about elk movements and resource selection to better understand the timing, direction, and duration of space use patterns.

Additionally, there is a need for robust methods to monitor abundance, survival, and recruitment annually that are not cost prohibitive so biologists can effectively manage this valuable population. The North Dakota Game and Fish (NDGF) routinely collects age-at-harvest data to assess the population status and harvest of elk. This information is cost-effective to collect and can be incorporated into a long-term monitoring program that includes a new statistical method called statistical population reconstruction (SPR; Skalski et al. 2010, Gast et al. 2013*a*, *b*). SPR offers a novel approach to assessing demographic parameters of harvested populations by providing robust and defensible estimates of annual age-specific abundance of harvested populations (Skalski et al. 2011, Gast et al. 2013*a*, Clawson 2015). Additionally, SPR allows estimation of survival, recruitment, harvest mortality, and abundance when one or more sets of auxiliary data, such as survival data from a radio telemetry study or independent abundance estimates, are incorporated into the model (Clawson et al. 2013). SPR models do not assume stable age distributions or a stationary population; they also use functional free forms for estimating annual recruitment. All estimates can be age-specific and include corresponding confidence intervals.

This research was designed to provide a comprehensive assessment of the elk population in western North Dakota, focused on assessing survival, movement, and resource selection, while also determining the impact of oil and gas development on these metrics and behaviors. Such information is critically important to help manage elk damage to private lands, mitigate impacts of oil and gas development projects, and identify areas for conducting annual elk counts. Knowledge of migratory behavior, if it exists, will allow for the maintenance of migration corridors and facilitate harvest management. Monitoring bull elk movements from SUTRNP will lead to a better understanding of how SUTRNP contributes to overall harvest levels, which will aid in sustainable harvest management. Finally, the second component of this research focused on the development of a long-term elk monitoring program which annually estimates abundance, natural survival, harvest rates and recruitment, based on data routinely collected by NDGF. The development of methods to annually monitor elk will allow for robust and defensible estimates of abundance and other important characteristics needed to sustainably manage the population.

Objectives

1) Determine elk movement patterns in western North Dakota including home range estimates, migration strategies and if migratory, identify corridors.
2) Evaluate resource selection of elk in western North Dakota.
3) Quantify elk survival and causes of mortality.
4) Develop a monitoring strategy for elk in western North Dakota that will provide methods to determine abundance, harvest rates, natural survival and recruitment rates annually using harvest data already collected by NDGF. This includes identifying seasonal areas of concentration to annually monitor elk abundance and calf production using ground or aerial counts.

Methods for all chapters

Study Area

We studied elk movement, resource selection, and population demographics in the Badlands Region of western North Dakota, within Billings, Dunn, Golden Valley, McKenzie, and Slope counties. The Badlands Region was characterized by highly eroded, steep clay canyons and buttes, distributed along the Little Missouri River and ranged in elevation from approximately 570 – 710 m above mean sea level (Hagen et al. 2005). Vegetation occurring in draws of the northern and eastern slopes were predominately Rocky Mountain juniper (*Juniperus scopulorum*) and green ash (*Fraxinus pennsylvanica*), while riparian areas contained cottonwood (*Populus deltoides*) stands. Southern and western slopes, plateaus, and bottomlands were often barren or contain short-grass prairie (Hagen et al. 2005). Grass species within the region included blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicate*), Indian ricegrass (*Achnatherum hymenoides*), western wheatgrass (*Pascopyrum smithii*), and little bluestem (*Schizachyrium scoparium*; Hagen et al. 2005).

The Killdeer Mountains Region was also located within the study area and represented a 60-km^2 island of elevated habitat connected to the Badlands Region by a few small drainages. This area rose 300 m above the surrounding prairie to 1,010 m and was comprised of a mosaic of open grassland and deciduous species, including green ash, quaking aspen (*Populus tremuloides*), burr oak (*Quercus macrocarpa*), paper birch (*Betula papyrifera*), western black birch (*Betula nigra*), and American elm (*Ulmus americana*), with a dense undergrowth of beaked hazelnut (*Corylus cornuta*; Hagen et al. 2005).

North Dakota has a relatively dry climate (42.7 cm mean annual precipitation) characterized by hot summers (record high 49°C) and cold winters (record low −51°C; Seabloom et al. 2011). Cattle grazing was the most common land use in the Little Missouri Badlands; however, oil and gas development was rapidly increasing within the region (Hagen et al. 2005). Our study area was a mosaic of public (49%) and private land (51%), with the western portion predominately public and the eastern portion predominantly private. Public lands within the study area included Theodore Roosevelt National Park (TRNP), the Little Missouri National Grasslands, Bureau of Land Management properties, North Dakota State Trust lands, and the North Dakota Game and Fish Department Killdeer Wildlife Management Area (Wilckens et al. 2016).

The Bakken and Three Forks Shale Formations largely overlapped the study area, and oil and gas development, including drilling rigs and actively producing wells, occurred throughout the area. The study area encompassed locations with more than 2 active well pads/km^2, which the Western Association of Fish and Wildlife Agencies guidelines (WAFWA; Lutz et al. 2011) considers a high level of development for ungulate habitat.

Elk living in the North Dakota badlands co-exist with mule deer, white-tailed deer, pronghorn (*Antilocapra americana*), and bighorn sheep. Most natural predators of elk were absent from the landscape except for a small mountain lion (*Puma concolor*) population. However, a mountain lion diet selection study completed in this system indicated elk comprise little of their diet (Wilckens et al. 2016). The study area included Game Management Units (GMU) E2, E3, and E4. Elk season for these units opened at the beginning of September and close at the end of December each year.

Field methods

We captured yearling (1.5-year-old) and adult (≥ 2.5-year-old) male and female elk using helicopter net-gunning in February 2019, January 2020, and January 2021. We attempted to capture elk in each of the 9 herds in proportion to the estimated number of elk within each herd. Elk were fitted with global positioning system (GPS) radio collars (G5-2D Iridium; Advanced Telemetry Systems, Isanti, Minnesota, USA) that were programmed to record a location every 2 hours. We programmed collars to drop off on 30 April 2022 for elk caught in 2019 and 2020, and on 30 April 2024 for elk caught in 2021. All animal captures were permitted by the University of Montana Animal Care and Use Committee Protocol # 058-18JMWB-111918 and the National Park Service Animal Care and Use Committee Protocol # MWR_THRO_Millspaugh_Elk_2018.A2. To ensure there were no effects of helicopter capture on elk movements, we removed the first two weeks of locations collected after capture (Jung et al., 2019).

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Chapter 1. Elk movements in western North Dakota

Objective

Determine elk movement patterns in western North Dakota including home range estimates, migration strategies and if migratory, identify corridors.

Methods

To ensure there were no effects of helicopter capture on elk movements, we removed the first two weeks of locations collected after capture (Jung et al., 2019). We also removed GPS collar locations from the dataset if they had a dilution of precision (DOP) value > 10 (D'eon and Delparte 2005), because those values indicated the GPS collar location accuracy was low (Jung et al. 2018). We then used Migration Mapper 3.1 (Merkle et al. 2022) to visually examine each elk's movements to determine if they were migratory or resident, if they dispersed, and if they moved to Montana. Elk within the South Unit Theodore Roosevelt National Park (SUTRNP) were managed differently than elk outside the park, so we visually examined the movements of elk collared within the park and quantified the number of elk that left the park, and in which season they left the park boundaries.

We then calculated the mean total daily displacement to determine how far an elk moved each day. To calculate this metric, we first measured the distance between successive GPS locations for each elk (also called step length). We summed these distances for each elk and day to get the total distance traveled each day for each elk. We then summarized these values by sex and season.

We used the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al., 2012) to estimate a 99% utilization distribution (UD) for the annual and seasonal home ranges for each elk. The dBBMM creates a UD by modeling the space use between two continuous locations as Brownian movement, a continuous random walk, in which movement is diffusive and equally likely in any direction (Horne et al., 2007). Creating a UD using the dBBMM accounts for the uncertainty associated with movements that could have occurred between GPS fixes. We defined seasons as winter (January 1 – March 31), spring (April 1 – May 31), summer (June 1 – August 31), and fall (September 1 – December 31).

Individual home ranges

Using the seasonal and annual home range UDs, we calculated annual and seasonal home range sizes for each elk (in km^2) and summarized these by sex and herd. To assess if individual elk shift their space use between seasons, we quantified the amount of overlap between seasonal home ranges for each elk. We used a simple measure of home range overlap to assess space use sharing between seasons, which ranged from 0% (no overlap of home range polygons) to 100% (complete overlap of home range polygons). We measured overlap between all pairs of seasons for each elk (fall/winter, fall/summer, fall/spring, winter/summer, winter/spring, spring/summer), then summarized these data by herd and season for females and males. To determine overall amounts of seasonal space use overlap, we also summarized these data across all seasons.

Herd level ranges

Male and female elk have different patterns of space use, with non-migratory females forming discrete social units (herds) and showing high fidelity to these herds (Millspaugh et al., 2004) and males making larger movements than females (Wallace & Krausman, 1997) and showing less fidelity to these herds (Montgomery et al., 2013). Therefore, we analyzed herd annual and seasonal home ranges in 3 different ways: 1) females only, 2) males only, and 3) all elk. To create herd annual and seasonal home ranges, we added the UDs of all elk within that herd and season together, then rescaled the resulting raster to values within 0 (low probability of use) and 1 (high probability of use; Sawyer et al., 2009). If an elk dispersed from the herd in which they were captured, we removed them from the data used to create that herd's home range. We then transformed these UD rasters to polygons and used the polygons to map annual and seasonal herd space use.

To assess the accuracy of herd delineation and potential interaction between herds, we first quantified overlap between annual home ranges of elk within the same herd, then quantified overlap between annual home ranges of elk within adjacent herds. We measured overlap for herds as defined using 1) females only, 2) males only, and 3) all elk. We used a simple measure of home range overlap to assess space use sharing among and within herds, which ranged from 0 (no overlap of home range polygons) to 1 (complete overlap of home range polygons).

Results

A total of 149 (105 female, 44 males) elk were collared, but collars on 2 adult females failed immediately after deployment. Therefore, we used data from 95 adult female, 8 yearling female, 6 adult male, and 38 yearling male elk that were GPS collared between 2019 and 2021. Between February 16, 2019, and August 31, 2023, we collected 1,094,003 locations, with a mean of 7,442 locations per elk (range = 384 – 19,764 locations per elk, standard deviation [SD] = 4,205). Between capture and April 3, 2024, the collars collected locations for an average of 679 days (females = 807 days, males = 379 days). Of the 120 collars deployed on elk that did not die during the study, there were 30 collars that collected locations for < 1 year (females = 6, males = 24), 31 collars that collected locations for ≥ 1 year and < 2 years (females = 22, males = 9), and 59 collars that collected locations for > 2 years (females = 55, males = 4). There were 13 collars that fell off prematurely (females = 3, males = 10) and 6 collars that were purposefully removed earlier than anticipated by SUTRNP capture efforts (females = 2, males = 4). If we assume 2 years is the minimum amount of time collar batteries should last, given our fix rate, we observed 52.5% (63 out of 120) of our collars fail prematurely.

On average, female elk moved 4.40 km per day (SD = 2.41) during the fall, 3.13 km per day (SD = 1.93) during the winter, 3.67 km per day (SD = 1.97) during the spring, and 3.58 km per day (SD = 1.97) in the summer. On average, male elk moved 5.30 km per day (SD = 3.57) during the fall, 2.81 km per day (SD = 1.90) during the winter, 4.74 km per day (SD = 2.77) during the spring, and 5.67 km per day (SD = 3.34) in the summer.

We observed 6 yearling males disperse (2 to Montana), 3 females disperse (1 to Montana), 5 other females move between North Dakota and Montana, and 1 female migrate (Figures A1 – A15). Please note that some of these elk (particularly the males) were collared < 1 year, so it is possible their dispersal movements were exploratory movements, migrations, or otherwise not true dispersals. The 6 males that dispersed traveled on average 81.5 km (median: 56.3 km, range: 24.5 – 236 km). The elk that made the largest dispersal movement traveled 236 km (straight line distance) or 885 km (total displacement) from their capture location within the Reservation herd to northwest South Dakota. The two male elk that moved into Montana were collared for < 1 year, so we do not know whether these elk remained in Montana or eventually returned to North Dakota. However, one of those males moved into Montana in May 2019 and was harvested in Montana in October 2022, suggesting he dispersed permanently to Montana.

All females that moved into Montana were collared for > 1 year, so we have more insight into their movements. Of the 6 females that made movements into Montana, 4 moved back and forth between North Dakota and Montana while they were collared, 1 went into Montana for < 1 season, then returned to North Dakota permanently, and 1 dispersed to Montana and never returned to North Dakota. The 3 females that dispersed traveled on average 28.0 km (median: 23.7 km, range: 11.8 – 48.7 km). The female elk that migrated was part of the Reservation herd and migrated approximately 40 km between their summer range southeast of Watford City to their winter range directly north by the Missouri River.

A total of 23 elk (13 female, 10 male) were collared within SUTRNP and 14 (8 female, 6 male) of those elk had at least one GPS location outside of the park boundary (Figures C1 – C8). There were 2 yearling males that dispersed from their capture area within SUTRNP to an area outside the park, and they never returned while they were collared. The 12 other elk that made movements outside the park did so during all months of the year, but the spring and summer months (April – August) had the largest number of locations made outside the park and the late fall/early winter (November – February) had the least (Figure 1).

Individual Home Ranges and Overlap

The average annual home range size was 129.11 km^2 for females (SD = 59.97) and 181.62 km^2 for males (SD = 108.95). The average seasonal home range sizes for females were 107.30 km^2 (SD = 65.76) in the fall, 87.88 km^2 (SD = 46.06) in the winter, 75.10 km^2 (SD = 41.03) in the spring, and 51.18 km^2 (SD = 27.58) in the summer. The average seasonal home range sizes for male elk were 124.07 km^2 (SD = 100.16) in the fall, 43.78 km^2 (SD = 35.73) in the winter, 109.42 km^2 (SD = 81.14) in the spring, and 115.10 km^2 (SD = 80.84) in the summer.

The average amount of seasonal home range overlap across all seasons and herds was 0.66 (SD = 0.19) for females and 0.49 (SD = 0.25) for males. For females, seasonal range overlap the least between their winter and summer ranges (mean = 0.57, SD = 0.20) and the most between their fall and summer ranges (mean = 0.75, SD = 0.15). For males, seasonal range overlap was the least between their winter and summer ranges (mean = 0.43, SD = 0.26) and the most between their winter and spring ranges (mean = 0.57, SD = 0.22) across herds. Figures 2 – 4 depict a breakdown of these home range overlap values by herd.

Herd Level Ranges

Bell Lake/Tommy O

The average annual home range size was 186.73 km^2 for females (SD = 63.52) and 292.32 km^2 for males (SD = 94.80). The average seasonal home range sizes for females were 159.44 km^2 (SD = 79.77) in the fall, 116.37 km^2 (SD = 50.87) in the winter, 104.22 km^2 (SD = 60.01) in the spring, and 60.24 km^2 (SD = 31.35) in the summer. The average seasonal home range sizes for male elk were 169.22 km^2 (SD = 77.47) in the fall, 61.91 km^2 (SD = 56.32) in the winter, 207.26 km^2 (SD = 97.49) in the spring, and 141.20 km^2 (SD = 95.69) in the summer.

Blue Buttes (Bulls Only)

The average annual home range size was 262.43 km^2 (SD = NA) for males. The average seasonal home range sizes for male elk were 233.18 km^2 (SD = NA) in the fall, 143.96 km^2 (SD = NA) in the winter, 121.10 km^2 (SD = NA) in the spring, and 171.82 km^2 (SD = NA) in the summer.

Devil's Slide

The average annual home range size was 185.57 km^2 for females (SD = 53.86) and 131.48 km^2 for males (SD = 15.66). The average seasonal home range sizes for females were 143.08 km^2 (SD = 74.94) in the fall, 83.05 km^2 (SD = 20.49) in the winter, 86.46 km^2 (SD = 27.99) in the spring, and 88.16 km^2 (SD = 25.67) in the summer. The average seasonal home range sizes for male elk were 93.36 km^2 (SD = NA) in the fall, 44.65 km^2 (SD = 35.34) in the winter, 75.34 km^2 (SD = 17.00) in the spring, and 110.96 km^2 (SD = 48.94) in the summer.

Elkhorn

The average annual home range size was 130.19 km^2 for females (SD = 23.62) and 221.28 km^2 for males (SD = 107.68). The average seasonal home range sizes for females were 68.07 km^2 (SD = 22.70) in the fall, 108.88 km^2 (SD = 29.69) in the winter, 89.05 km^2 (SD = 23.27) in the spring, and 71.26 km^2 (SD = 12.92) in the summer. The average seasonal home range sizes for male elk were 75.13 km^2 (SD = 41.64) in the fall, 30.92 km^2 (SD = 21.89) in the winter, 107.18 km^2 (SD = 86.15) in the spring, and 166.68 km^2 (SD = 114.54) in the summer.

Mormon Butte

The average annual home range size was 103.71 km^2 for females (SD = 55.23) and 107.80 km^2 for males (SD = 139.32). The average seasonal home range sizes for females were 110.91 km^2 (SD = 65.62) in the fall, 60.66 km^2 (SD = 35.17) in the winter, 59.65 km^2 (SD = 23.62) in the spring, and 41.27 km^2 (SD = 35.66) in the summer. The average seasonal home range sizes for male elk were 172.81 km^2 (SD = NA) in the fall, 16.19 km^2 (SD = 9.68) in the winter, 92.47 km^2 (SD = NA) in the spring, and 117.86 km^2 (SD = NA) in the summer.

Ranch Creek

The average annual home range size was 150.38 km^2 for females (SD = 47.75) and 163.57 km^2 for males (SD = 71.84). The average seasonal home range sizes for females were 136.82 km^2 (SD = 70.06) in the fall, 118.45 km^2 (SD = 63.24) in the winter, 101.19 km^2 (SD = 46.19) in the spring, and 40.82 km^2 (SD = 15.72) in the summer. The average seasonal home range sizes for male elk were 119.41 km^2 (SD = 18.26) in the fall, 81.76 km^2 (SD = 34.00) in the winter, 91.42 km^2 (SD = 35.40) in the spring, and 112.31 km^2 (SD = 27.66) in the summer.

Reservation

The average annual home range size was 136.15 km^2 for females (SD = 57.35) and 211.17 km^2 for males (SD = 32.23). The average seasonal home range sizes for females were

133.85 km^2 (SD = 66.11) in the fall, 98.33 km^2 (SD = 51.09) in the winter, 73.25 km^2 (SD = 40.12) in the spring, and 32.11 km^2 (SD = 22.28) in the summer. The average seasonal home range sizes for male elk were 111.44 km^2 (SD = 63.97) in the fall, 46.00 km^2 (SD = 27.80) in the winter, 75.91 km^2 (SD = 34.76) in the spring, and 82.09 km^2 (SD = 44.64) in the summer.

Scairt Woman

The average annual home range size was 142.62 km^2 for females (SD = 27.09) and 73.71 km^2 for males (SD = NA). The average seasonal home range sizes for females were 127.96 km^2 (SD = 40.42) in the fall, 84.74 km^2 (SD = 22.51) in the winter, 75.26 km^2 (SD = 24.12) in the spring, and 56.09 km^2 (SD = 14.69) in the summer. The average seasonal home range sizes for male elk were 39.77 km^2 (SD = NA) in the winter, 66.57 km^2 (SD = NA) in the spring, and 5.92 km^2 (SD = NA) in the summer.

State Park

The average annual home range size was 83.61 km^2 for females (SD = 13.16) and 189.59 km^2 for males (SD = 97.61). The average seasonal home range sizes for females were 78.70 km^2 (SD = 22.73) in the fall, 66.39 km^2 (SD = 28.11) in the winter, 44.15 km^2 (SD = 8.39) in the spring, and 43.19 km^2 (SD = 10.79) in the summer. The average seasonal home range sizes for male elk were 218.19 km^2 (SD = 227.10) in the fall, 37.84 km^2 (SD = 7.98) in the winter, 127.21 km^2 (SD = 54.80) in the spring, and 100.04 km^2 (SD = 28.30) in the summer.

TRNP

The average annual home range size was 47.68 km^2 for females (SD = 20.15) and 107.18 km^2 for males (SD = 110.99). The average seasonal home range sizes for females were 41.44 km^2 (SD = 16.94) in the fall, 34.27 km^2 (SD = 15.90) in the winter, 31.64 km^2 (SD = 19.25) in the spring, and 25.62 km^2 (SD = 7.57) in the summer. The average seasonal home range sizes for male elk were 93.44 km^2 (SD = 119.68) in the fall, 26.44 km^2 (SD = 17.16) in the winter, 74.23 km^2 (SD = 92.03) in the spring, and 63.33 km^2 (SD = 43.79) in the summer.

Herd Level Overlap

Overall, elk had high space use overlap with other elk within their herd (mean = 0.55, SD = 0.32, Table 1). When herds were defined using female elk only, there was higher overlap between elk within each herd (mean = 0.62, SD = 0.30) compared to when herds contained only males (mean = 0.39, SD = 0.32) and both males and females (mean = 0.53, SD = 0.32). The herd with the lowest individual space use overlap was the SUTRNP herd, which could potentially be split into a west and east herd (Figure A16).

There was little space use overlap between adjacent herds (mean = 0.02, SD = 0.08; Table 2). There was less overlap between adjacent herds when herds were defined using females only (mean = 0.01, SD = 0.06), compared to when herds were defined using males only (mean = 0.03, SD = 0.11) and when all elk were included (mean = 0.02, SD = 0.08). Herds with the largest amount of overlap were 1) Reservation and Mormon Butte, 2) Belle Lake/Tommy O and Elkhorn, and 3) SUTRNP and Elkhorn (Figures C1 – C5). The overlap between SUTRNP and Elkhorn was the result of 4 yearling males in Elkhorn and 3 yearling males in SUTRNP that moved farther than other elk within their respective herds. Elk that live in the western portion of the Reservation herd and the northern portion of the Mormon Butte herd overlap a significant amount. Two elk within the Mormon Butte herd and five elk within the Reservation herd overlap with each other but also overlap with elk within their own herds that are more spatially separate from this intersection.

Discussion

Within this section, we found that elk in western North Dakota were non-migratory and some males dispersed large distances (24.5 – 236 km) from their natal range. However, these elk largely showed high fidelity to their individual home ranges, and exhibited few shifts in space use seasonally, with at least half of their range overlapping among seasons on average. Females generally moved less than males, both in terms of average movement distances and home range sizes. Below we discuss how these movement behaviors align with other elk populations in North America and their implications for managers in western North Dakota.

Many elk populations in western North America are migratory (Barker et al. 2019, Kauffman et al. 2022, Poole et al. 2024). These large-scale seasonal movements enable elk to track spring forage green-up while migrating (Aikens et al. 2017, Middleton et al. 2018), access seasonally available forage during the summer (Albon and Langvatn 1992), evade harsh weather conditions during the winter (Kauffman et al. 2021), and potentially reduce predation risk (Hebblewhite and Merrill 2007). These advantages can confer fitness benefits to migratory elk as compared to resident elk (Middleton et al. 2018) and having a mix of migratory strategies within an elk population is thought to be beneficial (Hebblewhite and Merrill 2011, Eggeman et al. 2016). Given this ubiquity of migration among elk in western North America, and the many benefits associated with it, the lack of migratory movements within this population of elk might seem surprising.

However, there are many possible reasons why elk in western North Dakota do not migrate. First, migration is thought to be a learned behavior in ungulates, with knowledge gained through individual or social learning (Jesmer et al. 2018, Merkle et al. 2019, Kauffman et al. 2021). For example, bighorn sheep (*Ovis canadensis*) translocated into areas with existing herds learned to migrate more quickly than sheep translocated into novel areas with no existing sheep herd (Jesmer et al. 2018). Furthermore, sheep probability of migration increased as time since translocation increased; the probability of migration occurring each year reached 50% after 90 years post-translocation (Jesmer et al. 2018). Given that the current elk population in western North Dakota is the result of translocations occurring within SUTRNP in 1985, it is possible that not enough time has elapsed for elk to 'learn' to migrate. Elk were reintroduced to Arkansas between 1981-1985, to Kentucky between 1995-2002, and to Ontario between 1998-2001 (Popp et al. 2014) and they are also non-migratory populations. Yet, it is unlikely that limited time since translocation is the only reason why elk in North Dakota were non-migratory. Despite elk being reintroduced to Michigan and South Dakota around the same time (1914 - 1915; Popp et al. 2014, Simpson 2015), some elk in South Dakota are migratory (Benkobi et al. 2005), while those in Michigan are not migratory (Bender and Haufler 1999).

Many of the main benefits associated with elk migration are due to an elevational difference between summer and winter ranges. Elk often migrate from low elevation winter range, typically valleys where winter weather is milder, to high elevation summer range, typically mountain ranges where summer forage is of higher quality and quantity (Kauffman et al. 2021, 2022). While the exact elevations of summer and winter range vary depending on the location and local topography, there is often a 1000 m difference in elevation between the two ranges (Conner et al. 2001, Benkobi et al. 2005, Poole and Mowat 2005, Hebblewhite and Merrill 2007, Smith 2007, Nelson et al. 2012, Simpson 2015, Barker et al. 2019, Mikle et al. 2019). In elk habitat in this study, elevation ranged from 520 – 1,050 m and there were no distinct mountains or valleys, but rather steep canyons and buttes. While there are differences in temperature and plant communities across this elevational range, they are likely not different or large enough in size to warrant distinct seasonal movements.

Elk home range sizes vary greatly depending on the location and are affected by body size, sex, age, landscape composition, and disturbance (Anderson et al. 2005, Webb et al. 2011). Female elk in this study had similar annual home range sizes compared to resident female elk in South Dakota (99.7 – 175.65 km^2; Benkobi et al. 2005, Simpson 2015), smaller annual home range sizes compared to female elk in New Mexico (249.5 km^2; Webb et al. 2011), and larger home range sizes compared to female elk in Washington (1.34 – 29.79 km^2; Sevigny et al. 2018), Pennsylvania (40.67 km^2; Padilla et al. 2023), northeastern North Dakota (18.5 – 29.5 km^2) and south central North Dakota (31.9 km^2; Amor et al. 2019). These relationships generally agree with the expectation that home range sizes are larger for elk inhabiting grassland-dominated landscapes than those within a forest-grassland mosaic, where both forage and cover are more accessible (McCorquodale 1991, Anderson et al. 2005, Amor et al. 2019, Padilla et al. 2023). Additionally, disturbances such as oil and gas extraction, timber harvest, and infrastructure development can either decrease (Edge et al. 1985, Webb et al. 2011) or increase (Powell 2003) elk home range sizes, potentially depending on the surrounding landscape composition. While we did not examine the relationship between elk home range sizes and density of well pads within each home range, this could be an important avenue for future research if oil and gas development continues to increase within the area.

Elk home range sizes also fluctuate depending on the season, with smaller home range sizes expected during the summer because the increased availability of high-quality forage enables elk to move less to acquire necessary resources (Benkobi et al. 2005, Padilla et al. 2023). However, in some regions, particularly those where elk are supplementally fed in the winter, home range sizes are smaller in winter than summer (Rosatte 2016). Interestingly, we observed opposite relationships for females (winter = 87.88 km^2, summer = 51.18 km^2), and males (winter = 43.78 km^2, summer = 115.10 km^2), indicating that behavioral differences between sexes might also impact seasonal home range size. During the summer females give birth and raise calves, which might restrict their movements due to calf movement constraints and possible increased predation risk associated with increased movement (Berg et al. 2023). Conversely, during the summer males do not have this movement limitation and their increased selection for crops over woodlands could enable them to reduce their movements and thus home range size during the winter (see Resource Selection chapter).

In addition to differences in home range sizes, we observed differences in herd fidelity, dispersal distance and dispersal frequency between males and females. Females showed high fidelity to their herds in all seasons, while males dispersed farther and more often than females, and showed less fidelity to their herds. These movement and space use differences between sexes are found across elk populations (Millspaugh et al. 2004, Montgomery et al. 2013, Killeen et al. 2014, Padilla et al. 2023) and are related to the spatial segregation of sexes, potentially caused by differing forage requirements (Barboza and Bowyer 2000), commonly observed within cervids (Ruckstuhl and Neuhaus 2002). This spatial segregation results in male elk being more solitary, sometimes forming bachelor groups (Weckerly 2001), and females congregating in social groups that are maintained across seasons (Weckerly 1999). Additionally, because elk are polygynous, young males disperse, often large distances, from their natal range to avoid sexual competition with older, larger males (Long et al. 2008). While females do not compete for mates, they may also disperse to avoid inbreeding (Pusey and Wolf 1996), but their dispersals are shorter in distance and less frequent (Killeen et al. 2014). These differences in movement behaviors highlight the importance of monitoring both male and female elk within a population, particularly in a growing population where concerns of chronic wasting disease (CWD) and other diseases continue to increase.

Management Implications

Because elk in North Dakota are not migratory managers do not need to be concerned about protecting migration corridors or managing summer and winter range differently. While elk generally did not shift their space use between seasons, some yearling males dispersed large distances from their natal ranges, with one male traveling > 200 km. Additionally, both males and females made movements into Montana; some of these elk stayed in Montana and some returned to North Dakota. These long-distance and trans-boundary movements will be crucial to incorporate into disease planning efforts, particularly if CWD is found within eastern Montana or continues to increase in prevalence in northwest South Dakota. However, most of the collared elk remained within North Dakota, so managers and hunters should not be concerned that large numbers of elk are being drawn out of the state and reducing hunting opportunity. Annual and seasonal home range sizes were comparable to those seen in some other populations, but as oil and gas development increases within the area, managers should continue to monitor elk movements, home range sizes and home range fidelity. These movement metrics are all known to change as disturbances increase.

Space use overlap was high among elk within a herd and low between elk in adjacent herds, indicating the 9 herds delineated by NDGF are accurate groupings of elk across the landscape. The only exception would be the SUTRNP herd, which could be split into an east and a west herd, as there was some spatial separation within this herd. Additionally, more than half of the elk collared within the SUTRNP herd made movements outside the park, with most of these movements occurring in the summer. However, some movements outside the park were observed in the fall, particularly for males, indicating these elk are susceptible to harvest. The high fidelity and spatial delineation of herds makes herd specific management feasible should there be interest. For example, should depredation on agricultural crops in certain locations be a concern, tag allocation could be managed to promote harvest in those regions. Focusing harvest regionally would be effective given the spatial delineation of herds and their movements.

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Figures

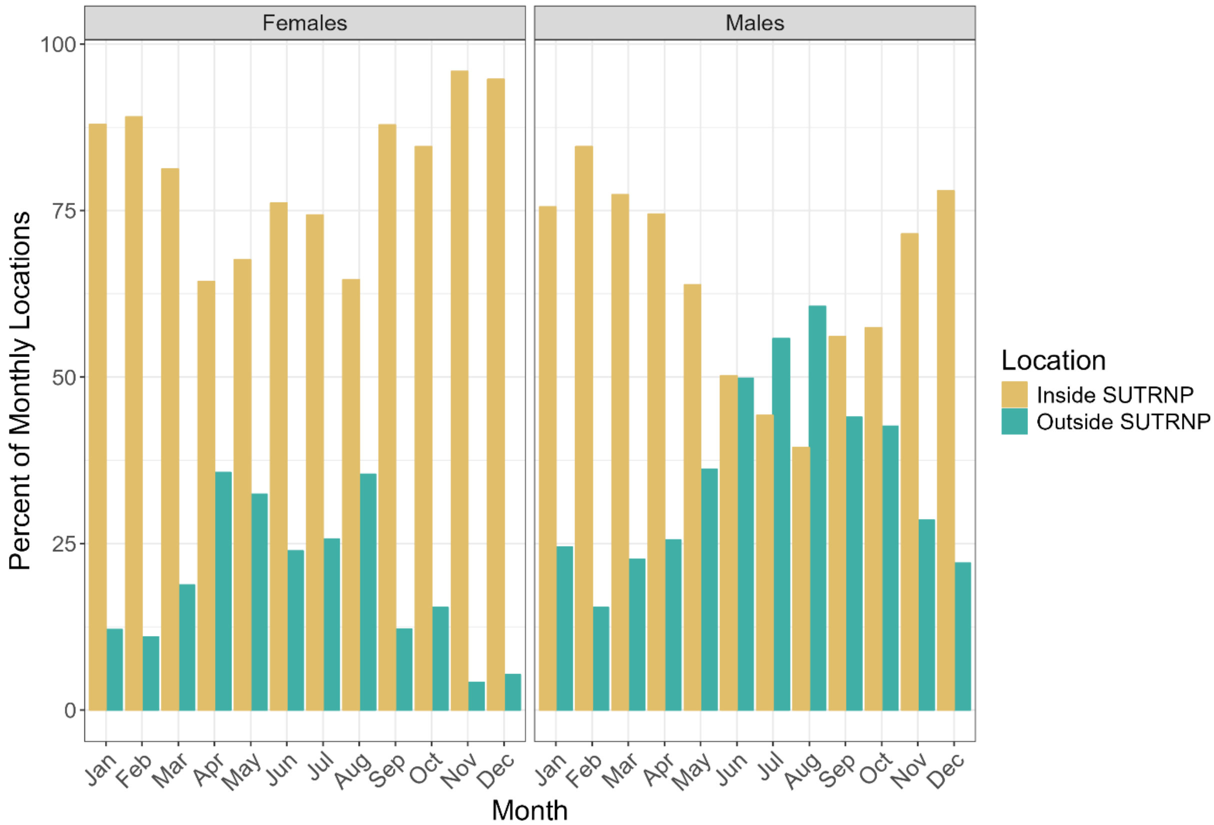

Figure 1. Percent of male and female elk locations located inside and outside of the South Unit Theodore Roosevelt National Park (SUTRNP) by month. These numbers are based on the 21 elk collared within SUTRNP that did not disperse from the park.

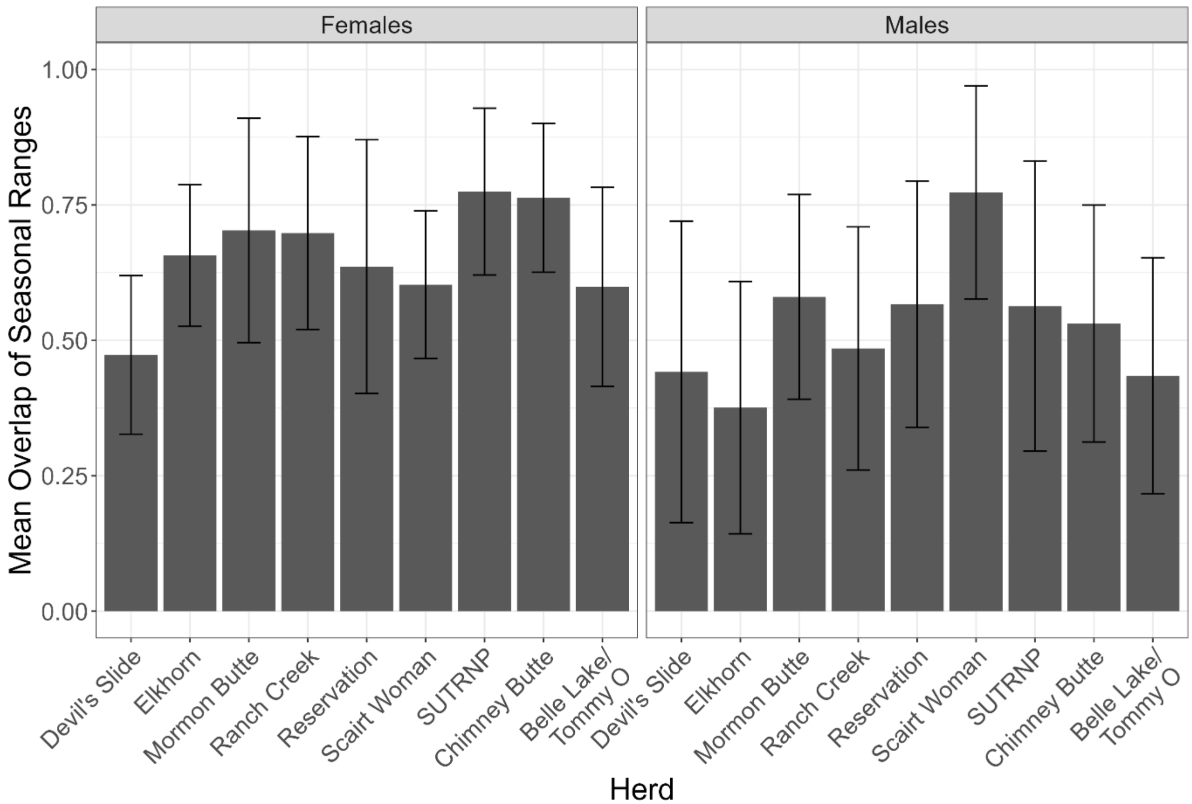

Figure 2. Mean seasonal home range overlap ± 1 standard deviation for male and female elk within the 9 elk herds in western North Dakota. Overlap values ranged from 0 (no space use overlap) to 1 (complete space use overlap).

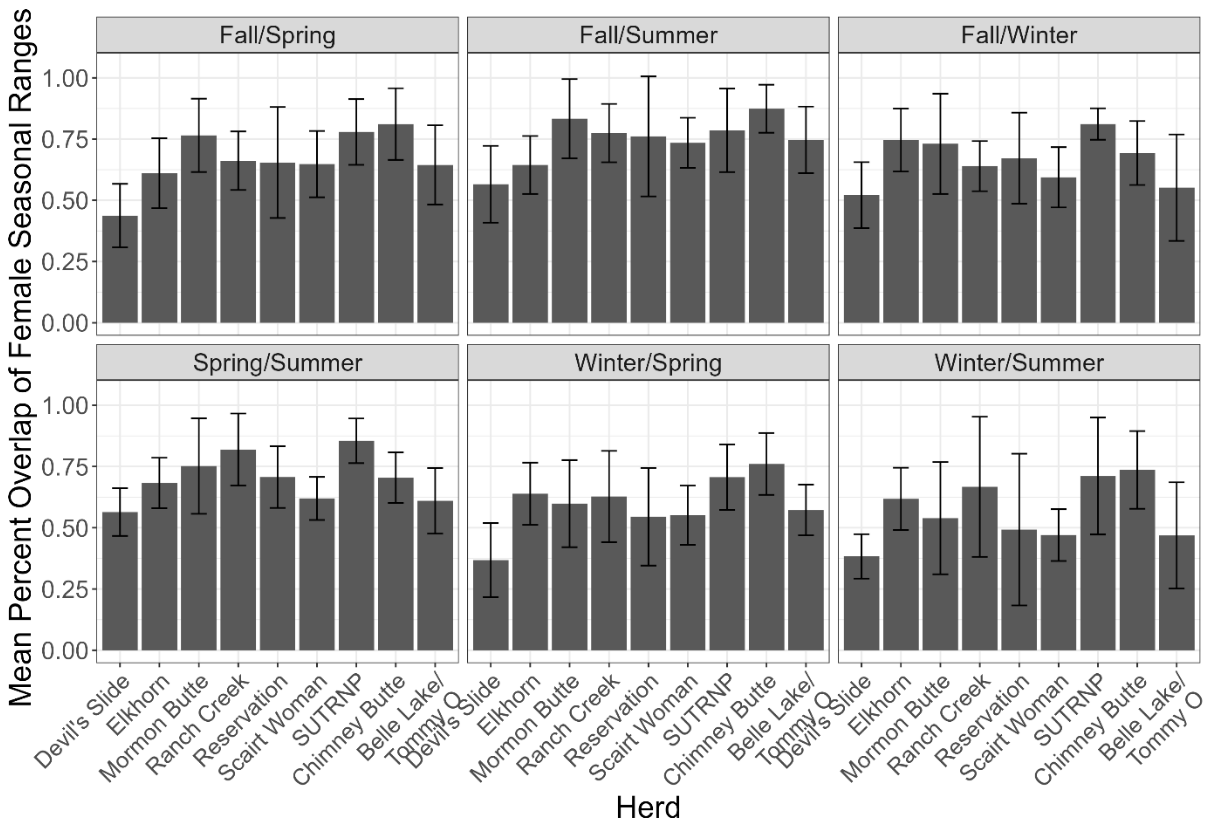

Figure 3. Mean seasonal home range overlap (broken up by season) ± 1 standard deviation for female elk within 9 elk herds in western North Dakota. Overlap values ranged from 0 (no space use overlap) to 1 (complete space use overlap).

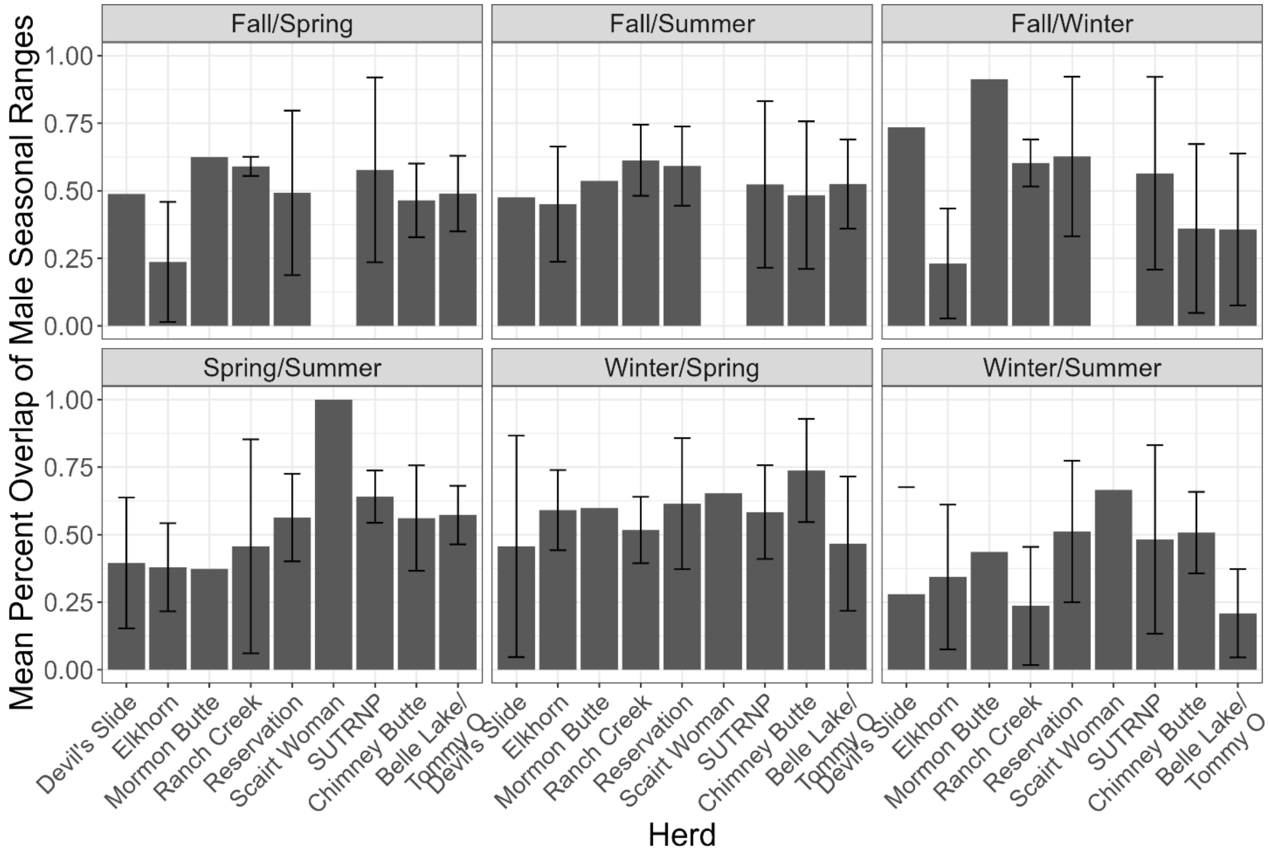

Figure 4. Mean seasonal home range overlap (broken up by season) ± 1 standard deviation for male elk within the 9 elk herds in western North Dakota. Overlap values ranged from 0% (no space use overlap) to 100% (complete space use overlap).

Tables

Table 1. Annual space use overlap values for elk within each herd. These values were calculated using males only, females only, and all elk to highlight the general trend that females exhibit higher fidelity to their herds than males. Overlap values ranged from 0 (no space use overlap) to 1 (complete space use overlap).

Herd	Type	Minimum	Mean	Maximum	Standard Deviation
Belle Lake/Tommy O	All Elk	0.01	0.59	1.00	0.26
	Females Only	0.01	0.57	1.00	0.29
	Males Only	0.43	0.68	0.96	0.20
Devil's Slide	All Elk	0.21	0.67	1.00	0.22
	Females Only	0.25	0.74	1.00	0.21
	Males Only	0.33	0.38	0.42	0.06
Elkhorn	All Elk	0.01	0.60	1.00	0.28
	Females Only	0.17	0.72	1.00	0.20
	Males Only	0.06	0.49	1.00	0.31
Mormon Butte	All Elk	0.01	0.56	1.00	0.32
	Females Only	0.14	0.66	1.00	0.26
	Males Only	0.03	0.51	1.00	0.69
Ranch Creek	All Elk	0.17	0.63	1.00	0.28
	Females Only	0.22	0.74	1.00	0.23
	Males Only	0.23	0.54	0.97	0.27
Reservation	All Elk	0.00	0.50	1.00	0.30
	Females Only	0.00	0.55	1.00	0.32
	Males Only	0.08	0.30	0.77	0.23
Scairt Woman	All Elk	0.38	0.75	0.99	0.15
	Females Only	0.44	0.78	0.99	0.13
Chimney Butte	All Elk	0.21	0.69	1.00	0.23
	Females Only	0.38	0.79	1.00	0.17
	Males Only	0.57	0.70	0.83	0.18

Herd	Type	Minimum	Mean	Maximum	Standard Deviation
SUTRNP	All Elk	0.00	0.24	1.00	0.31
	Females Only	0.00	0.32	1.00	0.36
	Males Only	0.00	0.23	1.00	0.28

Table 2. Annual space use overlap statistics for adjacent herds of elk in western North Dakota. These values were calculated using males only, females only, and all elk to highlight the general trend that females exhibit higher fidelity to their herds than males. Overlap values ranged from 0 (no space use overlap) to 1 (complete space use overlap).

Herds	Type	Minimum	Mean	Maximum	Standard Deviation
Belle Lake/Tommy O & SUTRNP	All Elk	0.00	0.006	0.354	0.030
	Males Only	0.00	0.013	0.354	0.049
Belle Lake/Tommy O & Elkhorn	All Elk	0.00	0.036	0.835	0.100
	Males Only	0.00	0.068	0.545	0.135
SUTRNP & Elkhorn	All Elk	0.00	0.010	1.000	0.083
	Males Only	0.00	0.024	0.890	0.111
Mormon Butte & Ranch Creek	All Elk	0.00	0.000	0.043	0.003
	Females Only	0.00	0.000	0.043	0.004
Ranch Creek & Chimney Butte	All Elk	0.00	0.000	0.038	0.003
	Females Only	0.00	0.000	0.038	0.004
SUTRNP & Scairt Woman	All Elk	0.00	0.001	0.093	0.007
Reservation & Mormon Butte	All Elk	0.00	0.057	1.000	0.148
	Females Only	0.00	0.020	1.000	0.088

Table 3. Mean annual home range sizes (km^2) for male and female elk within the 10 elk herds in western North Dakota.

Herd	**Sex**	**Mean Area (km^2)**	**Standard Deviation**	**Number of Elk**
Belle Lake/Tommy O	Females	186.73	63.52	15
	Males	292.32	94.80	6
Blue Buttes	Males	262.43	NA	1
Devil's Slide	Females	185.57	53.86	7
	Males	131.48	15.66	3
Elkhorn	Females	130.19	23.62	19
	Males	221.28	107.68	9
Mormon Butte	Females	103.71	55.23	10
	Males	107.80	139.32	2
Ranch Creek	Females	150.38	47.75	8
	Males	163.57	71.84	4
Reservation	Females	136.15	57.35	13
	Males	211.17	32.23	3
Scairt Woman	Females	142.62	27.09	10
	Males	73.71	NA	1
State Park	Females	83.61	13.16	8
	Males	189.59	97.61	4
TRNP	Females	47.68	20.15	13
	Males	107.18	110.99	10

Table 4. Mean seasonal home range sizes (km^2) for male and female elk within the 10 elk herds in western North Dakota.

Herd	Season	Sex	Mean Area (km^2)	Standard Deviation	Number of Elk
Belle Lake/Tommy O	Fall	Females	159.44	79.77	15
		Males	169.22	77.47	5
	Spring	Females	104.22	60.01	15
		Males	207.26	97.49	6
	Summer	Females	60.24	31.35	15
		Males	141.20	95.69	6
	Winter	Females	116.37	50.87	15
		Males	61.91	56.32	6
Blue Buttes	Fall	Males	233.18	NA	1
	Spring	Males	121.10	NA	1
	Summer	Males	171.82	NA	1
	Winter	Males	143.96	NA	1
Devil's Slide	Fall	Females	143.08	74.94	7
		Males	93.36	NA	1
	Spring	Females	86.46	27.99	7
		Males	75.34	17.00	3
	Summer	Females	88.16	25.67	7
		Males	110.96	48.94	2
	Winter	Females	83.05	20.49	7
		Males	44.65	35.34	3
Elkhorn	Fall	Females	68.07	22.70	19
		Males	75.13	41.64	8
	Spring	Females	89.05	23.27	19
		Males	107.18	86.15	9
	Summer	Females	71.26	12.92	19
		Males	166.68	114.54	9
	Winter	Females	108.88	29.69	19
		Males	30.92	21.89	9
Mormon Butte	Fall	Females	110.91	65.62	10
	Fall	Males	172.81	NA	1
	Spring	Females	59.65	23.62	10
		Males	92.47	NA	1
	Summer	Females	41.27	35.66	10
		Males	117.86	NA	1
	Winter	Females	60.66	35.17	10
		Males	16.19	9.68	2
Ranch Creek	Fall	Females	136.82	70.06	8
		Males	119.41	18.26	2
	Spring	Females	101.19	46.19	8
		Males	91.42	35.40	4

	Summer	Females	40.82	15.72	8
		Males	112.31	27.66	3
	Winter	Females	118.45	63.24	8
		Males	81.76	34.00	4
Reservation	Fall	Females	133.85	66.11	12
		Males	111.44	63.97	4
	Spring	Females	73.25	40.12	13
		Males	75.91	34.76	4
	Summer	Females	32.11	22.28	13
		Males	82.09	44.64	4
	Winter	Females	98.33	51.09	13
		Males	46.00	27.80	4
Scairt Woman	Fall	Females	127.96	40.42	10
	Spring	Females	75.26	24.12	10
		Males	66.57	NA	1
	Summer	Females	56.09	14.69	10
		Males	5.92	NA	1
	Winter	Females	84.74	22.51	10
		Males	39.77	NA	1
State Park	Fall	Females	78.70	22.73	8
		Males	218.19	227.10	3
	Spring	Females	44.15	8.39	8
		Males	127.21	54.80	4
	Summer	Females	43.19	10.79	8
		Males	100.04	28.30	4
	Winter	Females	66.39	28.11	8
		Males	37.84	7.98	4
TRNP	Fall	Females	41.44	16.94	13
		Males	93.44	119.68	6
	Spring	Females	31.64	19.25	13
		Males	74.23	92.03	8
	Summer	Females	25.62	7.57	13
		Males	63.33	43.79	7
	Winter	Females	34.27	15.90	13
		Males	26.44	17.16	10

Chapter 2. Elk resource selection in western North Dakota at two different spatial scales

Objective

Evaluate resource selection of elk in western North Dakota.

Methods

We evaluated elk resource selection during 5 seasons for male and female elk by comparing resource attributes at GPS points where elk were located (used locations) to attributes at randomly generated points (available locations). Resource selection is a scale dependent process and analyzing elk resource selection at varying spatial scales can provide valuable insights regarding elk perception of the landscape (Johnson 1980). Therefore, we determined elk resource selection at two distinct spatial scales, 1) within home range (hereafter referred to as the resource selection function [RSF]) and 2) at the individual step level (hereafter to referred to as the step selection function [SSF]). Using these two scales provided unique insights into how elk used resources given what was available within their entire home range (RSF) versus how they used resources given what was immediately available to them (SSF). Behavior at fine spatial scales can be the foundation for patterns found at coarser scales, leading to similarities in selection patterns across scales (Prokopenko et al. 2017*a*), but this is not always the case (Orians and Wittenberber 1991). We defined availability for the RSF by using individual home range polygons, created previously during the movement section, and buffering these polygons by twice the median step length (4.03 km for females, 5.10 km for males). Within each buffered home range, we randomly sampled 10 available locations for each used location (Fieberg et al. 2021). We defined the seasons as early fall (Sept 1 – Oct 31), late fall (Nov 1 – Dec 31), winter (Dec 31 – March 31), spring (Apr 1 – May 31), and summer (June 1 – August 31).

Covariates

We predicted terrain, vegetation type, oil/gas well pads, and roads would impact elk resource selection in all seasons (Table 5), so we downloaded remotely sensed data from various public repositories that represented these variables and extracted the data to each used and available location. We obtained a 30-m digital elevation model (DEM) from the US Geological Survey Earth Explorer. From the DEM we calculated slope (degrees) and aspect (north and east) using the terra package in R. We also used the DEM to derive the topographic wetness index (TWI), a measure of how local slope and upslope area contribute to water flow (Sørensen et al. 2006), using ArcGIS Spatial Analyst Tools (Environmental Systems Research Institute, Redlands, California, USA). Finally, we used the DEM to create a measure of terrain ruggedness (Vector Ruggedness Measure; Sappington et al. 2007) using the spatialEco package in R (Evans 2021).

We obtained Normalized Difference Vegetation Index (NDVI) as a proxy for forage availability (Hurley et al. 2014), Terrain Ruggedness Index (TRI), and snow water equivalent (SWE) as a proxy for snow cover through R (v. 4.4.2, R Core Team 2024) using package FedData (Bocinsky 2024). We obtained the 2019-2023 cropland data layers from the US Department of Agriculture (USDA) National Agricultural Statistics Service and reclassified the land cover types into 5 groups for the RSF: grassland (grassland/pasture, herbaceous wetlands, other hay/non-alfalfa), shrub (shrubland), woodland (coniferous forest, deciduous forest, mixed forest), other (water, developed, barren), and crop (corn, soybeans, alfalfa, wheat, and all other crop categories). For the SSF we classified the cropland data layer into 6 groups: grassland (grassland/pasture, herbaceous wetlands, other hay/non-alfalfa), shrub (shrubland), woodland (coniferous forest, deciduous forest, mixed forest), other (water, developed), barren, and crop (corn, soybeans, alfalfa, wheat, and all other crop categories). We created a landowner data layer with 3 categories, privately owned land, publicly owned land, and reservation land, by downloading landowner parcel data and other public land data (state and federal) from the North Dakota GIS hub data portal.

We downloaded road data for Montana from ArcGIS Hub provided by Montana State Library and for North Dakota from the North Dakota GIS Hub site provided by the North Dakota Department of Transportation and classified roads as either paved, improved, or unimproved. We obtained oil and gas well pad data for Montana from the Montana Board of Oil and Gas Conservation website and for North Dakota from the North Dakota Department of Mineral Resources Well Data Subscription Service and created separate monthly well pad layers from April 2019 – June 2023 for active, drilling, and inactive wells. We then created 'distance to' layers for paved roads, improved roads, unimproved roads and monthly 'distance to' layers for active wells, drilling wells, and inactive wells by measuring the shortest Euclidean distance (m) to each road or well feature. We also created well density rasters by calculating number of wells within 3 km per km^2 at a resolution of 30 x 30 m for each well type.

Collinearity, scaling, and functional forms – RSF

We pooled data across years, but we estimated RSFs separately for each sex and season, which resulted in 10 different models. We standardized all continuous covariates using the equation: $\frac{value-mean}{standard\ deviation}$. Before modeling, we screened all covariates for collinearity ($|r| < 0.6$) using Pearson's correlation coefficient and did not include correlated covariates in the same model. Slope and VRM were correlated in all sexes and seasons. We wanted to use the covariate with the highest predictive power, so we fit slope and VRM in univariate logistic regression models for the respective season and sex, ranked models using Akaike's Information Criterion scores corrected for small sample size (AICc), and chose the covariate within the top model as the covariate used in the RSF for that sex and season. In all models, slope was the top ranked covariate over VRM and was used in RSF modeling.

We conducted initial exploratory analyses to determine the best functional forms of elevation, slope, TWI, distance to paved roads, distance to improved roads, distance to unimproved roads, distance to active wells, distance to drillings wells, and distance to inactive wells. We evaluated the linear, pseudo-threshold ($[value + 0.5]$), and quadratic forms of elevation, slope, and TWI. For the 6 'distance to' variables, we only tested exponential decay terms $\left(1 - e^{-2 \times distance}\right)$ because these terms assume there is a threshold distance at which elk selection for the feature does not change beyond that distance (Whittington et al. 2011). The distances to roads and wells extended 10 – 148 km from used locations, which is likely far beyond the distance at which elk can perceive these disturbances on the landscape (Prokopenko et al. 2017*a*). In this analysis, we tested threshold distances of 500 m, 1 km, 2.5 km, 3.5 km, 5 km, and 10 km. We chose the best functional form of each covariate (Table 6) using the same univariate analysis approach as described for correlation.

Analysis – RSF

We used generalized linear mixed models with a binomial distribution and logit link to estimate resource selection with individual elk ID as a random intercept using the package glmmTMB (Brooks et al. 2017) in Program R. We weighted each available point with W = 1000 and used points with W = 1 (Fithian and Hastie 2013, Muff et al. 2020). We used forward manual selection to identify which covariates were included in the final model using the buildmer package (Voeten 2023). We evaluated model fit of the final model for each sex and season by 1) comparing plots of the predicted model output to plots of the raw use/availability data for each covariate, and 2) using k-fold cross validation with k=5 to assess predictive power, with a value > 0.70 considered adequate. After comparing plots of predicted output vs. raw data, we determined that the female models in winter and spring and the male models late fall and winter did not accurately predict elk responses to vegetation type. We determined that distance to improved roads and slope were collinear with vegetation type in those seasons. To account for this issue in the male models, we included an interaction between distance to improved roads and vegetation category. The female models fit best when vegetation category was not included in the final model. We therefore removed vegetation category from the final model and instead fit a separate model containing only vegetation category in the winter and spring.

Finally, we mapped the top RSF model on the exponential scale for each sex and season by predicting the top model over all spatial covariates included within that model. We divided the continuous selection probabilities into 100 equal area divisions with 1 representing low selection probability areas and 100 representing high selection probability areas. We clipped the prediction surfaces to the spatial extent of the available area to avoid making predictions beyond where we collected data.

Analysis – SSF

We used mixed effect step selection functions (SSFs) in a generalized linear mixed-effects model framework including random slopes for distance to and density covariates with individual elk ID as a random intercept using the package glmmTMB (Brooks et al. 2017) in Program R (Muff et al. 2020). To determine available steps, we fit a gamma distribution to observed step lengths and a Von Mises distribution to observed turn angles using Maximum Likelihood methods. We randomly drew 10 available steps per observed step using these distributions. We ranked a group of a priori models for each sex and season using Akaike's

Information Criterion scores corrected for small sample size (AICc). The global model was the top model for all sex and seasons, and therefore all results are based on these models.

Results

We used data from 146 GPS collared elk (early fall: 102 females, 30 males; late fall: 93 females, 21 males; spring: 103 females, 41 males; summer: 103 females, 38 males; winter: 103 females, 43 males) in this analysis. Female elk transmitted locations for an average of 733 days (median = 725) and male elk transmitted locations for an average of 350 days (median = 259). Between February 2019 and June 2023, the collars collected 1,064,642 locations, with a mean of 7,292 locations per elk (range = 384 – 19,023 locations per elk, standard deviation = 4,072).

Females Early Fall RSF – The top model for females in the early fall contained all covariates except VRM (it was correlated with slope; Table 7) and had a k-fold cross validation value of 1. The model predicted females selected northeast facing, wetter areas (higher TWI values) in intermediate elevations (~700 m) and on gentle slopes (0^{o} - 5^{o}; Table 8, Table D1, Figure E1 - Figure E5). They selected areas farther away from all road and well types but showed a higher selection strength to be farther away from paved roads, unimproved roads, and inactive wells than improved roads, active wells, and drilling wells (Figure 5). Females selected private land over reservation and public land (Table 10, Figure E6) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland (Table 12, Figure E7).

Females Early Fall SSF – The top model for females in the early fall contained all SSF covariates except SWE. The model predicted females selected for greater NDVI values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types, active wells and inactive wells. Selection for or against drilling well distance was insignificant. Female selection was unaffected by active well, drilling well, and inactive well densities (Figure 6). Females selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) grassland, 5) other, 6) barren (Table 13).

Females Late Fall RSF – The top model for females in the late fall contained all covariates except VRM (it was correlated with slope; Table 7) and had a k-fold cross validation value of 1. The model predicted females selected east facing, drier areas (low TWI values) in intermediate elevations (~700 m) and on gentle slopes (0^{o} - 5^{o}; Table 8, Table D2, Figure E1 - Figure E5). They selected areas farther away from all road and well types but showed a higher selection strength to be farther away from paved roads and inactive wells than improved roads, unimproved roads, active wells, and drilling wells (Figure 7). Females selected private land over reservation and public land (Table 10, Figure E6) and ranked vegetation types in the following order: 1) crop, 2) woodland, 3) grassland, 4) shrub, 5) other (Table 12, Figure E7).

Females Late Fall SSF – The top model for females in the early fall contained all SSF covariates except NDVI. The model predicted females selected for greater SWE values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road and well types. They selected areas with lower active and inactive well densities but selected for areas with higher drilling well densities (Figure 8). Females selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) crop, 2) woodland, 3) grassland, 4) shrub, 5) other, 6) barren (Table 13).

Females Winter RSF – The top model for females in the winter contained all covariates except VRM (it was correlated with slope) and vegetation category (Table 7) and had a k-fold cross validation value of 0.99. The model predicted females selected southeast facing, drier areas (low TWI values) in intermediate elevations (~750 m) and slopes (~10°; Table 8, Table D3, Figure E1 - Figure E5). They selected areas farther away from all road and well types but showed a higher selection strength to be farther away from paved roads than all other road and well types (Figure 9). Females selected private land over reservation and public land (Table 10, Figure E6) and the univariate vegetation model predicted females ranked vegetation types in the following order: 1) woodland, 2) crop, 3) grassland, 4) shrub, 5) other (Table 12, Figure E7).

Females Winter SSF – The top model for females in the early fall contained all SSF covariates except NDVI. The model predicted females selected for greater SWE values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types, active wells and drilling wells. Selection for or against inactive well distance was insignificant. They selected areas with lower active and inactive well densities, but no significant effects were observed for drilling well densities (Figure 10). Females selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) crop, 2) grassland, 3) woodland, 4) shrub, 5) barren, 6) other (Table 13).

Females Spring RSF – The top model for females in the spring contained all covariates except VRM (it was correlated with slope) and vegetation category (Table 7) and had a k-fold cross validation value of 1. The model predicted females selected northeast facing, wetter areas in intermediate elevations (~750 m) and steeper slopes (~15°; Table 8, Table D4, Figure E1 - Figure

E5). They selected areas farther away from all road and well types except inactive wells and showed a higher selection strength to be farther away from paved roads than all other road and well types (Figure 11). Females selected private land over reservation and public land (Table 10, Figure E6) and the univariate vegetation model predicted females ranked vegetation types in the following order: 1) woodland, 2) shrub, 3) crop, 4) grassland, 5) other (Table 12, Figure E7).

Females Spring SSF – The top model for females in the early fall contained all SSF covariates except SWE. The model predicted females selected for greater NDVI values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types and active wells. Selection for or against drilling and inactive well distance was insignificant. Female selection was unaffected by active well, drilling well, and inactive well densities (Figure 12). Females selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) grassland, 5) other, 6) barren (Table 13).

Females Summer RSF – The top model for females in the spring contained all covariates except VRM (Table 7) and had a k-fold cross validation value of 1. The model predicted females selected northeast facing, wetter areas in intermediate elevations (~750 m) and steeper slopes (~15°; Table 8, Table D5, Figure E1 - Figure E5). They selected areas farther away from all road and well types except inactive wells and showed a higher selection strength to be farther away from paved roads than all other road and well types (Figure 13). Females selected private land over reservation and public land (Table 10, Figure E6) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland (Table 12, Figure E7).

Females Summer SSF – The top model for females in the early fall contained all SSF covariates except SWE. The model predicted females selected for greater NDVI values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types, active wells and drilling wells. Selection for or against inactive well distance was insignificant. They selected areas with lower active and drilling well densities but selected for areas with higher inactive well densities (Figure 14). Females selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland, 6) barren (Table 13).

Males Early Fall RSF – The top model for males in the late fall contained all covariates except VRM (Table 7) and had a k-fold cross validation value of 0.99. The model predicted males selected northeast facing, wetter areas in intermediate elevations (~700 m) and slopes (~10-15^{o}; Table 8, Table D6, Figure E8 - Figure E12). They selected areas farther away from all road and well types and showed a slightly higher selection strength to be farther away from paved and unimproved roads than all other road and well types (Figure 15). Males selected private land over reservation and public land (Table 10, Figure E13) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland (Table 12, Figure E14).

Males Early Fall SSF – The top model for males in the early fall contained all SSF covariates except SWE. The model predicted males selected for greater NDVI values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types, active wells and drilling wells. Selection for or against inactive well distance was insignificant. They selected areas with lower active well density but selected for areas with higher drilling and inactive well densities (Figure 16). Males selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland, 6) barren (Table 13).

Males Late Fall RSF – The top model for males in the early fall contained all covariates except VRM and included an interaction between vegetation type and distance to improved roads (Table 7). The top mode had a k-fold cross validation value of 0.95 and predicted males selected east facing, wetter areas in intermediate elevations (~750 m) and steeper slopes (~15^{o}; Table 8, Table D7; Figure E8 - Figure E12). The interaction predicted males selected to be farther away from improved roads, but the strength of selection depended on the vegetation type (Table 12, Figure E15). Close to improved roads (~40 m away), males ranked vegetation types in the following order: 1) crop, 2) woodland, 3) shrub, 4) grassland, 5) other. Farther from improved roads (~4,200 m away) males ranked vegetation types in the following order: 1) woodland, 2) shrub, 3) grassland, 4) crop, 5) other. Males selected private land over reservation and public land (Table 10, Figure E14), and they selected areas farther away from all road and well types but showed a slightly higher selection strength to be farther away from active wells than all other road and well types (Figure 17).

Males Late Fall SSF – The top model for males in the early fall contained all SSF covariates except NDVI. The model predicted males selected for greater SWE values but selection for terrain ruggedness was insignificant (Table 9). They selected areas farther away from all road types and active wells. Selection for or against drilling and inactive well distance was insignificant. They selected areas with lower drilling and inactive well densities, but no significant effects were observed for active well densities (Figure 18). Males selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) crop, 2) woodland, 3) shrub, 4) grassland, 5) other, 6) barren (Table 13).

Males Winter RSF – The top model for males in the early fall contained all covariates except VRM and included an interaction between vegetation type and distance to improved roads (Table 7). The top mode had a k-fold cross validation value of 1 and predicted males selected southeast facing, drier areas in intermediate elevations (~750 m) and steeper slopes (~15°; Table 8, Table D8, Figure E8 - Figure E12). The interaction predicted males selected to be farther away from improved roads, but the strength of selection depended on the vegetation type (Table 12, Figure E15). Close to improved roads (~40 m away), males ranked vegetation types in the following order: 1) crop, 2) woodland, 3) other, 4) grassland, 5) shrub. Farther from improved roads (~4,200 m away) males ranked vegetation types in the following order: 1) woodland, 2) shrub, 3) grassland, 4) crop, 5) other. Males selected public land over reservation and private land (Table 10, Figure E14), and they selected areas farther away from all road and well types but showed a slightly higher selection strength to be farther away from paved and unimproved roads than other road and well types (Figure 19).

Males Winter SSF – The top model for males in the early fall contained all SSF covariates except NDVI. The model predicted males selected for greater SWE values and for more rugged terrain (TRI; Table 9). They selected areas farther away from all road types, active wells, and drilling wells. Selection for or against inactive well distance was insignificant. They selected areas with lower drilling well densities, but no significant effects were observed for active and inactive well densities (Figure 20). There was no significant selection according to landowner type (Table 11) but males ranked vegetation types in the following order: 1) crop, 2) woodland, 3) shrub, 4) grassland, 5) other, 6) barren (Table 13).

Males Spring RSF – The top model for males in the spring contained all covariates except VRM (Table 7) and had a k-fold cross validation value of 0.99. The model predicted males selected northeast facing, wetter areas in intermediate elevations (~700 m) and slopes (~15 - 20^{o}; Table 8, Table D9, Figure E8 - Figure E12). They selected areas farther away from all road and well types except unimproved roads and showed a slightly higher selection strength to be farther away from drilling wells than all other road and well types (Figure 21). Males selected public land over reservation and private land (Table 10, Figure E13) and ranked vegetation types in the following order: 1) woodland, 2) shrub, 3) other, 4) crop, 5) grassland (Table 12, Figure E14).

Males Spring SSF – The top model for males in the early fall contained all SSF covariates except SWE. The model predicted males selected for greater NDVI values and less rugged terrain (lower TRI; Table 9). They selected areas farther away from all road types, active wells and drilling wells but selected areas closer to inactive wells. They selected areas with lower active, drilling, and inactive well densities (Figure 22). Males selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) grassland, 5) other, 6) barren (Table 13).

Males Summer RSF – The top model for males in the summer contained all covariates except VRM (Table 7) and had a k-fold cross validation value of 0.99. The model predicted males selected northeast facing, wetter areas in higher elevations (~850 m) and steeper slopes (~15 - 20°; Table 8, Table D10, Figure E8 - Figure E12). They selected areas closer to inactive wells and farther away from all road and well types (Figure 23). Males selected private land over reservation and public land (Table 10, Figure E13) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) other, 4) crop, 5) grassland (Table 12, Figure E14).

Males Summer SSF – The top model for males in the early fall contained all SSF covariates except SWE. The model predicted males selected for greater NDVI values but selection for terrain ruggedness was insignificant (Table 9). They selected areas farther away from all road types and active wells but selected areas closer to inactive wells. Selection according to drilling well distance was insignificant. They selected areas with lower active, drilling, and inactive well densities (Figure 24). Males selected private land over public land (Table 11) and ranked vegetation types in the following order: 1) woodland, 2) crop, 3) shrub, 4) other, 5) grassland, 6) barren (Table 13).

Discussion

We analyzed male and female elk habitat selection across five seasons and within two spatial scales and found elk generally selected for similar resources by scale and season, with some notable differences. At both the home range and step level, woodlands and crops ranked highest by males and females as the top vegetation categories and selected sites farther away from all road types and active wells. Additionally, females selected areas farther from paved roads in all seasons, had no response to inactive wells in the spring and summer, and selected private land over public land in all seasons. Finally, males in the summer selected sites closer to inactive wells and selected private land over public land in all seasons except winter and spring.

Within their home ranges, all elk selected east facing sites at intermediate elevations that were farther from drilling wells in all seasons. In the winter, males and females selected south facing, drier sites, the opposite of their selection patterns during other seasons at the home range scale. At the individual step level, elk selected areas with greater SWE values, and females selected areas with less rugged terrain in all seasons. These strategies highlight the consistent negative influence of roads and the more nuanced impacts of oil and gas wells on elk selection, in addition to the importance of crops as high value food resources, and the effects of winter weather conditions.

Throughout their range, elk select areas that provide a mix of both high-quality forages, often found in open canopy areas, and cover, often found in wooded areas (Anderson et al. 2005, Baasch et al. 2010, Amor et al. 2019, Smith et al. 2019, Hinton et al. 2020). Elk in western North Dakota are no exception, as we found that in 18 of our 20 models (2 sexes, 5 seasons, 2 spatial scales) males and females selected woodland and crop vegetation over all other vegetation categories. Elk select agricultural crops because they are higher in protein and more easily digestible than most grasses and browse (Mould and Robbins 1981), and in areas where crops are abundant, the carrying capacity of elk populations is higher because of this increased availability of high-quality forage (Walter et al. 2010). Therefore, we expected elk to select crops, particularly in the late summer and fall when natural forages senesce and crops reach maturity (Walter et al. 2010, Guthrie 2020). Interestingly, elk also selected crops outside of the growing season in the winter, indicating the possible presence of waste grain in these fields (Walter et al. 2010). In the spring at the home range level, crops were ranked the third and fourth selected vegetation type, while at the step level crops were ranked second. These results indicate that elk are not moving within their home range to actively find crops in the spring, but if there are crops in the immediate vicinity, then they will still choose crops over shrubs and grasslands. Perhaps crops are less preferred in this season because the excess grains from winter are depleted, and new crops have not grown in yet. Elk are responsible for causing more crop damage than any other species (Conover 2001) and mitigating these damages will likely be a challenge for NDGF as the elk population continues to grow (Wagner et al. 1997, Guthrie 2020).

Elk use forested areas presumably for thermal refugia in both the summer (Millspaugh et al. 1998) and winter (Amor et al. 2019), and as hiding cover from predators (Rowland et al. 2018). In western North Dakota, adult predation risk is low outside the hunting season, given the lack of an established wolf population and a low-density cougar population (Johnson et al. 2019). Therefore, elk selection of woodlands during winter, spring, and summer, when hunting is not allowed, is likely caused more by thermoregulation concerns than predation risk. The woodland canopy would provide shelter from deep snow and harsh winds in the winter (Amor et al. 2019) and comfort from the sun in summer (Millspaugh et al. 1998). Additionally, in the summer female elk might select woodlands for the security cover they provide elk calves from coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and other neonatal predators (Rohm et al. 2007, Pitman et al. 2014, 2024). During the hunting season, elk likely prioritize woodlands because they provide visual hiding cover from hunters (Ranglack et al. 2017), the main source of elk mortality in this study. Additionally, woodlands comprise only about 10% of the landscape in western North Dakota. Therefore, their low relative availability combined with their importance to elk likely leads to an increased positive selection response compared to other important, but abundant, vegetation types in the region. Regardless of the mechanisms driving elk selection of woodlands, they are a critical vegetative community for elk in the region throughout the year.

Elk avoidance of roads is another common behavioral response (Wisdom et al. 2004, Sawyer et al. 2007, Buchanan et al. 2014, Prokopenko et al. 2017*b*) that we observed within both spatial scales of our analysis. Elk likely selected areas far away from all road types in all seasons because humans are the main source of mortality for elk in this system, and therefore areas close to roads are perceived as risky due to their high human use (Prokopenko et al. 2017*b*). Traffic patterns can affect the degree to which elk respond to roads, with high traffic roads avoided more intensely than lower traffic roads (Gagnon et al. 2007, Montgomery et al. 2013). While we did not measure traffic patterns within this study, our results support this theory as we expected paved roads to have the highest traffic, followed by improved and then unimproved roads. Female elk were more likely to select areas farther away from paved roads than improved or unimproved roads in all seasons at both levels of availability, but particularly in the winter, spring, and summer when the selection response to paved roads was almost three times that of other road types. Similarly, male elk showed the smallest selection response to unimproved roads in the spring at the home range level, when these roads have further reduced traffic because they are likely of poor condition to be traveled regularly by vehicles.

We expected elk behavioral responses to oil and gas wells to follow a similar pattern – highest avoidance of drilling wells, where human activity, noise and disturbance is the greatest, and lowest avoidance of inactive wells, where human activity is very low (Sawyer et al. 2009, Northrup et al. 2015). We observed this pattern for males in the winter and spring at the home range level but did not for all other sexes and seasons. Females reacted similarly to drilling and active wells across seasons, selecting areas > 2.5 km away, and interestingly showed the greatest avoidance of inactive wells in the early and late fall, selecting areas > 5 km away. Elk harvest is facilitated by oil and gas wells (Dorning et al. 2017), likely because these areas are cleared of natural vegetation and have large road networks, which could increase hunter access and sightlines. Inactive well pads may be preferentially used by hunters over other well types because they do not have oil and gas activity occurring on them, thus leading to increased elk avoidance during the hunting season. In the spring and summer, females at the home range level selected locations that were only > 500 m from inactive wells, and males in the summer at both the home range and step level selected areas closer to inactive wells, supporting our theory that elk avoid inactive wells in the fall due to hunting activity.

The avoidance of well pads and roads effectively translates to habitat loss (Northrup et al. 2015), which could limit resource acquisition and thus reduce survival rates (Owen-Smith 2002). Male elk responded the most negatively to drilling wells in the winter and spring, stressful seasons for elk in which their body condition is at its lowest point of the year (Cook et al. 2013). Habitat loss through disturbance avoidance could exacerbate the negative effects brought on by winter (Williams et al. 2021). Additionally, actively fleeing from these disturbances increases energetic costs to elk (Ydenberg and Dill 1986, Cassirer et al. 1992), and spending more time being vigilant in these risky areas decreases the amount of time spent foraging (Fortin et al. 2004), both of which could increase mortality rates (Frid and Dill 2002). Although this elk population is increasing, and currently there is little evidence that human development is negatively impacting elk fitness (survival chapter), these relationships could change in the future as the elk population grows and disturbance continues to increase.

Management Implications

Woodlands were consistently selected by male and female elk in all seasons and levels of availability, highlighting the importance of wooded areas for elk in western North Dakota. Therefore, managers could prioritize the conservation of woodlands in the face of increased oil and gas development and the conversion of land for agriculture. Additionally, males and females consistently showed high selection probabilities for crops and private lands, indicating crop depredation and damage to private lands will continue as the elk population grows. Therefore, managers will need to find ways to mitigate these damages to reduce subsequent elk-human conflicts. Fencing most effectively reduces crop damage but is unfeasible at large spatial scales (Craven and Hygnstrom 1994, Johnson et al. 2014), and non-lethal deterrents such as repellents, frightening devices and hazing are only temporarily effective (Walter et al. 2010, Johnson et al. 2014). Therefore, the most feasible lethal method to reduce conflict is increased harvest; managers could increase landowner harvest tags and encourage landowners to increase hunter access to their land either directly or through the Private Land Open to Sportsmen (PLOTS) program. Given the herd organization identified through our movement analyses, it becomes possible to identify the spatial boundaries of the elk herd causing depredation and target that herd to reduce conflict. Increasing elk use of grasslands through weed control or prescribed burning could also help alleviate crop damage and conflicts.

To increase harvest success and stakeholder satisfaction, managers could use the results of these analyses to direct where hunters focus their efforts during the early and late fall. Specifically, hunters could look for elk within woodlands and crops on private land at intermediate elevations (700 – 750 m) and in less rugged terrain that are at least ~0.5 – 2.5 km away from improved and unimproved roads and > 5 km from paved roads. Slowing or reducing industrial growth is often not feasible, but changing the configuration of how the infrastructure is built can help ameliorate the negative effects to elk. For example, existing roads could be used as much as possible instead of creating new ones, oil and gas well pads could be built > 2.5 km apart, to ensure that elk can be their preferred distance away from these disturbances, or multiple wells should be drilled on one well pad to reduce the geographic footprint of this disturbance. Additionally, new wells could be built in low-quality elk habitat – low elevation (600 – 650 m), west facing grasslands or barren areas that are in rugged terrain (see Figures C1 – C10 for predicted elk selection maps).

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Figures

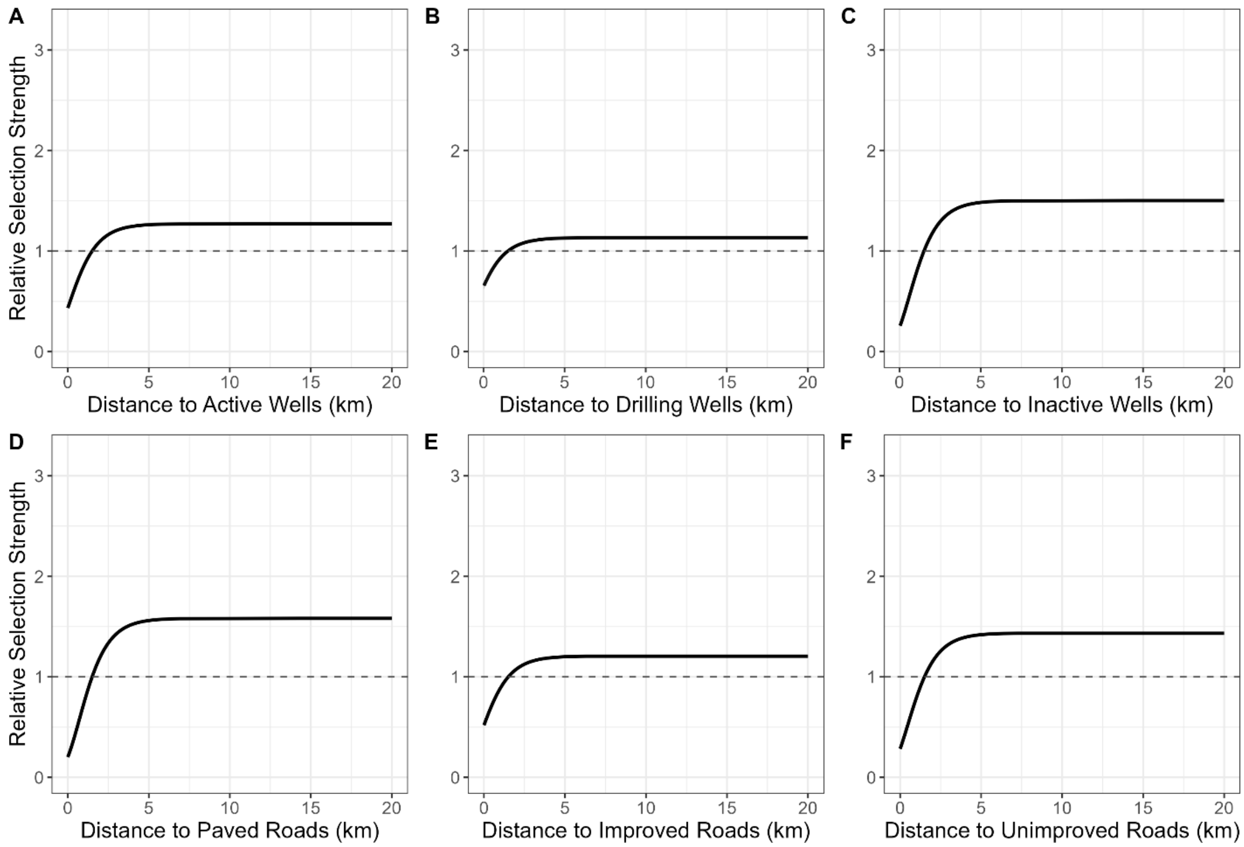

Figure 5. RSF Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for female resource selection during the early fall. Each panel compares the relative selection strength of an elk moving from a location 1.5 km away from that particular to feature to a location 0-20 km away from that feature. Values above 1 indicate selection of that distance compared to 1.5km and values below 1 indicate avoidance compared to 1.5km. Figures 2-10 contain the same results and comparisons for each sex and season

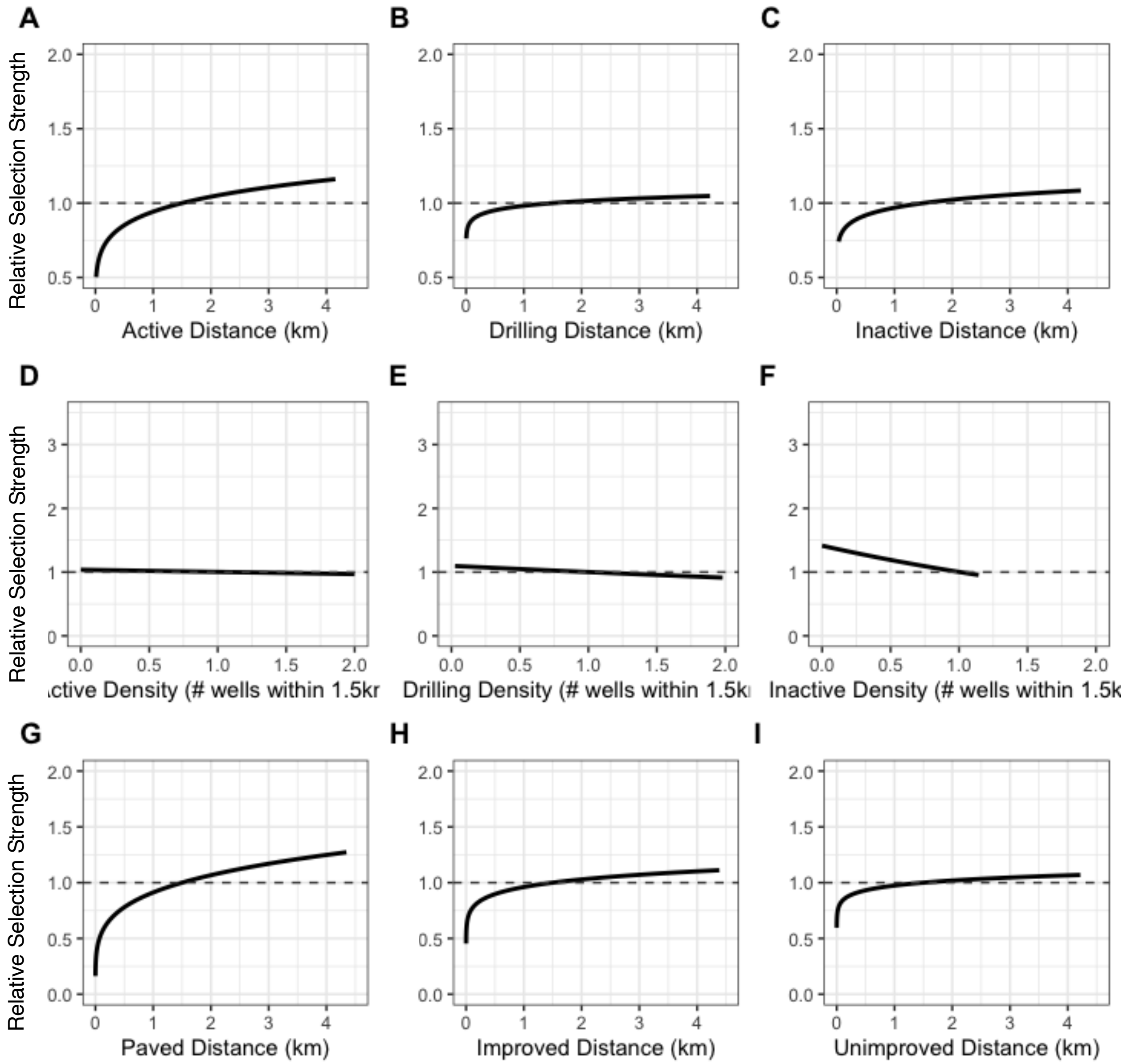

Figure 6. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for female step selection during the early fall. Each distance panel compares the relative selection strength of an elk moving from a location 1.5 km away from that feature to a location 0-5 km away from that feature. Values above 1 indicate selection of that distance compared to 1.5km and values below 1 indicate avoidance compared to 1.5km.

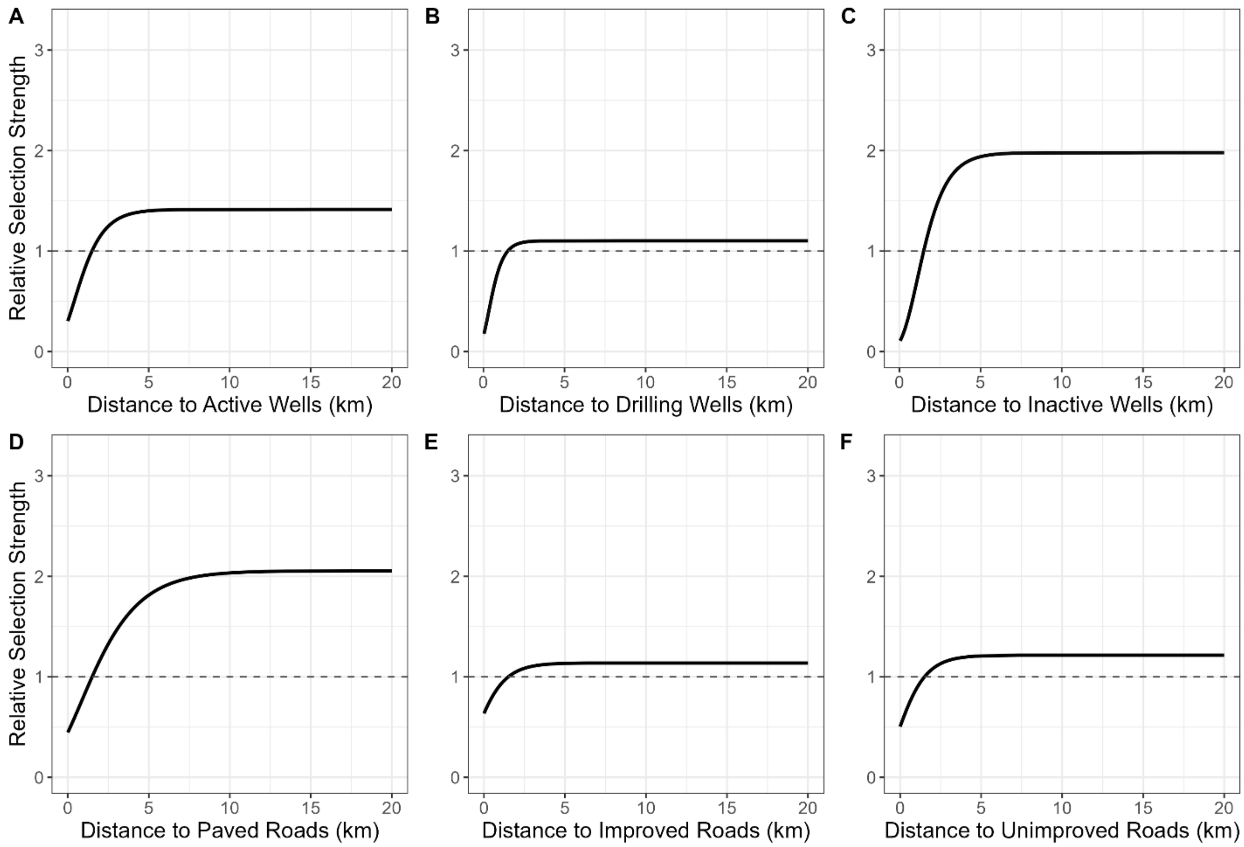

Figure 7. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for female resource selection during the late fall.

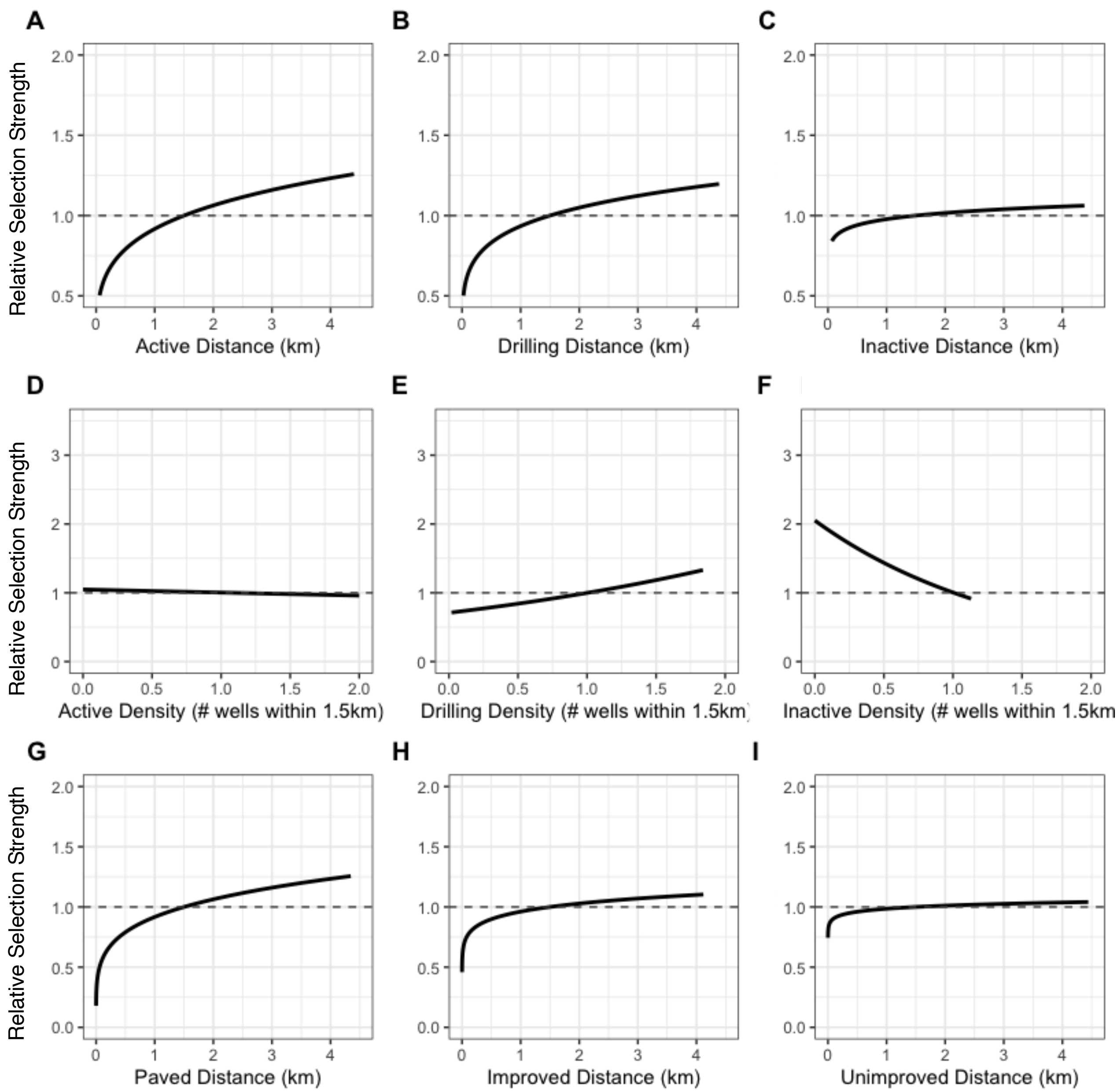

Figure 8. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for female step selection during the late fall.

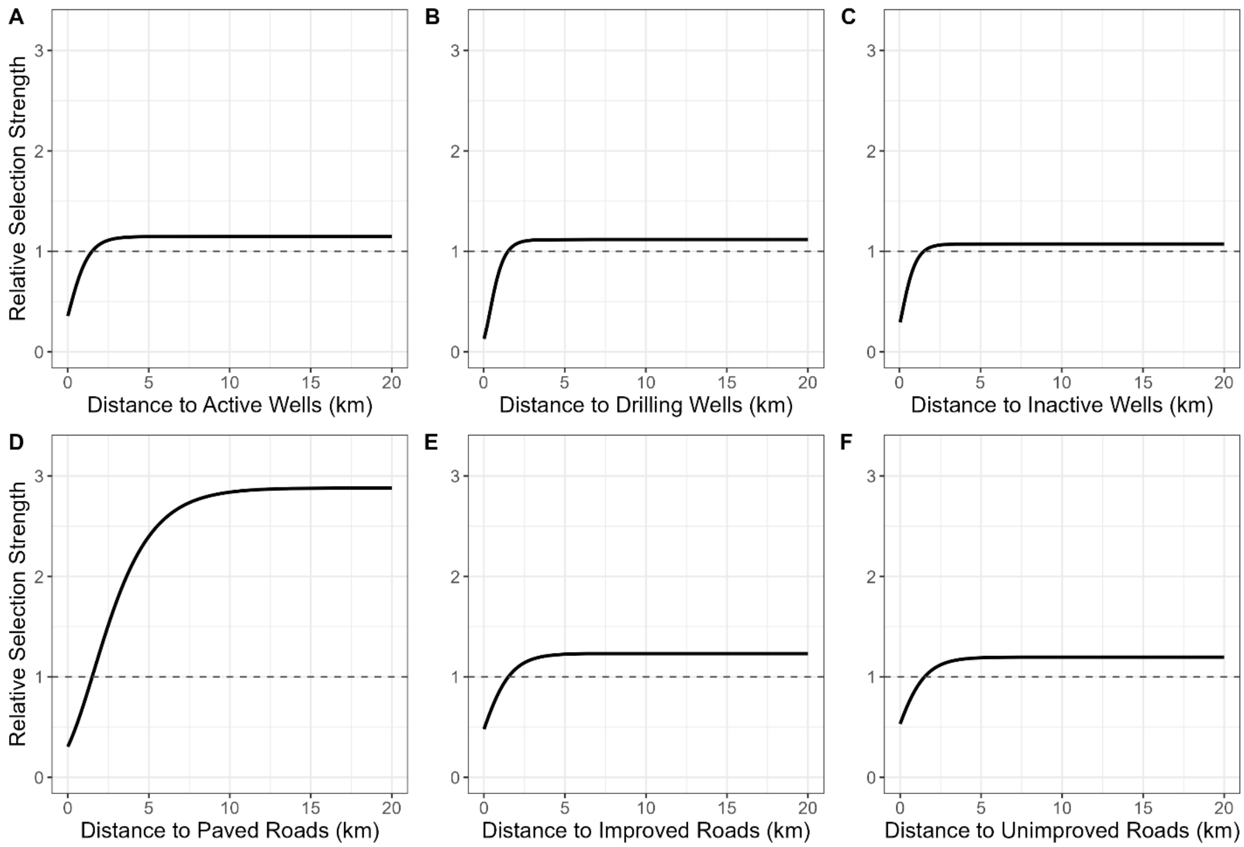

Figure 9. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for female resource selection during the winter.

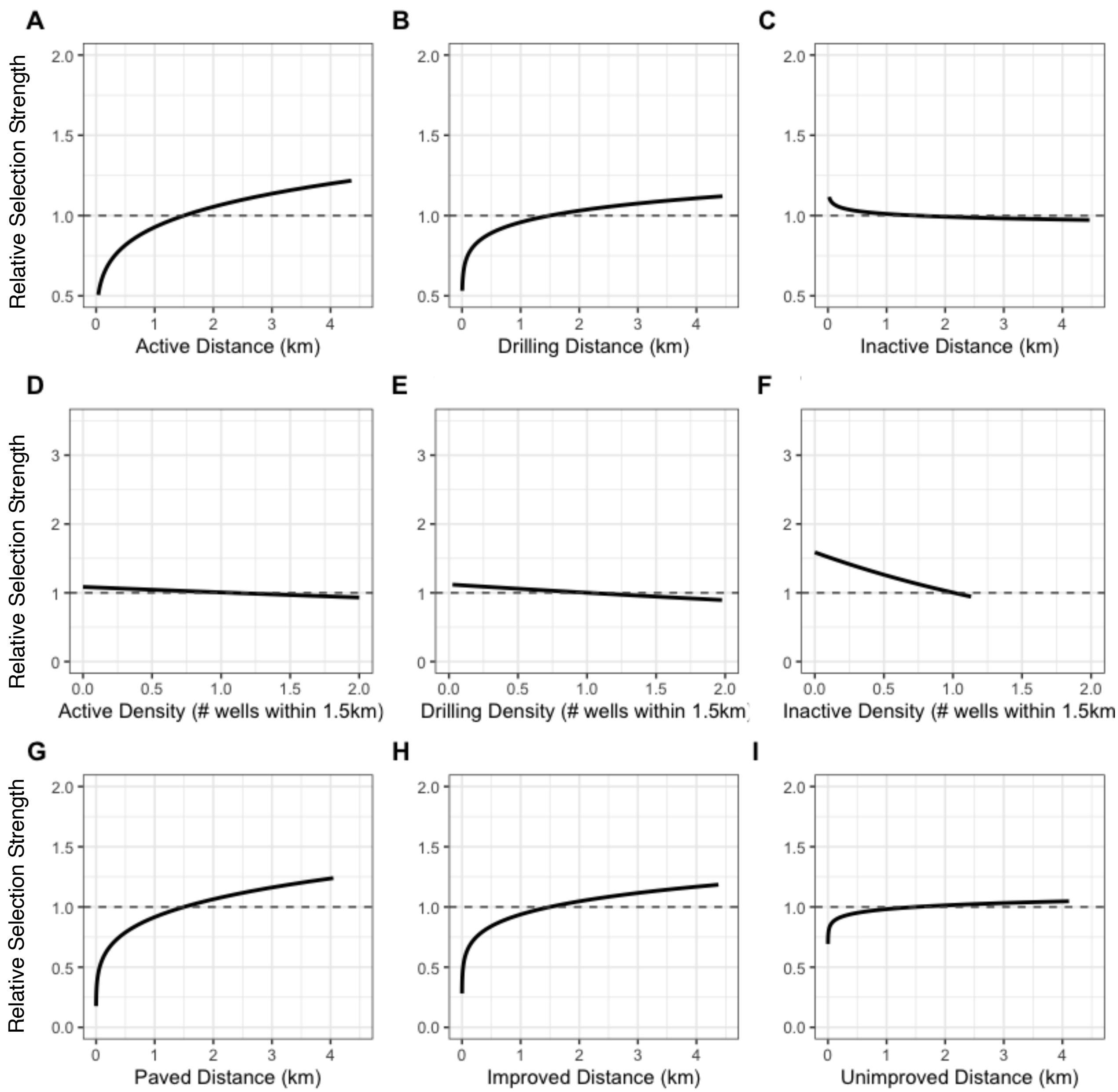

Figure 10. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for female step selection during the winter.

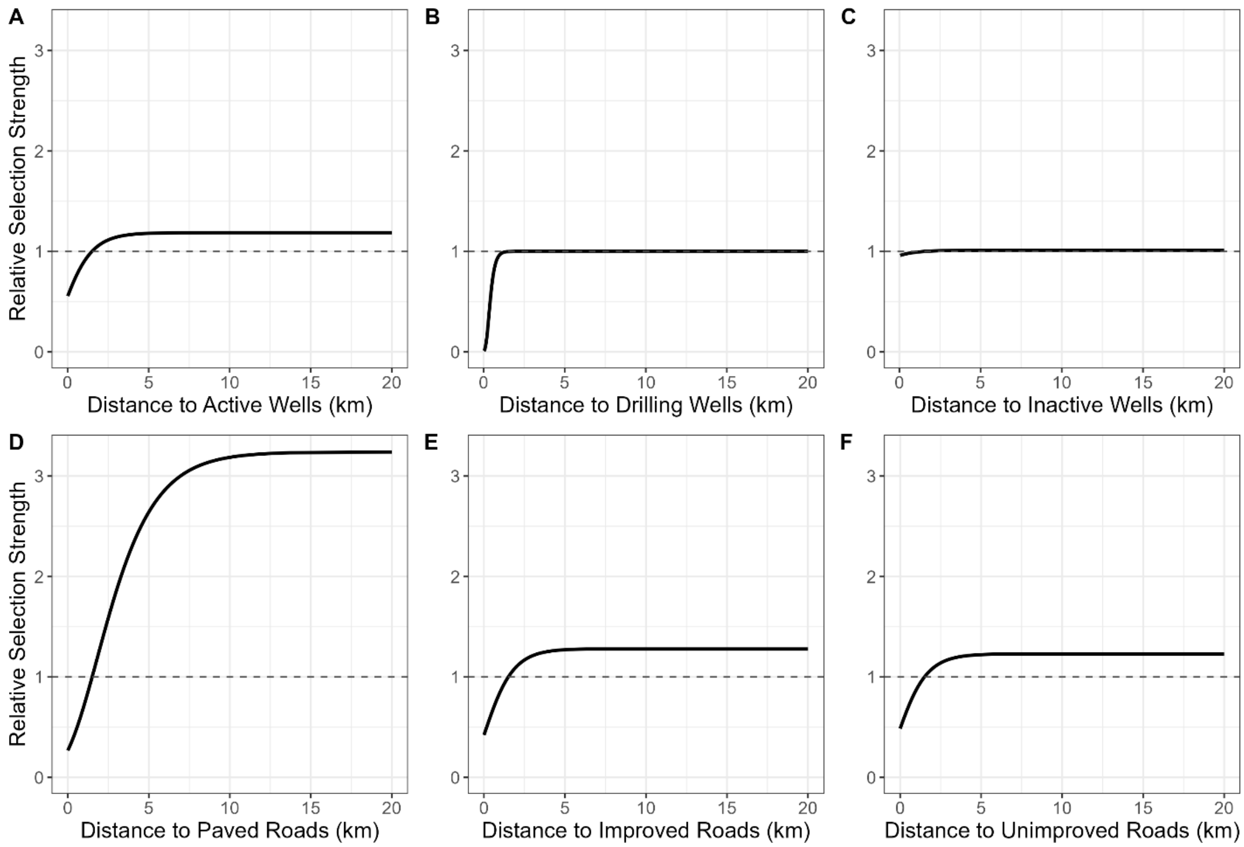

Figure 11. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for female resource selection during the spring.

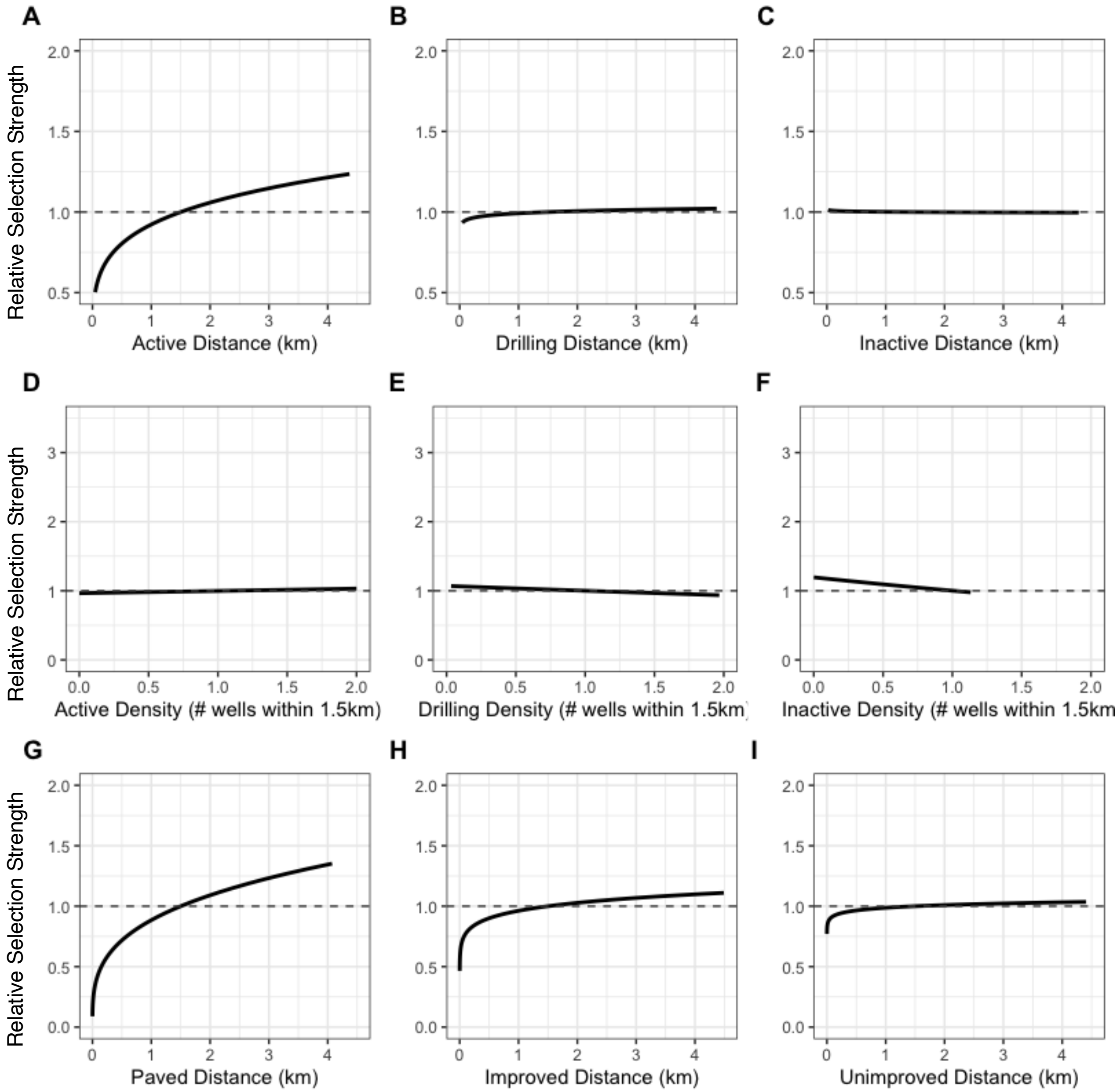

Figure 12. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for female step selection during the spring.

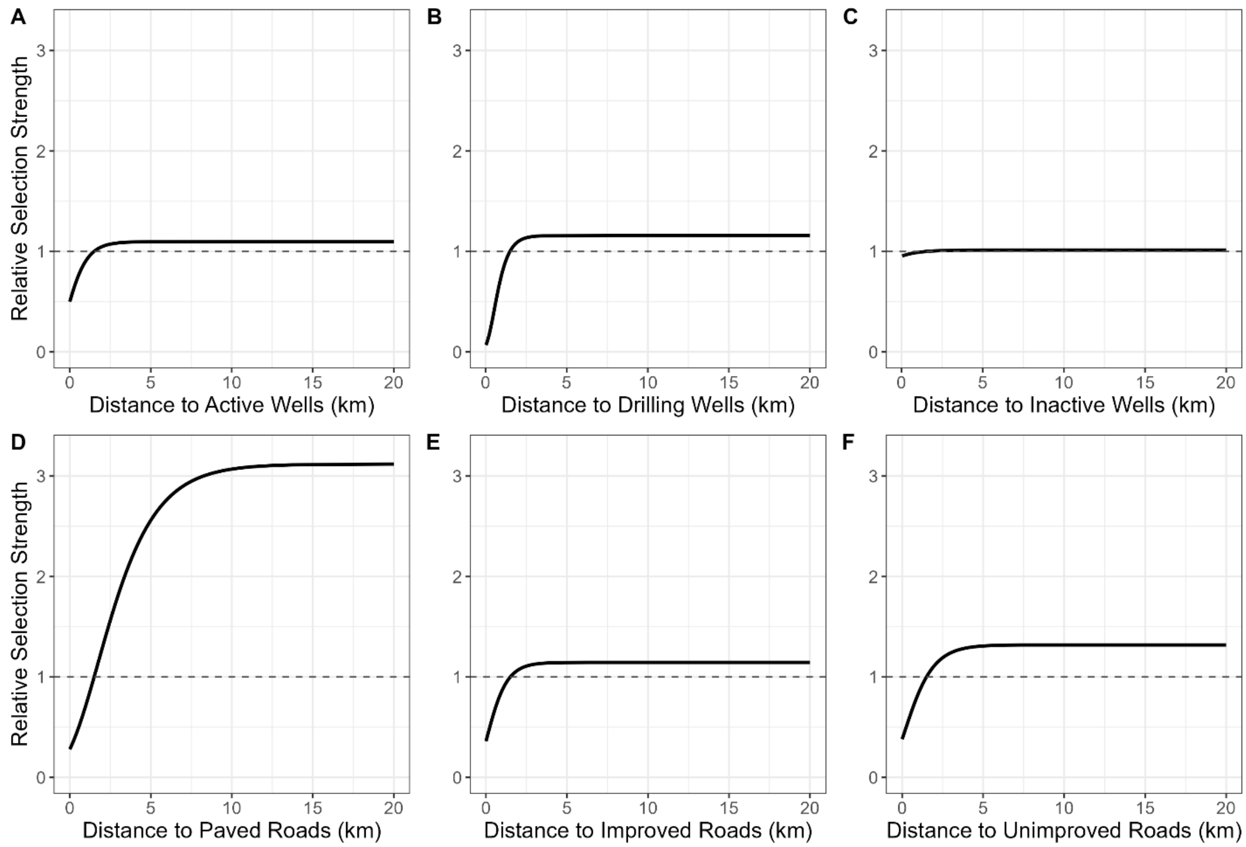

Figure 13. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for female resource selection during the summer.

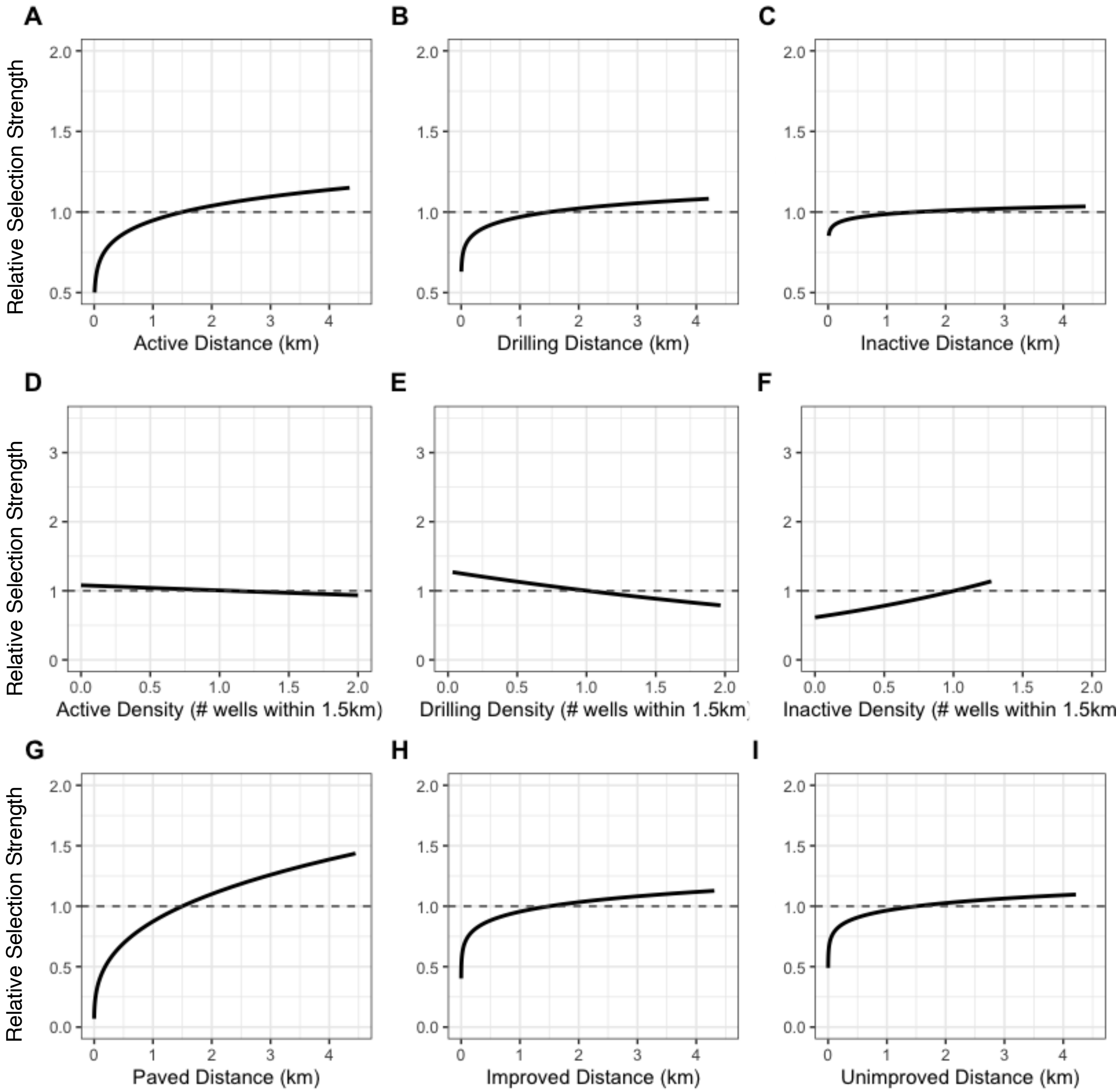

Figure 14. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for female step selection during the summer.

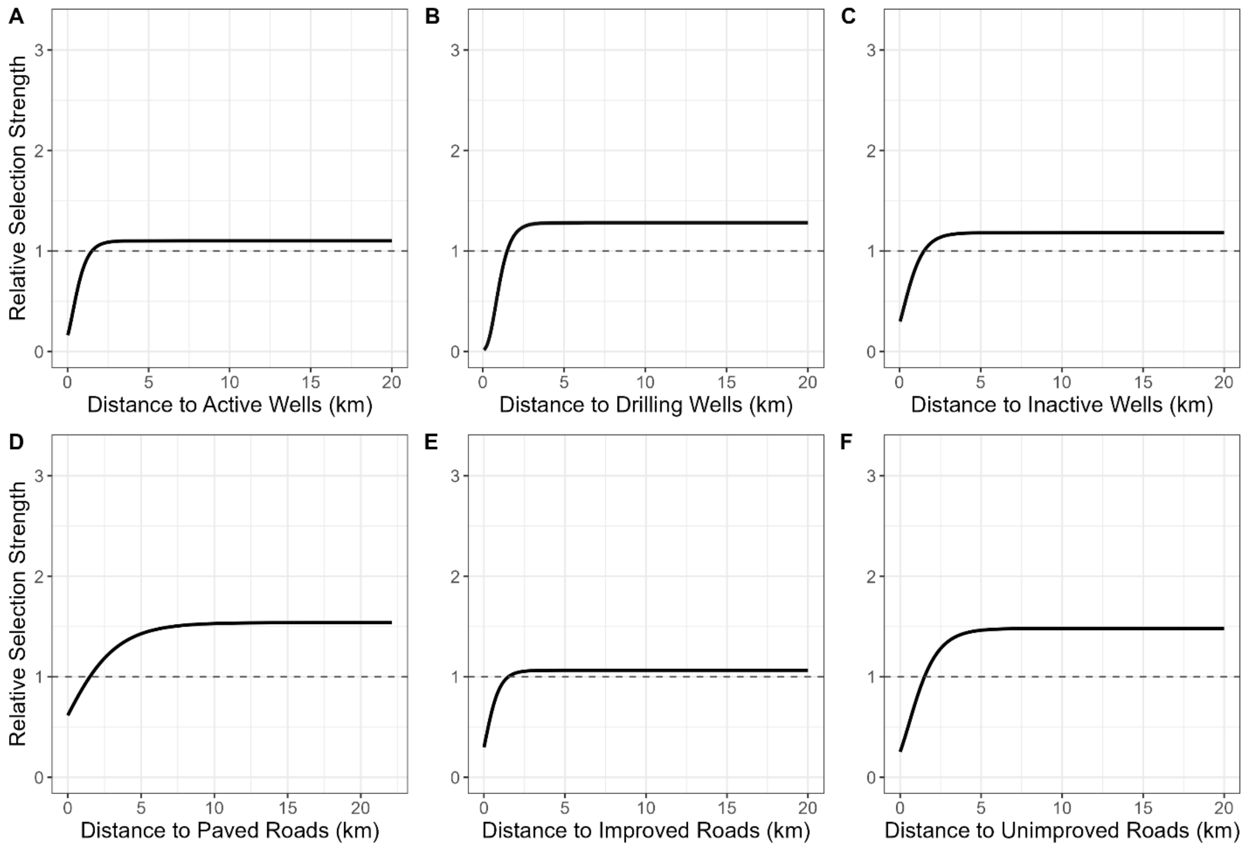

Figure 15. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for male resource selection during the early fall.

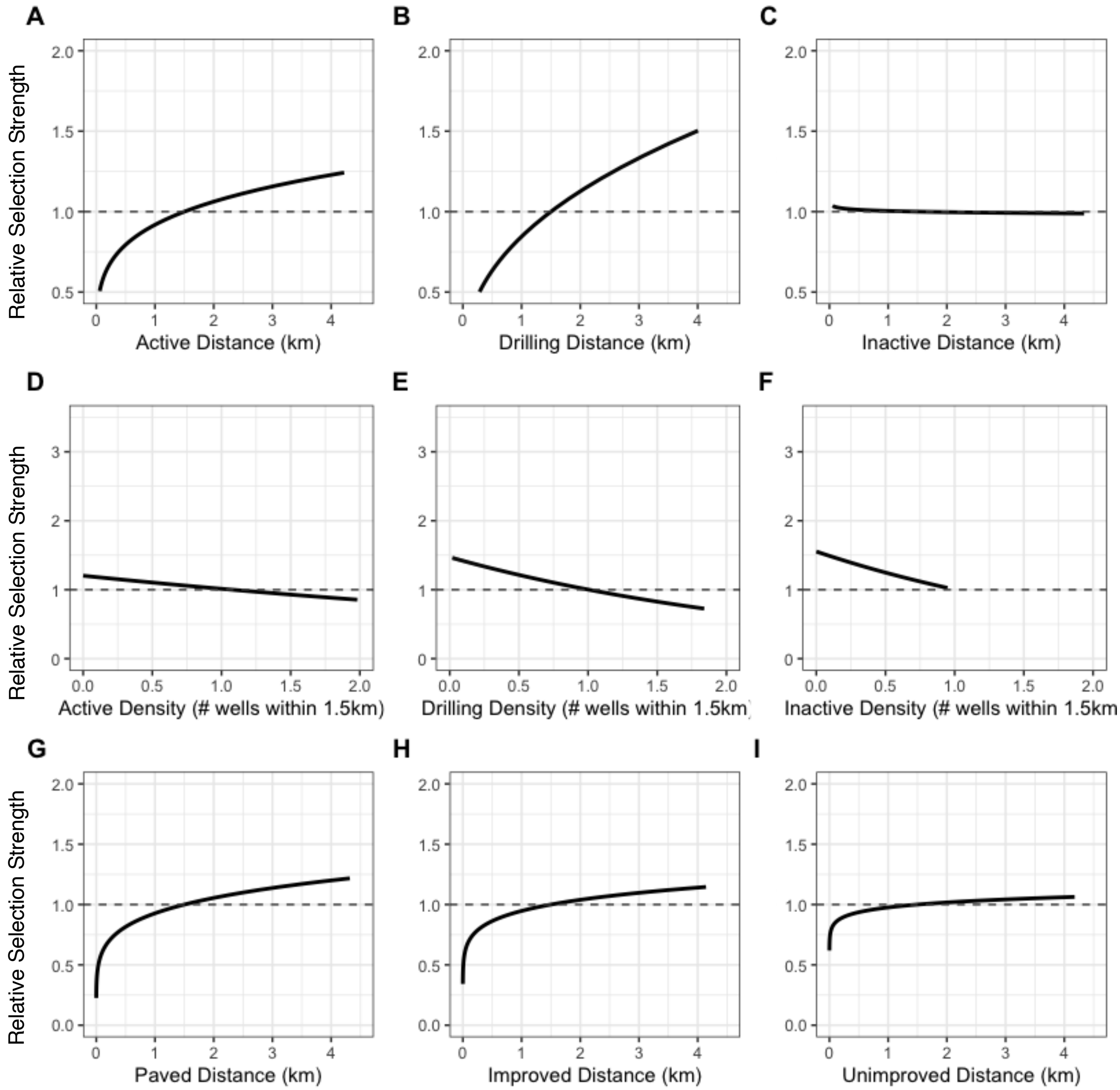

Figure 16. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for male step selection during the early fall.

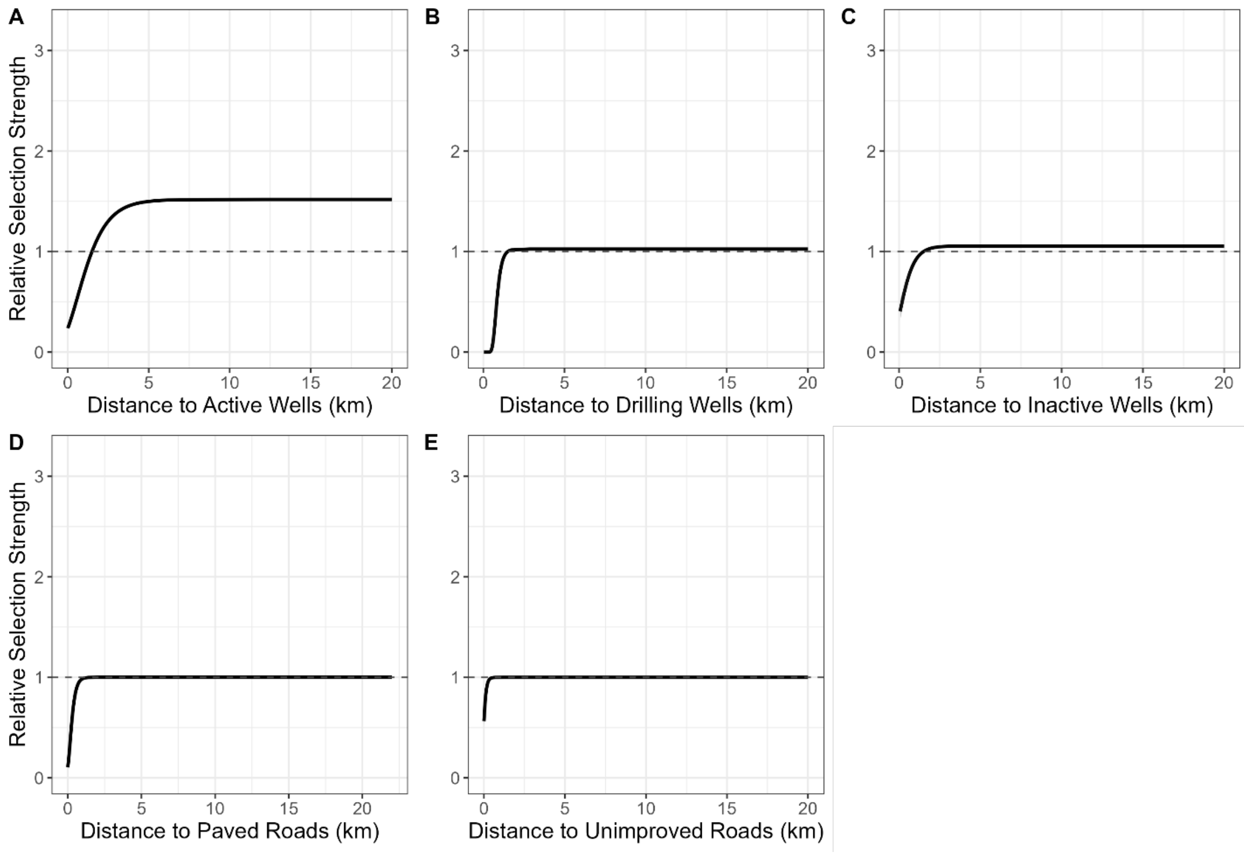

Figure 17. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads and E) distance to unimproved roads in the final model for male resource selection during the late fall.

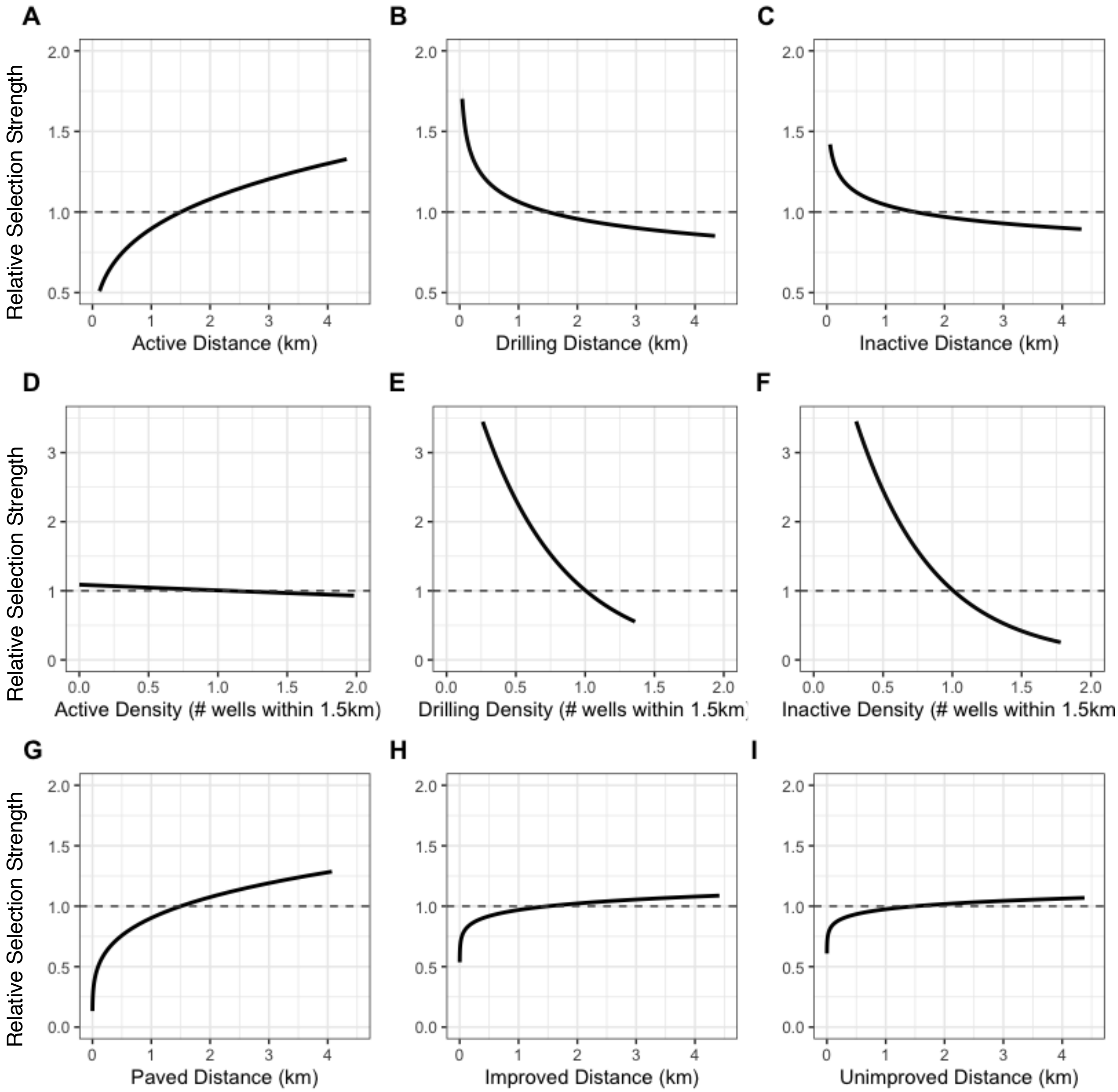

Figure 18. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for male step selection during the late fall.

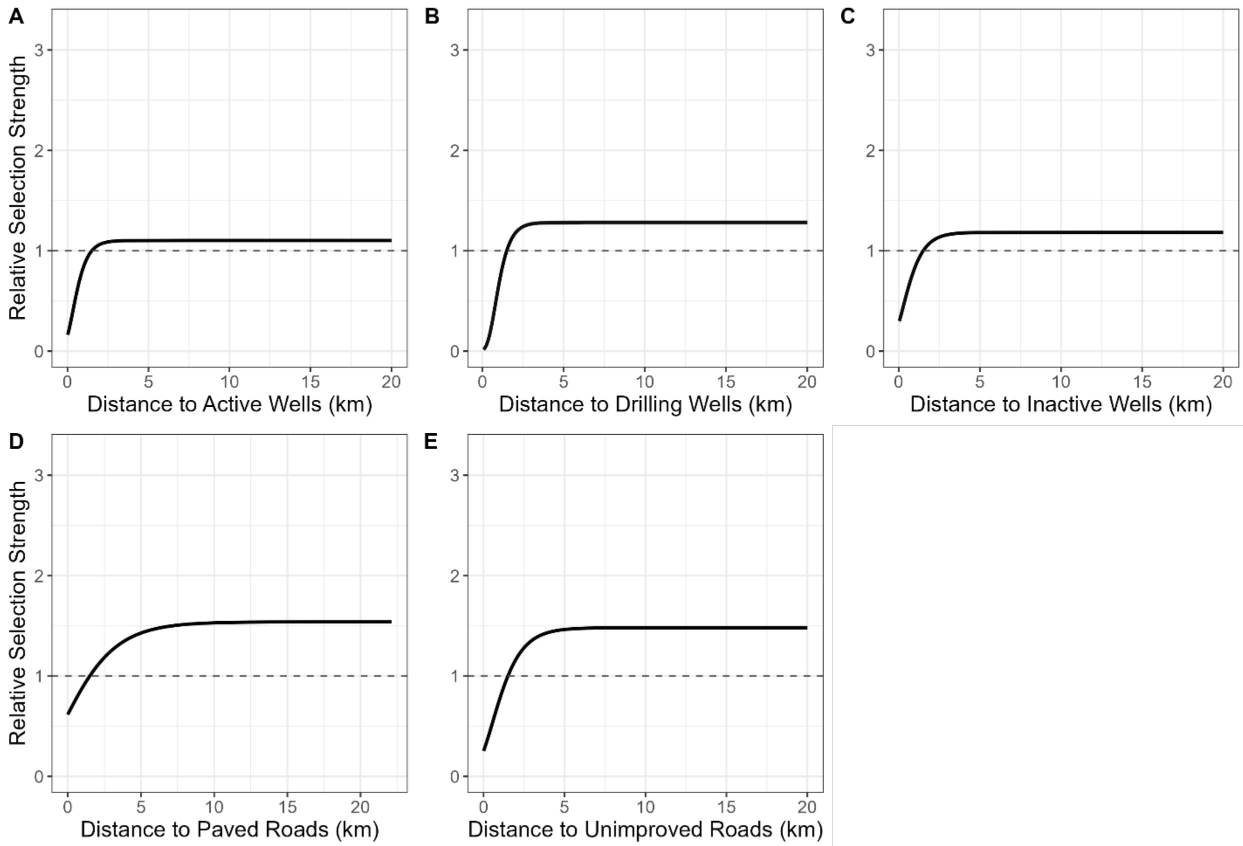

Figure 19. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads and E) distance to unimproved roads in the final model for male resource selection during the winter.

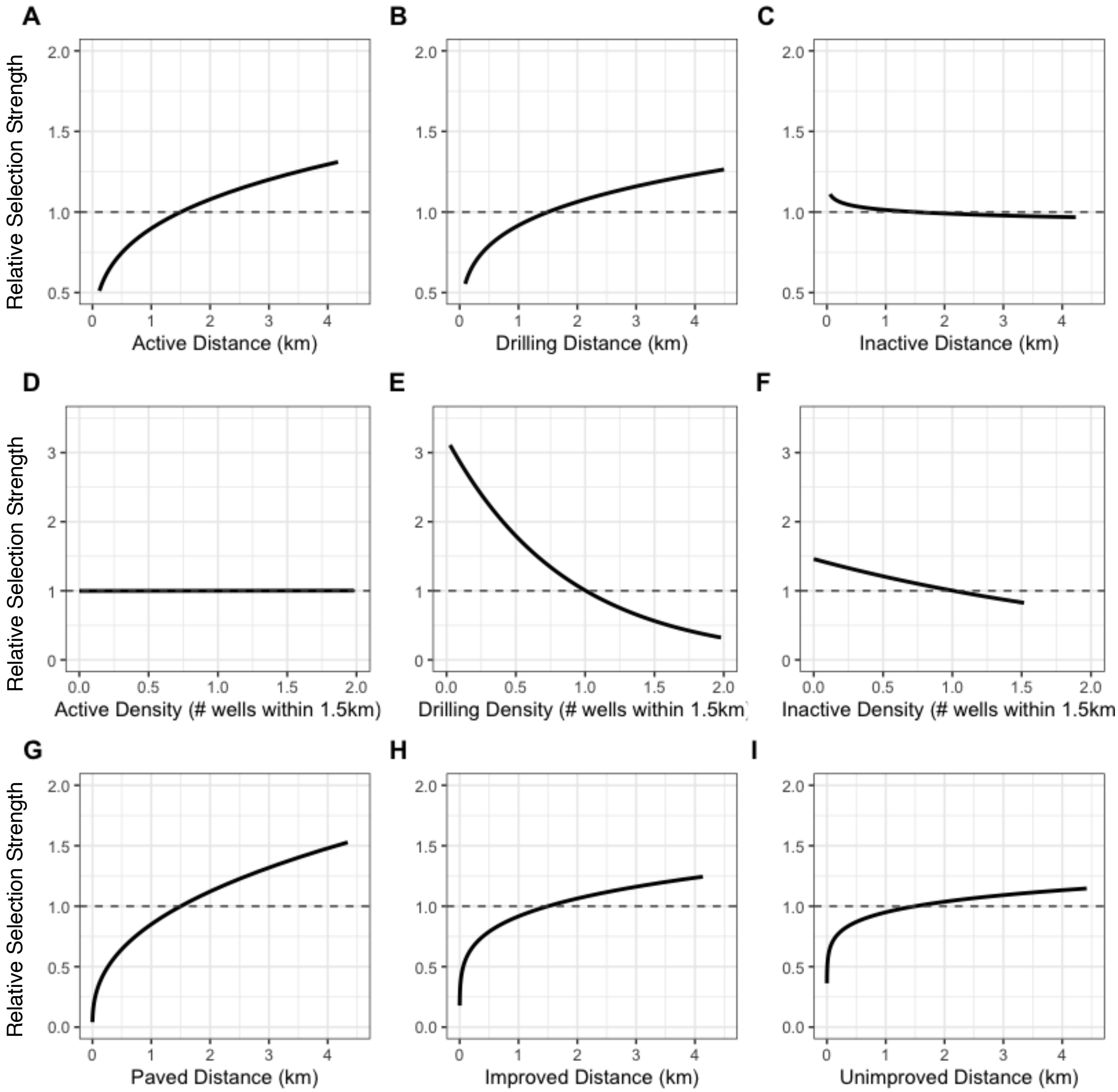

Figure 20. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for male step selection during the winter.

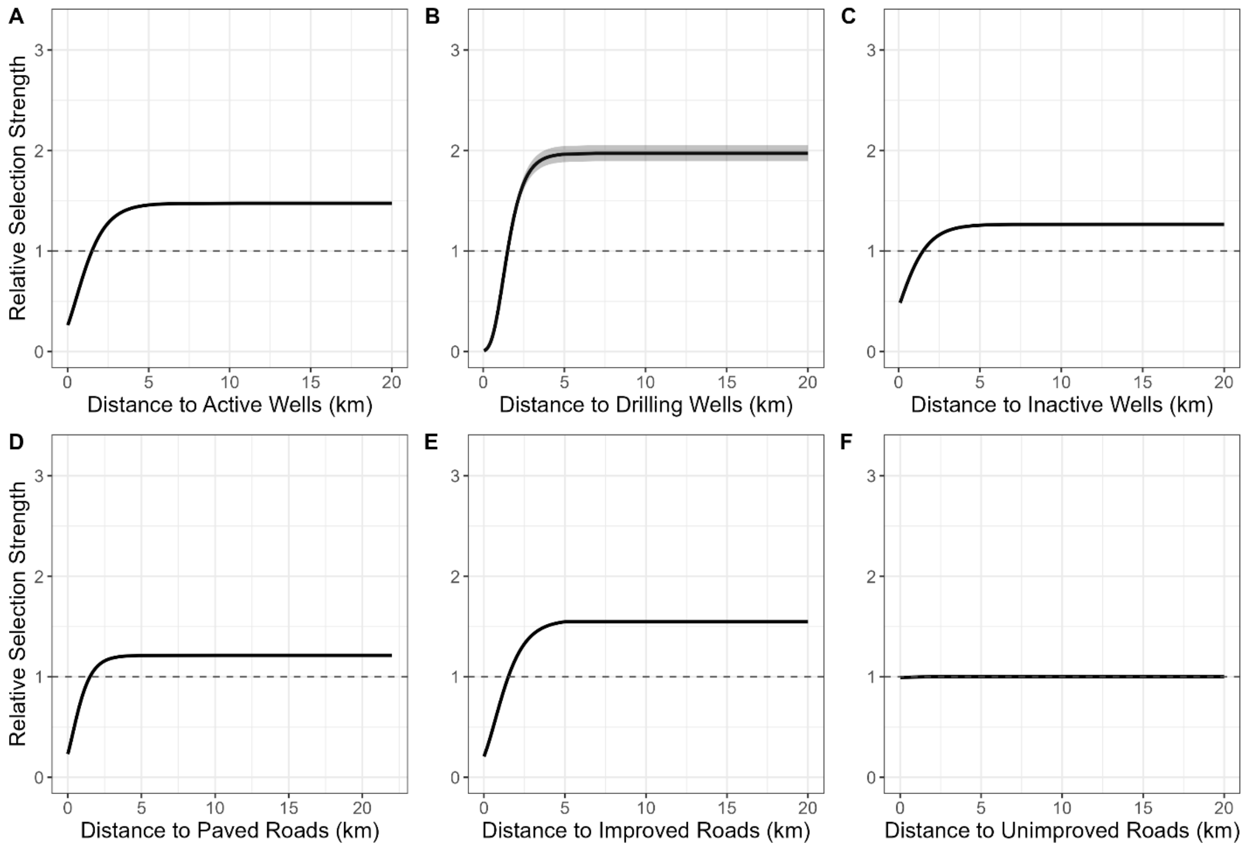

Figure 21. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for male resource selection during the spring.

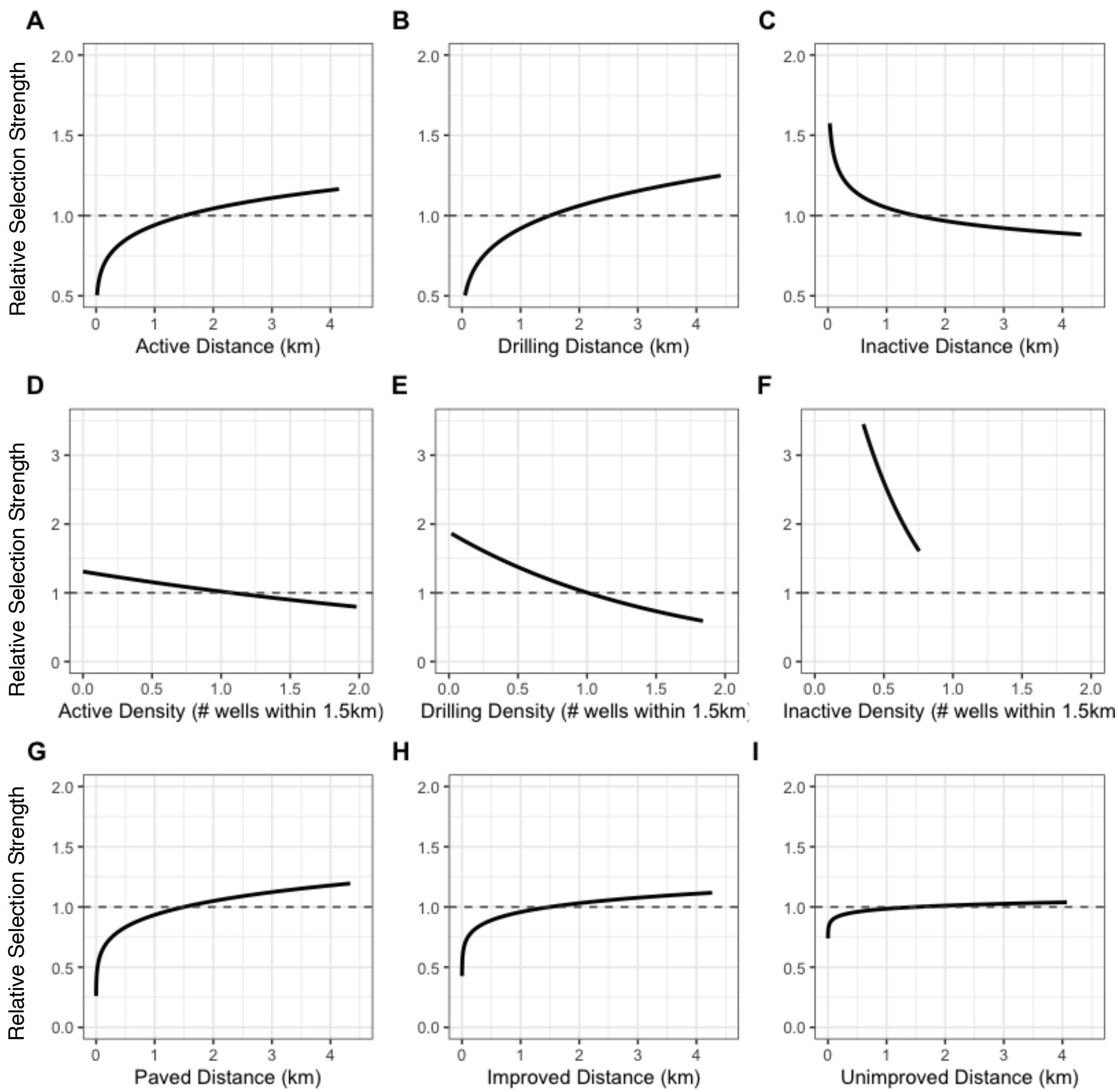

Figure 22. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for male step selection during the spring.

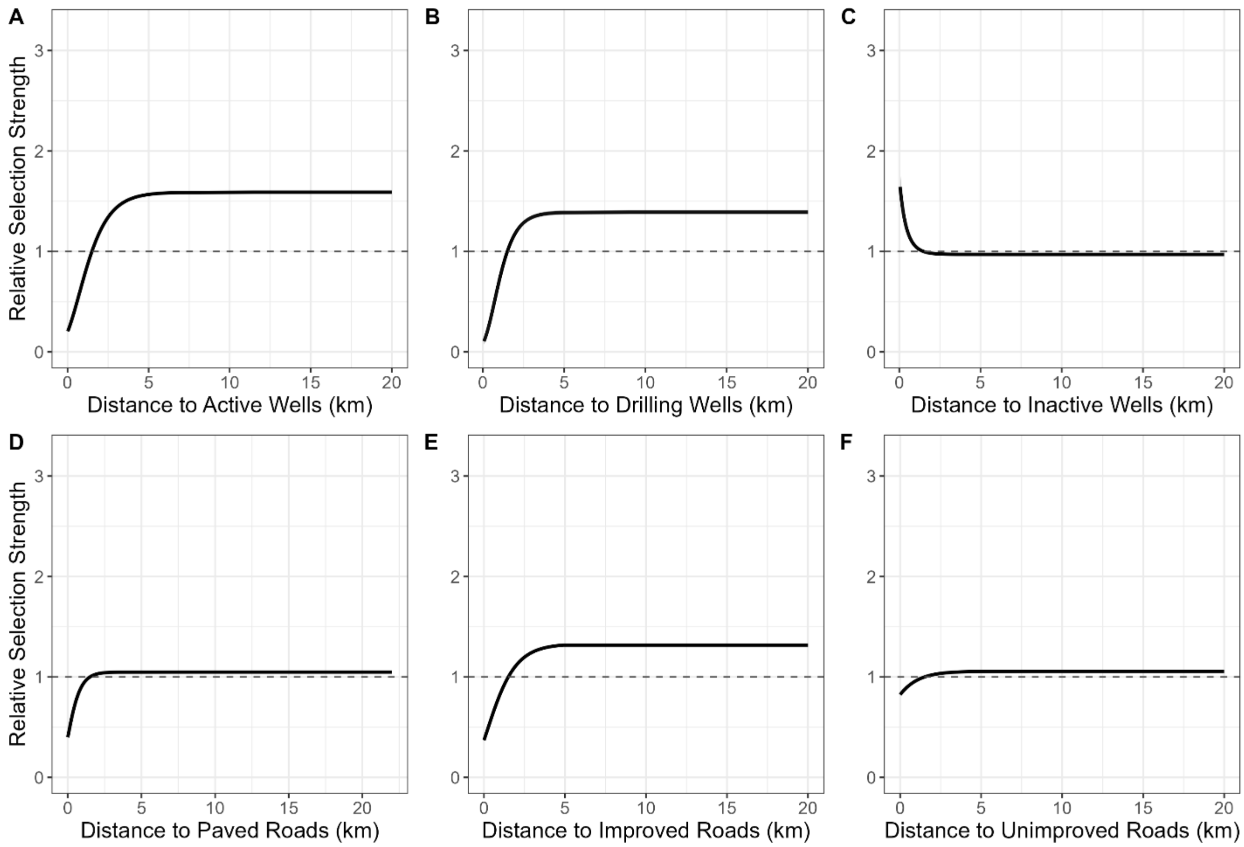

Figure 23. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) distance to paved roads, E) distance to improved roads and F) distance to unimproved roads in the final model for male resource selection during the summer.

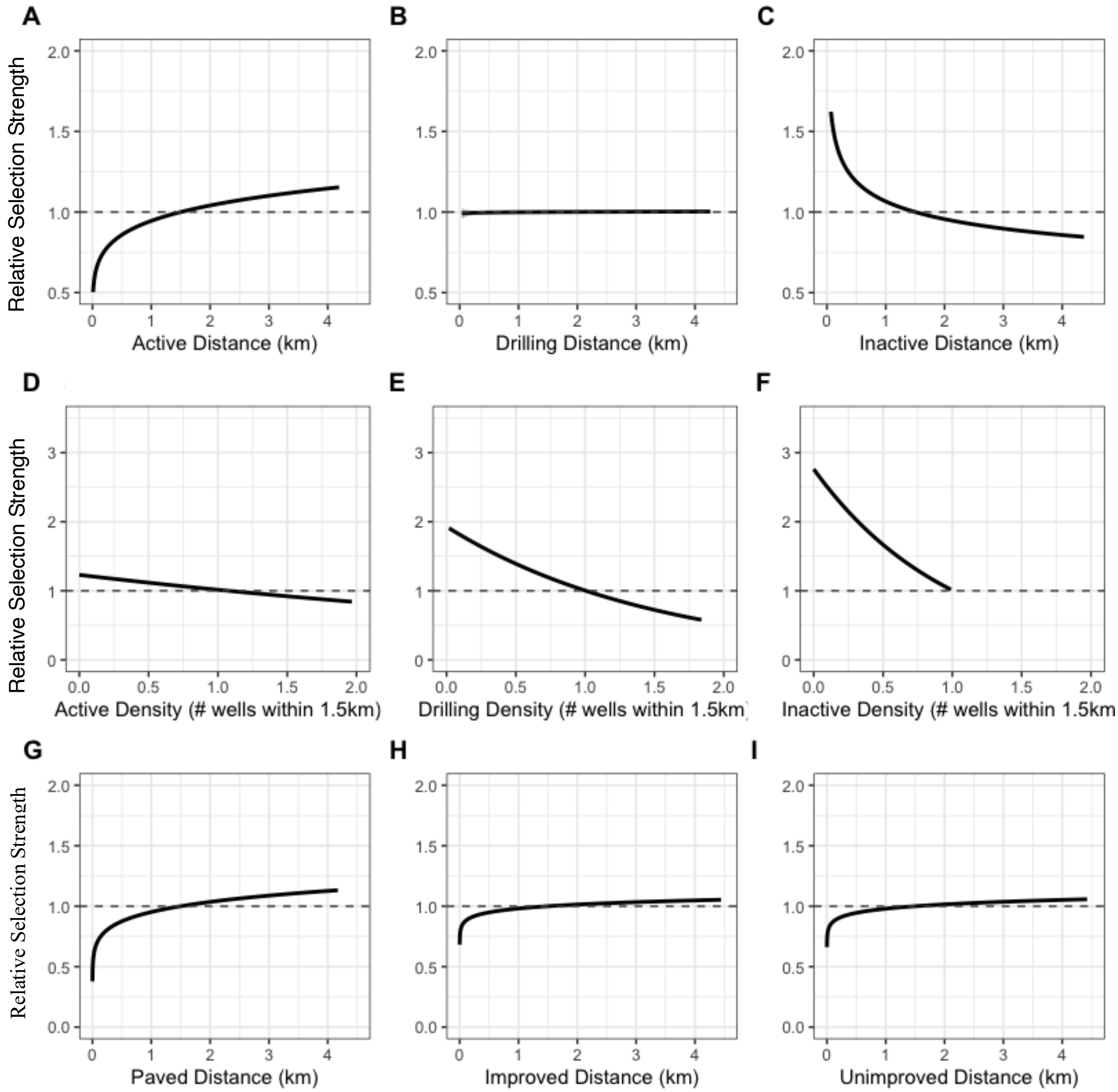

Figure 24. Plots of relative selection strength for A) distance to active wells, B) distance to drilling wells, C) distance to inactive wells, D) active well density, E) drilling well density, F) inactive well density, G) distance to paved roads, H) distance to improved roads and I) distance to unimproved roads in the final model for male step selection during the summer.

Tables

Table 5. Covariates used in the resource selection analysis of elk in western North Dakota 2019 – 2023.

Predictor Variable	*Description*	*Source*	*Functional form[1]*	*Model Inclusion*
Elevation	Elevation in meters	30 m digital elevation map (DEM) was sourced from the U.S. Geological Survey	Linear, quadratic, or pseudo-threshold	RSF
Slope	Steepness (degrees) calculated from the DEM using Spatial Analyst.	Derived from DEM	Linear, quadratic, or pseudo-threshold	RSF
Topographic wetness index (TWI)	Measure of topographic control on hydrological processes	Derived from DEM	Linear, quadratic, or pseudo-threshold	RSF
Vector ruggedness measure (VRM)	Variation in slope and aspect (Sappington et al. 2007)	Derived from DEM	Linear	RSF
Aspect	Two variables North: -1 = south facing, 1 = north facing East: -1 = west facing, 1 = east facing	Derived from DEM	Linear	RSF
Vegetation	Category of vegetation see description above	USDA National Agricultural Statistics Service cropland data layer 2019-2023	Categorical	RSF, SSF
Landowner type	Category of landownership – public, private, reservation	North Dakota parcel data	Categorical	RSF, SSF
Distance to paved road	Linear distance to the closest paved road	Montana State Library, North Dakota Department of Transportation	Exponential decay, pseudo-threshold	RSF, SSF

Distance to improved road	Linear distance to the closest improved road	Montana State Library, North Dakota Department of Transportation	Exponential decay, pseudo-threshold	RSF, SSF
Distance to unimproved road	Linear distance to the closest unimproved road	Montana State Library, North Dakota Department of Transportation	Exponential decay, pseudo-threshold	RSF, SSF
Distance to active well	Linear distance to the closest active well pad	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Exponential decay, pseudo-threshold	RSF, SSF
Distance to drilling well	Linear distance to the closest drilling well pad	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Exponential decay, pseudo-threshold	RSF, SSF
Distance to inactive well	Linear distance to the closest inactive well pad	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Exponential decay, pseudo-threshold	RSF, SSF
Active Well Density	Density of active wells within 3 km	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Linear, quadratic, or pseudo-threshold	SSF
Drilling Well Density	Density of drilling wells within 3 km	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Linear, quadratic, or pseudo-threshold	SSF
Inactive Well Density	Density of inactive wells within 3 km	Montana Board of Oil and Gas Conservation, ND Department of Mineral Resources	Linear, quadratic, or pseudo-threshold	SSF
Normalized Difference Vegetation Index (NDVI)	Proxy for forage availability (Hurley et al. 2014)	Program R (v. 4.4.2, R Core Team 2024) using package FedData (Bocinsky 2024)	Linear, quadratic, or pseudo-threshold	SSF
Terrain Ruggedness Index (TRI)	Amount of elevation difference between adjacent cells in a DEM	Program R (v. 4.4.2, R Core Team 2024) using package FedData (Bocinsky 2024)	Linear	SSF

Snow Water Equivalent (SWE)	Proxy for amount of snow present (Burkholder et al. 2022)	Program R (v. 4.4.2, R Core Team 2024) using package FedData (Bocinsky 2024)	Linear, quadratic, or pseudo-threshold	SSF

Table 6. Top ranked functional forms of each covariate included in the RSF analysis, as chosen by ranking univariate models with AICc.

Sex	Season	Functional forms
Females	Early Fall	Elevation^2, log(Slope), TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 5 km, Distance to Paved Road – 5 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Late Fall	Elevation^2, log(Slope), TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 2.5 km, Distance to Paved Road – 10 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Winter	Elevation^2, Slope^2, log(TWI), Distance to Active Well – 3.5 km, Distance to Inactive Well – 2.5 km, Distance to Drilling Well – 2.5 km, Distance to Paved Road – 10 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Spring	Elevation^2, Slope^2, TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 1 km, Distance to Paved Road – 10 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Summer	Elevation^2, Slope^2, TWI^2, Distance to Active Well – 3.5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 2.5 km, Distance to Paved Road – 10 km, Distance to Improved Road – 3.5 km, Distance to Unimproved Road – 5 km
Males	Early Fall	Elevation^2, Slope^2, TWI, Distance to Active Well – 2.5 km, Distance to Inactive Well – 3.5 km, Distance to Drilling Well – 2.5 km, Distance to Paved Road – 10 km, Distance to Improved Road – 2.5 km, Distance to Unimproved Road – 5 km
	Late Fall	Elevation^{2,} Slope^2, TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 2.5 km, Distance to Drilling Well – 1 km, Distance to Paved Road – 1 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 500 m
	Winter	Elevation^2, Slope^2, TWI^2, Distance to Active Well – 3.5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 2.5 km, Distance to Paved Road – 3.5 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Spring	Elevation^2, Slope^2, TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 5 km, Distance to Drilling Well – 3.5 km, Distance to Paved Road – 3.5 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km
	Summer	Elevation^2, Slope^2, TWI^2, Distance to Active Well – 5 km, Distance to Inactive Well – 2.5 km, Distance to Drilling Well – 3.5 km, Distance to Paved Road – 2.5 km, Distance to Improved Road – 5 km, Distance to Unimproved Road – 5 km

Table 7. Final best fit RSF model structure for each elk sex and season.

Sex	Season	Final Model
Females	Early Fall	$Elevation^2$ + log(Slope) + TWI^2 + North + East + Vegetation + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 5km + Distance to Inactive Well – 5km + Distance to Paved Road – 5km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km
	Late Fall	$Elevation^2$ + log(Slope) + TWI^2 + East + Vegetation + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 2.5km + Distance to Inactive Well – 5km + Distance to Paved Road – 10km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km
	Winter	$Elevation^2$ + $Slope^2$ + log(TWI) + East + North + Landowner + Distance to Active Well – 3.5km + Distance to Drilling Well – 2.5km + Distance to Inactive Well – 2.5km + Distance to Paved Road – 10km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km
	Spring	$Elevation^2$ + $Slope^2$ + TWI^2 + East + North + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 1km + Distance to Inactive Well – 5km + Distance to Paved Road – 10km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km
	Summer	$Elevation^2$ + $Slope^2$ + TWI^2 + East + North + Vegetation + Landowner + Distance to Active Well – 3.5km + Distance to Drilling Well – 2.5km + Distance to Inactive Well – 5km + Distance to Paved Road – 10km + Distance to Improved Road – 3.5km + Distance to Unimproved Road – 5km
Males	Early Fall	$Elevation^2$ + $Slope^2$ + TWI + North + East + Vegetation + Landowner + Distance to Active Well – 2.5km + Distance to Drilling Well – 2.5km + Distance to Inactive Well – 3.5km + Distance to Paved Road – 10km + Distance to Improved Road – 2.5km + Distance to Unimproved Road – 5km
	Late Fall	$Elevation^2$ + $Slope^2$ + TWI^2 + North + East + Vegetation × Distance to Improved Road – 5km + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 1km + Distance to Inactive Well – 2.5km + Distance to Paved Road – 1km + Distance to Unimproved Road – 500m
	Winter	$Elevation^2$ + $Slope^2$ + TWI^2 + North + East + Vegetation × Distance to Improved Road – 5km + Landowner + Distance to Active Well – 3.5km + Distance to Drilling Well – 2.5km + Distance to Inactive Well – 5km + Distance to Paved Road – 3.5km + Distance to Unimproved Road – 5km
	Spring	$Elevation^2$ + $Slope^2$ + TWI^2 + North + East + Vegetation + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 3.5km + Distance to Inactive Well – 5km + Distance to

		Paved Road – 3.5km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km
	Summer	Elevation^2 + Slope^2 + TWI^2 + North + East + Vegetation + Landowner + Distance to Active Well – 5km + Distance to Drilling Well – 3.5km + Distance to Inactive Well – 2.5km + Distance to Paved Road – 2.5km + Distance to Improved Road – 5km + Distance to Unimproved Road – 5km

Table 8. RSF Model results for continuous covariates from male and female elk resource selection functions in western North Dakota. Green boxes with '+' indicate that the covariate was positive (elk selected larger values of that covariate), green boxes with a '*' indicate that the covariate was positive and was included in an interaction with another covariate, red boxes with '-' indicate the covariate was negative (elk selected smaller values of that covariate), blue boxes with '≈' indicate elk selected intermediate values of that covariate (because the covariate was included with exponential terms), and white boxes indicate the covariate was not significant in that sex/season. As a note, green boxes for the 'distance to' covariates indicate elk selected for areas farther away from that feature (green = larger = farther away), larger positive values for the east covariate indicates east facing areas, smaller negative values for the east covariate indicates west facing areas, larger, positive values for the north covariate indicate north facing areas, and smaller, negative values for the north covariate indicate south facing areas.

Sex	**Season**	**Elevation**	**Slope**	**East**	**North**	**TWI**	**Distance to Paved Rd**	**Distance to Improved Rd**	**Distance to Unimproved Rd**	**Distance to Active Well**	**Distance to Drilling Well**	**Distance to Inactive Well**
Females	Early Fall	≈	-	+	+	+	+	+	+	+	+	+
	Late Fall	≈	-	+		-	+	+	+	+	+	+
	Winter	≈	≈	+	-	-	+	+	+	+	+	+
	Spring	≈	≈	+	+	+	+	+	+	+	+	
	Summer	≈	≈	+	+	+	+	+	+	+	+	
Males	Early Fall	≈	≈	+	+	+	+	+	+	+	+	+
	Late Fall	≈	≈	+		+	+	*	+	+	+	+
	Winter	≈	≈	+	-	-	+	*	+	+	+	+
	Spring	≈	≈	+	+	+	+	+		+	+	+
	Summer	+	≈	+	+	+	+	+	+	+	+	-

Table 9. Model results from male and female elk step selection functions in western North Dakota. Green boxes with '+' indicate that the covariate was selected for, red boxes with '-' indicate the covariate was selected against, and white boxes indicate the covariate was not significant in that sex/season. As a note, green boxes for the 'distance to' covariates indicate elk selected for areas farther away from that feature (green = larger = farther away), smaller values for the well densities, larger values for the snow water equivalent (SWE) covariate, larger values for the terrain ruggedness index (TRI) covariate, and larger values for the normalized difference vegetation index (NDVI) covariate. SWE was only included in the Late Fall and Winter models while NDVI was only included in the Spring, Summer, and Early Fall models. Significance Codes: ***(0.0001), **(0.001), *(0.01), none(> 0.1)

Sex	Season	SWE	TRI	Active Well Density	Drilling Well Density	Inactive Well Density	Distance to Paved Rd	Distance to Improved Rd	Distance to Unimproved Rd	Distance to Active Well	Distance to Drilling Well	Distance to Inactive Well
Females	Early Fall		-***				+***	+***	+***	+***		+**
	Late Fall	+*	-***	-*	+**	-***	+***	+***	+***	+***	+***	+*
	Winter	+***	-***	-***		-***	+***	+***	+***	+***	+**	
	Spring		-***				+***	+***	+***	+***		
	Summer		-***	-**	-**	+***	+***	+***	+***	+***	+***	
Males	Early Fall		-***	-**			+***	+***	+**	+***	+***	
	Late Fall	+**			-***	-**	+***	+***	+***	+***		
	Winter	+***	+***		-**		+***	+***	+***	+***	+**	
	Spring		-**	-***	-*	-***	+***	+***	+**	+***	+*	+*
	Summer			-***	-*	-**	+***	+***	+***	+***		+***

Table 10. Landowner type selection rankings obtained from male and female elk resource selection functions in western North Dakota. In each model, selection of public and reservation land was compared to selection of private land. In the table below, stars (*) indicate if public and reservation were selected significantly differently from private land. We used the beta coefficients from the top model to rank each landowner type from 1 to 3, with 1 being the most preferred landowner type within that sex/season and 3 being the least preferred.

Sex	Season	Private	Public	Reservation
Females	Early Fall	1	3*	2*
	Late Fall	1	2*	3*
	Winter	1	2*	3*
	Spring	1	2*	3*
	Summer	1	3*	2*
Males	Early Fall	1	2*	3*
	Late Fall	1	2*	3*
	Winter	2	1*	3*
	Spring	2	1*	3*
	Summer	1	3*	2*

Table 11. Landowner type selection rankings obtained from male and female elk step selection functions in western North Dakota. In each model, selection of public land was compared to selection of private land. In the table below, stars (*) indicate if public was selected significantly differently from private land. Each landowner type is ranked from 1 to 2, with 1 being the most preferred landowner type within that sex/season and 2 being the least preferred.

Sex	Season	Private	Public
Females	Early Fall	1	2*
	Late Fall	1	2*
	Winter	1	2*
	Spring	1	2*
	Summer	1	2*
Males	Early Fall	1	2*
	Late Fall	1	2*
	Winter	2	1
	Spring	1	2*
	Summer	1	2*

Table 12. Vegetation type selection rankings obtained from male and female elk resource selection functions in western North Dakota. In each model, the selection of woodland, grassland, other, and shrub was compared to selection of crops. In the table below, stars (*) indicate if these vegetation types were selected significantly differently from crops. We used the beta coefficients from the top model to rank each vegetation type from 1 to 5, with 1 being the most preferred vegetation type within that sex/season and 5 being the least preferred. The models for males in the late fall and winter included an interaction between vegetation type and distance to improved road. Therefore, there are two rankings for these seasons – one ranking for when elk are close (~40 m) to improved roads and one ranking for when elk are far (~4,200 m) from improved roads.

Sex	Season	Crop	Woodland	Grassland	Other	Shrub
Females	Early Fall	2	1*	5*	4*	3*
	Late Fall	1	2*	3*	5*	4*
	Winter	2	1*	3*	5*	4*
	Spring	3	1*	4*	5*	2*
	Summer	2	1*	5*	4*	3*
Males	Early Fall	2	1*	5*	4*	3*
	Late Fall*	Close: 1 Far: 4	Close: 2 * Far: 1	Close: 4* Far: 3	Close: 5* Far: 5	Close: 3* Far: 2
	Winter*	Close: 1 Far: 4	Close: 2* Far: 1	Close: 4* Far: 3	Close: 3* Far: 5	Close: 5* Far: 2
	Spring	4	1*	5*	3	2*
	Summer	2	1*	5*	3*	4*

Table 13. Vegetation type selection rankings obtained from male and female elk step selection functions in western North Dakota. Each vegetation type is ranked from 1 to 6, with 1 being the most preferred vegetation type within that sex/season and 6 being the least preferred.

Sex	Season	Crop	Woodland	Grassland	Shrub	Barren	Other
Females	Early Fall	2	1	4	3	6	5
	Late Fall	1	2	3	4	6	5
	Winter	1	3	2	4	5	6
	Spring	2	1	4	3	6	5
	Summer	2	1	5	3	6	4
Males	Early Fall	2	1	5	3	6	4
	Late Fall	1	2	4	3	6	5
	Winter	1	2	4	3	6	5
	Spring	2	1	4	3	6	5
	Summer	2	1	5	3	6	4

Chapter 3. Elk survival in western North Dakota

Objective

Quantify elk survival and causes of mortality.

Methods

We estimated annual adult survival rates using the Kaplan-Meier estimator (Pollock et al. 1989). We started the year on June 1, the average birth date for elk in northern regions (Griffin et al. 2011). Setting the start date on June 1 means we left-truncated the dataset between February and May 2019, but no mortalities occurred within this time frame, so it did not bias our results. We stratified estimates by sex, year, and herd, then used log-rank tests to test for significant differences in survival among these groups (Pollock et al. 1989). We summarized cause specific mortality sources by sex, age, herd, and year. We included all mortalities that occurred between the start of the study and January 7, 2023.

Results

We captured and fitted GPS collars on 97 adult female, 8 yearling female, 6 adult male, and 38 yearling male elk between 2019 and 2021 (Table 14). Collars on 2 adult females stopped working immediately after deployment, so we had a total sample size of 147 collared elk. We observed 27 mortalities: 22 legal harvest (16 female, 6 male), 2 wounding loss (1 female, 1 male), 1 probable epizootic hemorrhagic disease (EHD), 1 malnutrition due to a tongue abscess, and 1 unknown (Table 15, Figures 26 and 27). One male captured as a yearling dispersed to Montana where he was legally harvested in October 2022. However, his GPS collar stopped working before harvest, so we did not include this elk in our mortality sample (White and Garrott 1990).

The annual Kaplan-Meier survival estimate for all elk was 0.88 (95% confidence interval [CI] = 0.84 – 0.92; Figure 28), with no significant difference between male and female elk (P = 0.10). However, we ran separate Kaplan-Meier survival models for males and females for reporting purposes. Annual Kaplan-Meier survival estimates were 0.90 (95% CI = 0.85 – 0.94) for females (Figure 29A), and 0.80 (95% CI = 0.67 – 0.95) for males (Figure 29B). Survival was significantly lower (P = 0.004) in 2020 (survival = 0.76, 95% CI = 0.66 – 0.88) compared to 2019 (survival = 0.93, 95% CI = 0.87 – 0.99), 2021 (survival = 0.94, 95% CI = 0.88 – 1.00), and 2022 (survival = 0.91, 0.82 – 1.00; Figure 30). There weren't enough mortalities within each herd to assess differences in survival between herds. All elk caught as yearlings aged up to adults (2-year-old) in June of the year they were caught, and no yearlings died within this period. Therefore, we were not able to distinguish survival differences between yearlings and adults for male or female elk.

Discussion

Survival estimates for female elk in North Dakota are comparable to what has been recorded in Montana elk populations. Overall elk survival of badlands elk was 0.88, which is similar to survival reported for hunted populations of elk in western North America by Brodie et al. (0.85; 2013). Our adult female survival estimate of 0.90 for female elk is the same as female elk survival in Montana (0.90, Hansen et al. 2024). Montana reported male survival for those available for harvest, which are brow tined bulls only, resulting in bulls typically 2-years-old or more. Our male survival at 0.80 is much higher than male elk survival in Montana (0.60, Hansen et al. 2024). However, natural survival of elk in North Dakota is higher than most other elk populations. Harvest accounted for 98% of all the mortalities during our study, much greater than what was observed for a study evaluating other western elk populations where harvest accounted for 49% and predation accounted for 23% of all mortalities (Keller et al. 2015).

In fact, elk in the badlands face very little risk of predation at all. Most natural predators of elk are absent from the landscape except for a small mountain lion (*Puma concolor*) population. However, a mountain lion diet selection study completed in this system indicates elk make up little to none of their diet (Wilckens et al. 2015). So, harvest is the key factor managing elk populations in the badlands. But even harvest rates are lower in ND than other western elk populations. While the female harvest rate of western ND elk (0.052) is only slightly lower than female harvest rate of elk in NW Montana (0.062), the harvest rate for adult male elk in western ND at its highest in 2020 was only 0.24 compared to a much higher rate of 0.76 reported for males in NW Montana (Hansen et al. 2024).

The fact that harvest was almost the exclusive cause of mortality for elk in the badlands of North Dakota is useful for managers, since harvest is the main lever for elk population management. Further, harvest can be more easily controlled unlike other sources of mortality like predation or disease. Managers can increase or decrease licenses depending on their population goals and landowner tolerance which results in greater control over elk numbers in specific locations. However, managers face additional challenges managing harvests related to hunter access.

Many hunters rely on public land for access to hunt elk in western North Dakota. But only approximately 7% of land in North Dakota is publicly owned (NDGF Plots Fact Sheet). Although elk can be found on public land, studies suggest elk shift space use towards private land refuges during rifle hunting seasons, which includes the entire elk hunting season in North Dakota (Burcham et al. 1999, Proffitt et al. 2013). Many hunters chose to pay fees for access to private land elk hunting, but most hunters willing to pay fees do so for the opportunity to harvest bull elk. A 2020 study of elk hunters found that antlerless elk hunters were much less likely to pay trespass fees to harvest female elk (Grunterad and Chizinski 2020). With harvest of females having the most influence on elk population management, landowners in areas where elk are perceived as above tolerance should work with hunters to provide access for female elk harvests.

The survival estimates produced by the Kaplan-Meier Estimate were similar to survival estimates produced by the Statistical Population Reconstruction (SPR) Model developed for the elk in the badlands of North Dakota (see Chapter 4 – Population Monitoring) confirming that using SPR models to produce survival estimates is a viable alternative to conducting expensive collaring efforts to get survival estimates using Kaplan-Meier in the future. Since NDGF have collected various data sources used by SPR and plan to continue collecting that same data into the future, SPR modeling will fit their needs to produce reliable and cost-effective survival estimates for the foreseeable future.

Management Implications

Elk in western North Dakota have high natural survival. Only 3 elk in our study died from natural causes. Thus, hunting is the main management tool to effectively manipulate elk numbers. The remaining mortalities were all due to hunter harvest. The survival rates found using the Kaplan-Meier estimator were extremely close to what the SPR model estimated. This emphasizes that harvest is the main tool for population management of these elk and survival estimates from the SPR model can be used to evaluate survival of western North Dakota elk in the future. It also highlights the need for landowners with elk conflicts to work with and allow public hunters access to hunt on their land. These survival results also may help persuade landowners to join the Private Land Open To Sportsman (PLOTS) program to alleviate depredation from higher elk numbers.

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Figures

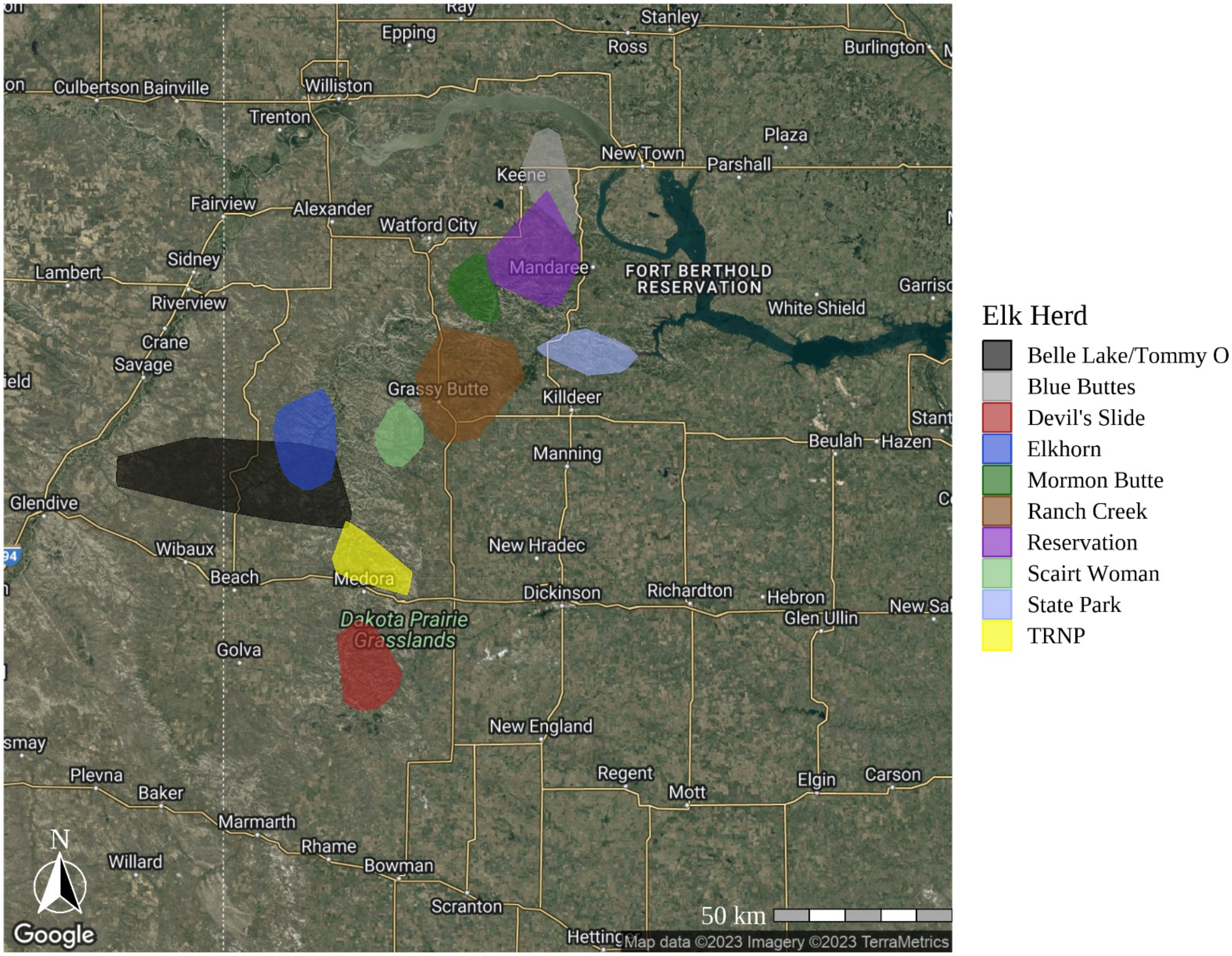

Figure 25. Map of elk herd winter ranges in western North Dakota.

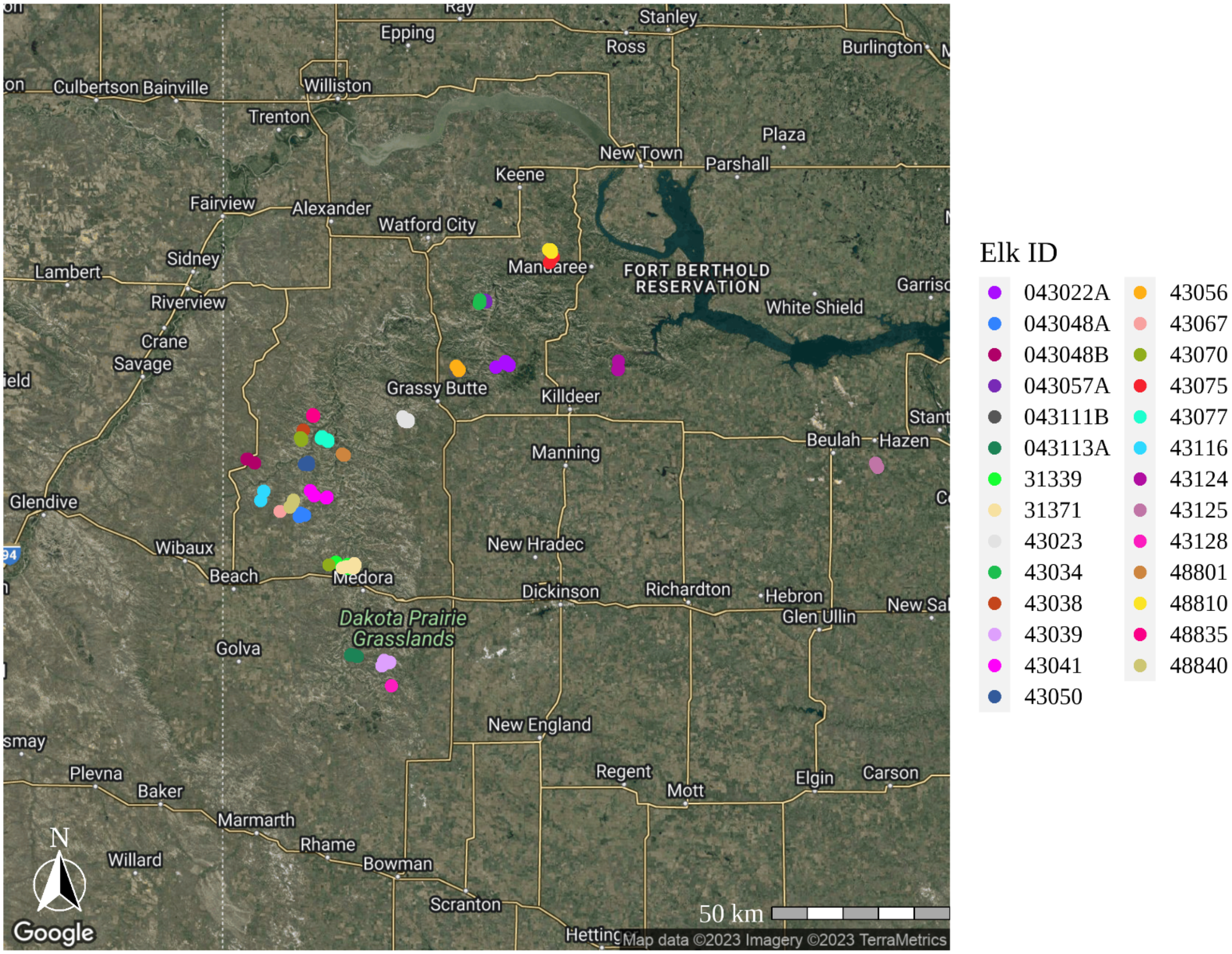

Figure 26. Map of individual elk GPS locations on the day they died in western North Dakota during 2019 – 2023.

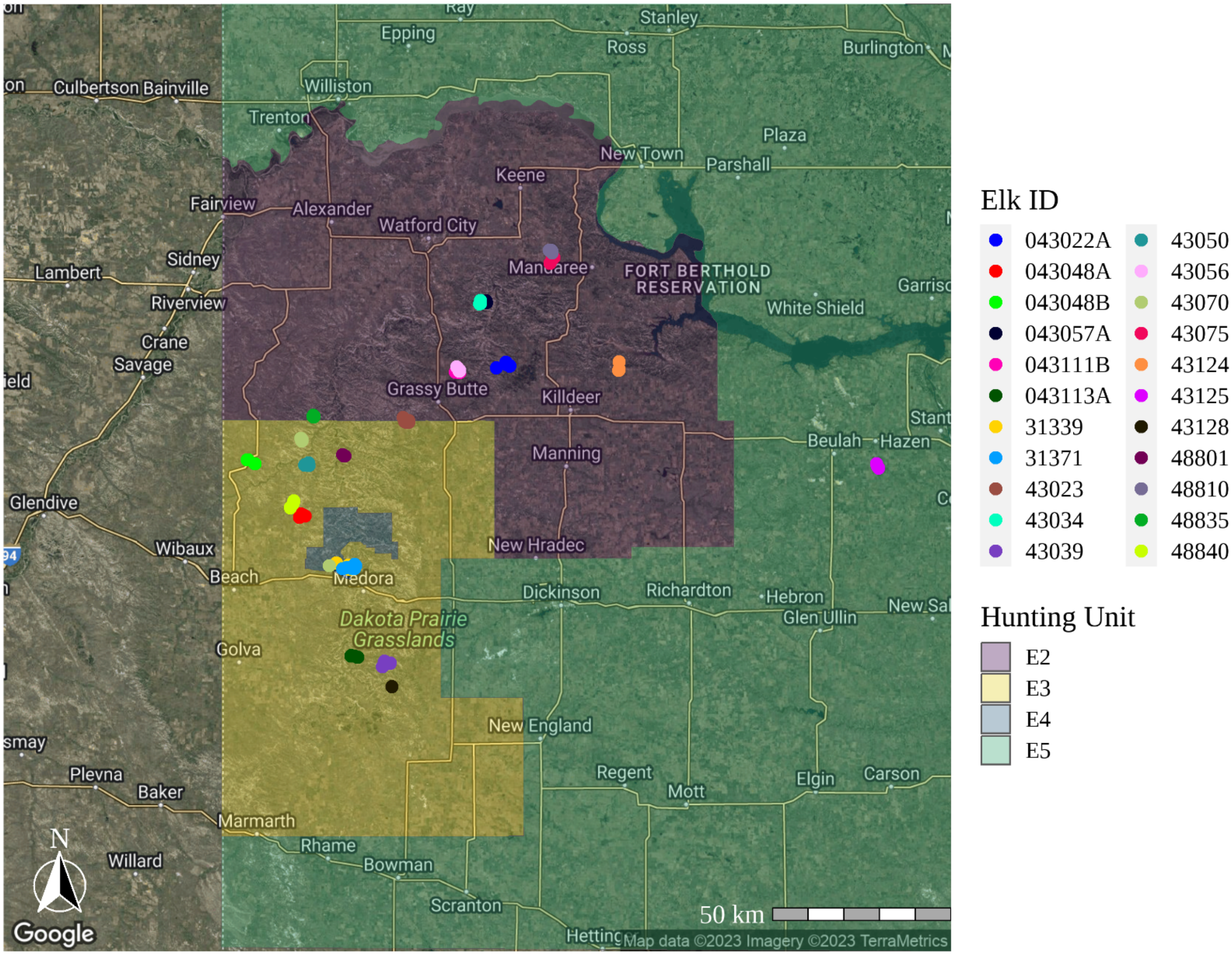

Figure 27. Map of elk hunting units and individual elk GPS locations on the day they were harvested in western North Dakota during hunting seasons 2019-20 through 2022-23.

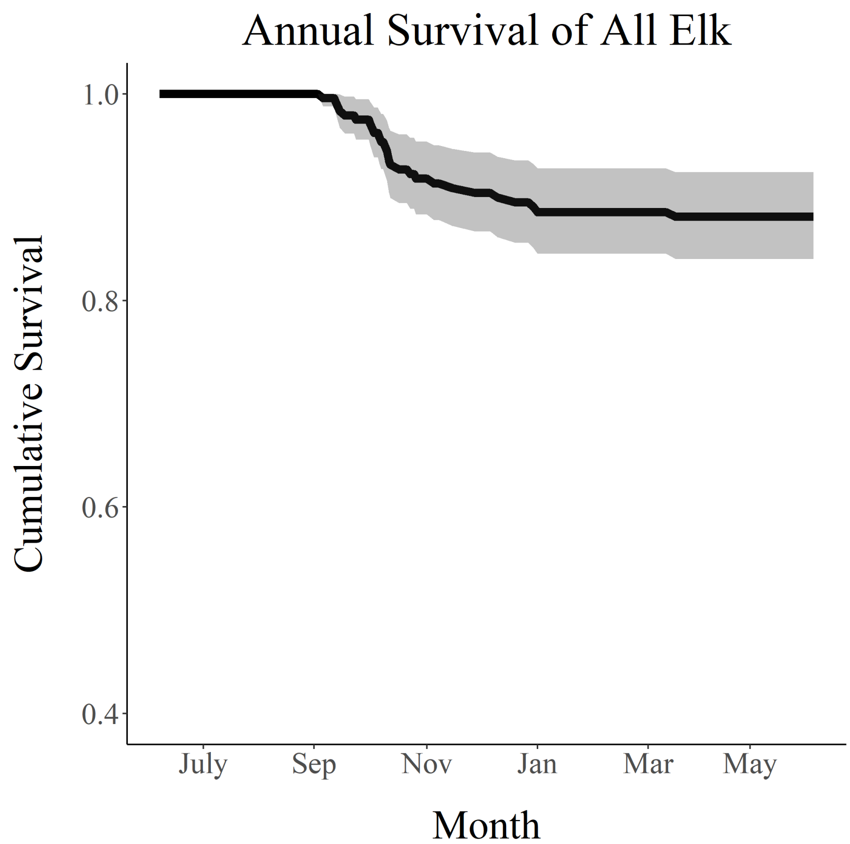

Figure 28. Annual Kaplan-Meier survival curve for elk in western North Dakota during 2019 – 2023. Note the y-axis is truncated between 0.40 and 1.0.

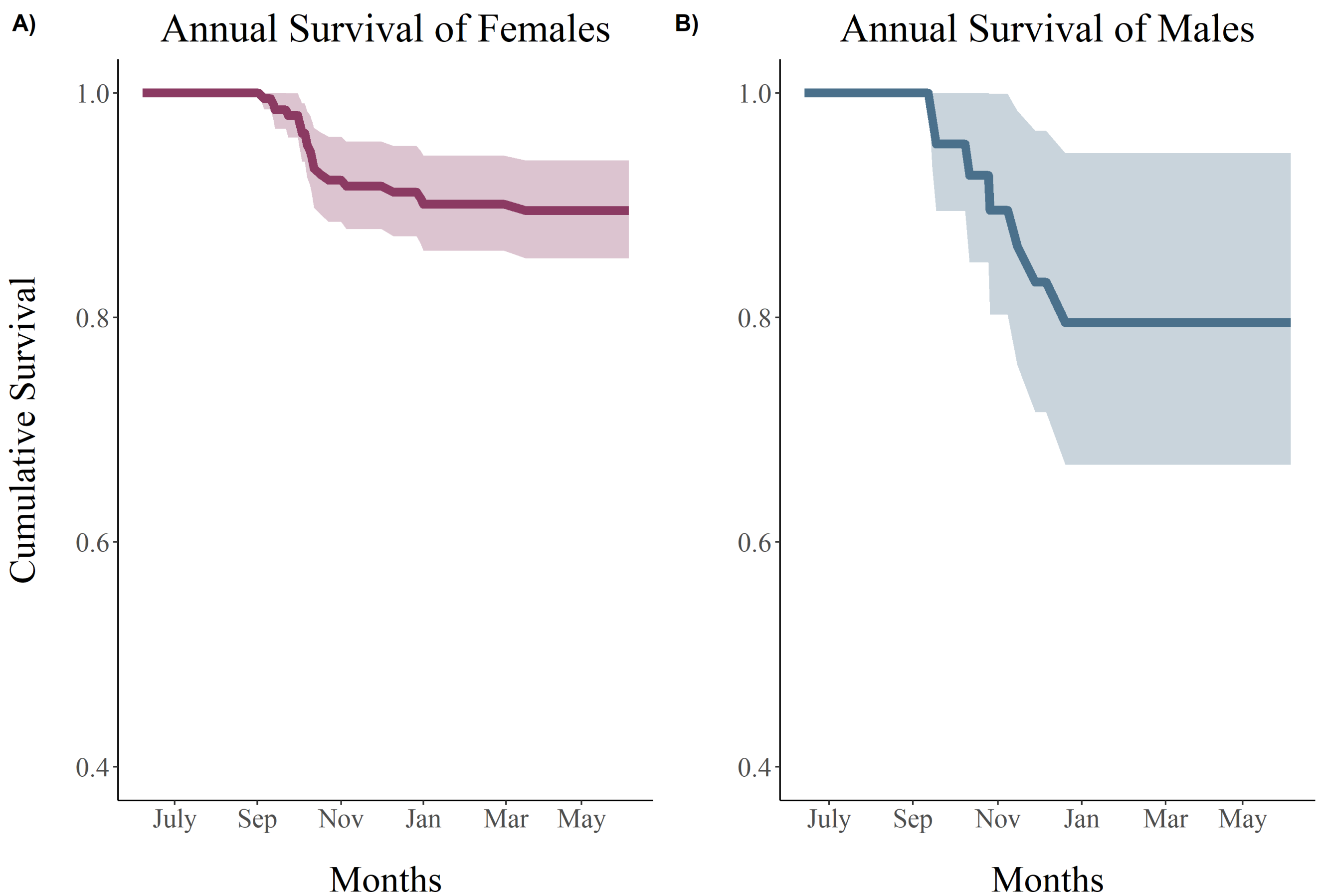

Figure 29. Annual Kaplan-Meier survival curve for A) female and B) male elk in western North Dakota during 2019 – 2023. Note the y-axis is truncated between 0.40 and 1.0.

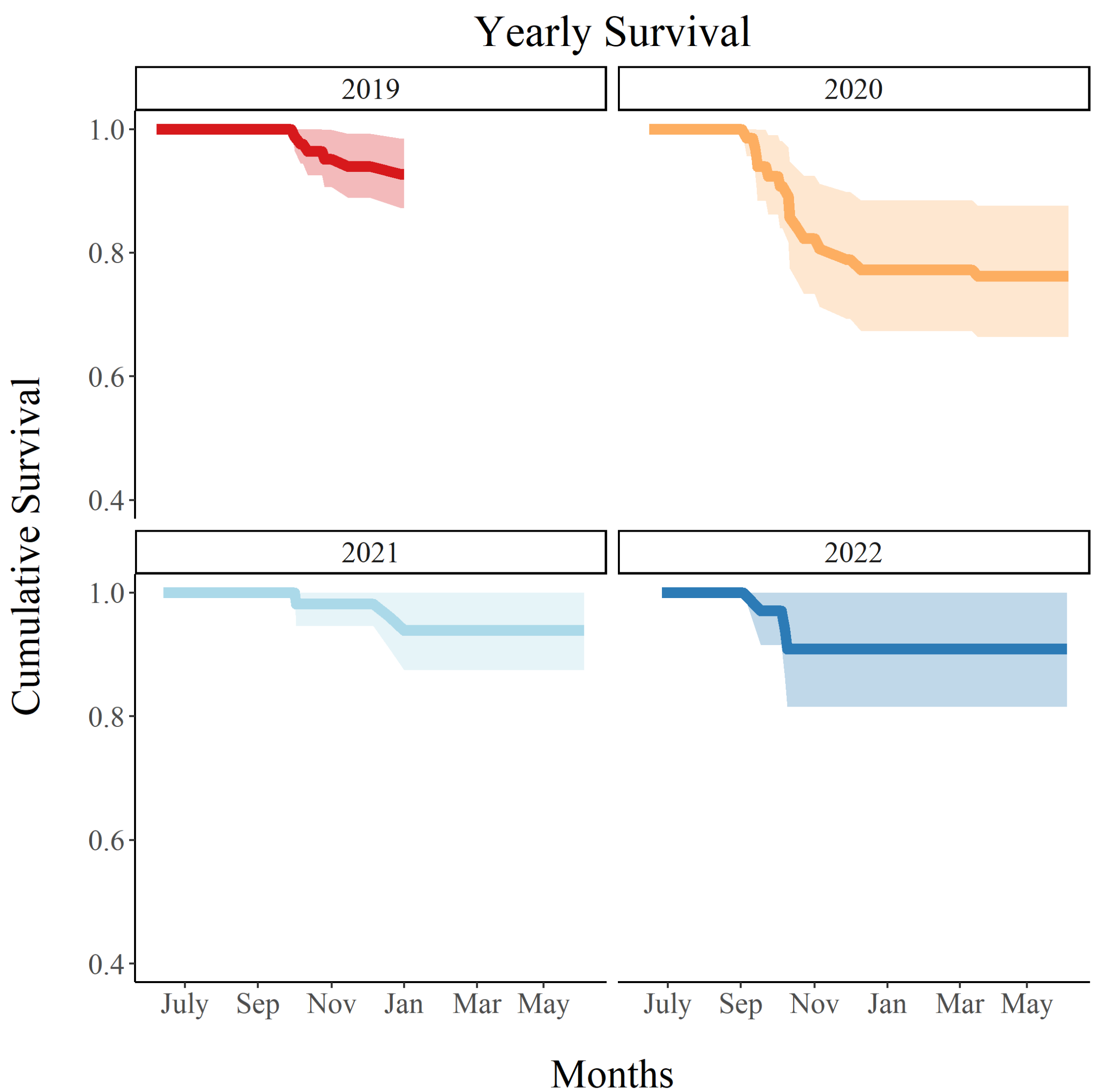

Figure 30. Yearly Kaplan-Meier survival curves for collared elk in western North Dakota. Survival was significantly lower in 2020 compared to 2019, 2021, and 2022. Note the y-axis is truncated between 0.40 and 1.0. The survival curve for 2019 only shows half the year because we set the start date for this analysis as June 1. No mortalities occurred between February and May 2019, so the estimate of annual survival is not affected by this decision. We only monitored survival until the end of the hunting season in 2023 (January 7) so there were not enough data to estimate survival in 2023.

Tables

Table 14. Elk capture summary by herd, sex, and age at capture. The Count column is the total number of collars deployed into each herd.

Herd	Sex	Capture Age	Count
Elkhorn	Female	Adult	18
Belle Lake/Tommy O	Female	Adult	14
Reservation	Female	Adult	13
TRNP	Female	Adult	12 [a]
Mormon Butte	Female	Adult	10
Scairt Woman	Female	Adult	9
State Park	Female	Adult	8
Devil's Slide	Female	Adult	7
Ranch Creek	Female	Adult	6 [a]
Ranch Creek	Female	Yearling	3
TRNP	Female	Yearling	2
Belle Lake/Tommy O	Female	Yearling	1
Elkhorn	Female	Yearling	1
Scairt Woman	Female	Yearling	1
TRNP	Male	Yearling	10
Elkhorn	Male	Yearling	9
Belle Lake/Tommy O	Male	Yearling	4
Reservation	Male	Yearling	4
State Park	Male	Yearling	3
Ranch Creek	Male	Adult	2
Devil's Slide	Male	Yearling	2
Mormon Butte	Male	Yearling	2
Ranch Creek	Male	Yearling	2
Belle Lake/Tommy O	Male	Adult	1
Devil's Slide	Male	Adult	1
Reservation	Male	Adult	1
State Park	Male	Adult	1
Blue Buttes	Male	Yearling	1
Scairt Woman	Male	Yearling	1

[a.] One collar stopped working immediately after deployment.

Table 15. Causes of elk mortality summarized by herd, sex, approximate age at death, and mortality cause. If we caught elk as yearlings, we were able to estimate their age at death. However, for elk caught as adults we had no way of knowing their specific age class at death and these are listed as 'adults'. The Count column is how many mortalities occurred from each herd.

Herd	Sex	Age at death	Cause of mortality	Year	Count
Belle Lake/Tommy O	Female	Adult	Legal Harvest	2019	1
Mormon Butte	Female	Adult	Legal Harvest	2019	1
Reservation	Female	Adult	Legal Harvest	2019	1
Ranch Creek	Female	2-year-old	Legal Harvest	2019	1
Belle Lake/Tommy O	Female	Adult	Legal Harvest	2020	1
Elkhorn	Female	Adult	Legal Harvest	2020	2
Mormon Butte	Female	Adult	Legal Harvest	2020	1
Ranch Creek	Female	Adult	Legal Harvest	2020	1
TRNP	Female	Adult	Legal Harvest	2020	2
Devil's Slide	Female	Adult	Legal Harvest	2020	1
Ranch Creek	Female	Adult	Legal Harvest	2020	1
Scairt Woman	Female	3-year-old	Legal Harvest	2020	1
Elkhorn	Female	Adult	Legal Harvest	2022	1
Reservation	Female	Adult	Legal Harvest	2022	1
Belle Lake/Tommy O	Female	Adult	Malnutrition	2020	1
Elkhorn	Female	Adult	Probable EHD	2021	1
Elkhorn	Female	Adult	Unknown	2020	1
Belle Lake/Tommy O	Female	Adult	Wounding Loss	2021	1
Devil's Slide	Male	Adult	Legal Harvest	2019	1
State Park	Male	3-year-old	Legal Harvest	2020	2
TRNP	Male	3-year-old	Legal Harvest	2020	1
Elkhorn	Male	2-year-old	Legal Harvest	2021	1
Belle Lake/Tommy O	Male	3-year-old	Legal Harvest	2022	1
Belle Lake/Tommy O	Male	Adult	Wounding Loss	2019	1

Chapter 4. Population Monitoring

Objective

Develop a monitoring strategy for elk in western North Dakota that will provide methods to determine abundance, harvest rates, natural survival and recruitment rates annually using harvest data already collected by NDGF. This includes identifying seasonal areas of concentration to annually monitor elk abundance and calf production using ground or aerial counts.

Methods

Monitoring Techniques

There are several techniques biologists use to monitor wildlife populations. One of the methods used extensively by state agencies responsible for monitoring large game species is aerial counts. Biologists fly designated areas counting all the individuals they see, giving them a count for that year that can be compared to previous years providing trend data about that population. However, this method underestimates population sizes (Slade and Blair 2000), ultimately leading to conservative license allocations (Banfield and Rosenberry 2020).

More advanced techniques that provide more accurate information such as abundance with confidence intervals and survival rates have since been developed that are now being used by many agencies. Recent developments in Statistical Population Reconstruction models provide robust and defensible estimates of annual age-specific abundance of harvested populations using harvest data that is already collected by and available to wildlife management agencies (Conn et al. 2008, Skalski et al. 2011, Gast et al. 2013, Clawson et al. 2015). Additionally, SPR allows estimation of natural survival, recruitment, and harvest mortality simultaneously to abundance when one or more sets of auxiliary data are incorporated into the model, such as survival data from a radio-tracking study or independent abundance estimates (Clawson et al. 2013). Aerial survey counts like the ones performed by NDGF can be used as auxiliary data in such a model.

Aerial Survey

Prior to this study, elk populations in the western North Dakota Badlands were monitored with aerial searches of large areas known to have elk. These large areas were searched in conjunction with annual aerial mule deer surveys in the fall and spring. Many years elk areas were not flown due to weather constraints and lower priority. This uncertain source of data was of limited use that provided a weak measure of population trend. To facilitate the development of regular flight routes for elk aerial surveys, we estimated 99% utilization distributions (UD) for the range of each herd from January 1 through the end of February, which corresponds with the timing of flights. We used these UDs to create annual elk count flight routes to count elk during the specified period. These routes were uploaded to both OnX Maps and ForeFlight to be used by the survey pilots to navigate the survey routes.

This process was first completed for elk herd locations collected during 2019 and 2020 to create a route for the 2021 count. For 2021, we separated the survey area into 2 categories; high elk use that included any location within the boundaries of the 99% UDs and low elk use that included all areas outside of the UDs but within hunting units E2 and E3 (Figure 31). We used a random transect generator in ArcMap to create 20 transects within the high elk use areas and 10 transects within the low elk use areas, to make up 30 transects allowed by time and resource constraints of NDGF personnel and equipment. All transects were 50 km in length, spaced at least 1 km apart, with randomized orientation bounded between 150 degrees and 200 degrees (Fleming and Tracy 2008).

Based on NDGF observer feedback from the 2021 aerial survey, we created a new transect route for 2022. Since surveys took less time to complete than anticipated, the total number of surveys was increased to 40 transects passing through the UDs extending 3 miles outside each UD edge. The 3-mile extension outside the UD was added to account for areas elk may expand to in the future. The transects were distributed proportionately across the herd UDs according to their size. In addition, transects were placed 3 miles outside each herd UD to account for future elk expansion into the unused areas resulting in 18 more transects (Figure 32).

After additional NDGF observer feedback was received from the 2022 aerial survey, more improvements were incorporated to create a new transect route for 2023 and beyond. Observers described difficulty with observability of elk during transects oriented East/West due to sun glare, so transects were oriented North/South, spaced 1 mile apart, and extended 3 miles to the north, south, east, and west of each UD to account for future elk expansion outside of the existing home range (Figure 33). An additional new survey requirement of clear skies was added to improve detectability of elk, since past surveys during overcast skies made it harder to observe elk in the broken landscape of the Badlands. Each survey started at sunrise when elk were more likely to be active.

We attempted to set up and conduct a distance sampling protocol to estimate elk abundance, however that effort proved unsuccessful. NDGF can fly elk surveys in the winter when elk are grouped up. With the open landscape of the Badlands, most of the observed elk were seen in the E Band (furthest band of survey from the flight path). Distance sampling assumes that observability is greater closer to the flight path, an assumption that was not aligned with the conditions observed in western North Dakota. Therefore, abundance estimates were skewed and overestimated elk abundance. We suspected there could be some observer bias resulting in detecting elk further away, so we attempted to fly surveys recording video. The video could then be reviewed after so that closer observations might not be missed. However, this attempt did not improve results.

Statistical Population Reconstruction (SPR) Analysis

We used the program PopRecon (Lady and Skalski 2015), Version 3 to produce a Statistical Population Reconstruction (SPR) model for elk within the study unit. The program is an integrated population model that pairs age-at-harvest and hunter-effort data with auxiliary information to estimate annual age-specific abundance, survival, and harvest rates, and their associated variances (Clawson et al. 2017). SPR has numerous advantages over other methods in that maximum likelihood methods are used to estimate annual hunter-harvest probabilities that, in turn, are used to estimate age-class and annual abundance (Gast et al. 2013). This approach provides better optimization and more realistic estimates of SEs and confidence intervals. It also allows age structures to change annually with yearly variation in recruitment. The age-at-harvest data we used for our model were provided by NDGF for years ranging from 2014 through 2022. Ages of elk harvested over that period ranged from 0.5 to 15 years old for both males and females. GPS collar data provided the number of elk at risk at the beginning of each year and if those elk were harvested, died of other causes, or survived until the next year and was input into the model as an auxiliary data source.

PopRecon 3 requires users to specify several settings and parameters when building a model. First, the data structure must be defined to establish the number of distinct age classes present in the age-at-harvest data. PopRecon 3 allows for pooling of age classes. For example, all individuals greater than a certain age would be pooled into one overall age class. The benefit of pooling age classes is that it reduces the variance in the model caused by low numbers of elk harvested within older age classes, resulting in better estimates. For this analysis, we set the number of age classes at 10 and we pooled elk for age classes 9 and older (Appendix F). The second step is to define the harvest processes by setting a minimum and maximum harvest percentage for each sex as well as defining the age at which an individual becomes an adult. Age classes at and above the adult age share the same harvest susceptibility. For males, we set the minimum harvest at 0.02, the maximum harvest at 0.4, and the first adult age at 4 (Appendix G). For females, we set the minimum harvest at 0.04, the maximum harvest at 0.15, and the first adult age at 1 (Appendix H). The minimum and maximum harvest parameters were set for each sex slightly below the lowest and above the highest recorded harvest rates present in the data for each sex. The next step is to define the natural survival processes by setting minimum and maximum survival of elk without accounting for harvest mortality as well as the age at which natural survival would become constant. For males, we set the minimum survival at 0.9, the maximum survival at 0.99, and the first adult age at 2 (Appendix I). For females, we set the minimum survival at 0.9, the maximum survival at 0.99, and the first adult age at 1 (Appendix J). Next, the annual schedule for harvest and natural survival must be set. In this model, harvest was set to start September 5 and to end December 31 each year with natural survival occurring the entire year (Appendix K). Finally, auxiliary data is entered. As stated above, we used GPS collar data with the number of elk at risk at the beginning of each year and if those elk were harvested, died of other causes, or survived until the next year. These data are entered for each year the GPS collars were active, which for our study ranged from 2019 through 2021. For ease of readability, the data entered in this step (Appendix L) are provided (Table 17, Table 18). The procedure to update the SPR model in the future has been provided (Appendix M). Additionally, we included aerial count data as auxiliary data in the model.

Results

Winter Counts

Winter counts by herd for the 2022 aerial survey in hunting unit E3 were 270 for Elkhorn, 185 for Bell Lake, 50 for Scairt Woman, 35 for Devils Slide, and 65 for Devils Slide South with a total of 605 elk counted. Winter counts by herd for the 2022 aerial survey in hunting unit E2 were 130 for Burnt Creek, 140 for Ranch Creek, 70 for Chimney Butte, and 65 for Mormon Butte with a total of 405 elk counted (Table 16).

Winter counts by herd for the 2023 aerial survey in hunting unit E3 were 525 for Elkhorn, 290 for Bell Lake, 65 for Scairt Woman, 80 for Devils Slide, and 65 for Devils Slide South with a total of 1,025 elk counted. Winter counts by herd for the 2022 aerial survey in hunting unit E2 were 140 for Burnt Creek, 175 for Ranch Creek, 100 for Chimney Butte, and 90 for Mormon Butte with a total of 505 elk counted (Table 16).

SPR Model

Abundance Estimates from SPR Model

Male elk abundance ranged from 324.3 (50.5 SE) to 545.4 (127.9 SE) between 2014 and 2022 (Table 18, Figure 34). Female elk abundance ranged from 583.2 (180.6 SE) to 1,947.6 (688.3 SE) between 2014 and 2022 (Table 20, Figure 37). Total elk abundance ranged from 907.5 (188.7 SE) to 2393.4 (710.9 SE) between 2014 and 2022 (Table 23, Figure 40).

Survival Estimates

Male elk survival estimates ranged from 0.847 (0.079 SE) to 0.955 (0.015 SE) for calves, from 0.916 (0.037 SE) to 0.969 (0.011 SE) for yearlings, from 0.625 (0.101 SE) to 0.859 (0.038 SE) for 2-year-olds, from 0.468 (0.082 SE) to 0.732 (0.044 SE) for 3-year-olds, and from 0.418 (0.047 SE) to 0.667 (0.035 SE) for males 4 years old or older (Table 19, Figure 35). Female elk survival estimates ranged from 0.889 (0.026 SE) to 0.939 (0.015 SE) for calves and from 0.877 (0.028 SE) to 0.926 (0.018 SE) for yearling and older females (Table 22, Figure 38).

Harvest Estimates

Male elk harvest probabilities ranged from 0.022 (0.009 SE) to 0.089 (0.049 SE) for calves, from 0.014 (0.008 SE) to 0.046 (0.023 SE) for yearlings, from 0.083 (0.023 SE) to 0.225 (0.069 SE) for 2-year-olds, from 0.153 (0.025 SE) to 0.323 (0.056 SE) for 3-year-olds, and from 0.160 (0.020 SE) to 0.362 (0.037 SE) for males 4 years old or older (Figure 36). Female elk harvest probabilities ranged from 0.035 (0.011 SE) to 0.060 (0.015 SE) for calves and from 0.035 (0.011 SE) to 0.061 (0.015 SE) for yearling and older females (Figure 39).

Discussion

Aerial Survey Improvement

Recognizing elk population trends is important for wildlife managers when it comes to making decisions related to updating harvest numbers and regulations. Assuring surveys are uniformly performed and optimizing the observability of elk during the surveys by limiting flights to mornings, when elk are more active, and clear sky days only, when the sunshine makes elk stand out on the landscape, can help managers better monitor trends in elk populations in western North Dakota. When these data are summarized into a meaningful index of abundance, population changes can be tracked over time (Amundson et al. 2019, Finch et al. 2021). However, these indices can be subject to bias if observer error is not constant through time (Davis et al. 2022). Fortunately, these data can also help tune and improve abundance estimates of a more robust population monitoring tool when included as auxiliary data in such model, especially when other auxiliary data are not available (Skalski et al. 2007).

Statistical Population Reconstruction Model

The total annual abundance estimates from the SPR model for 2023 were within 329 individuals more than the counts from the aerial survey, a result that should be expected assuming an observer will never be able to count all elk within the study area (Pollock and Kendall 1987, Samuel et al. 1987). Further, the aerial counts are a post hunting season count while the SPR estimates abundance pre hunting season. So, if we subtract the number of elk harvested during the hunting season the SPR estimate and the aerial count was within 4% for 2023. Although the counts are not as accurate as a true abundance estimate, we believe they are close to the actual number of elk due to the openness of the landscape and relatively small size of the area. Therefore, we can assume our SPR model estimates are reliable and can be used to make determinations on harvest allotments to manage the population.

The geometric mean ($\bar{\lambda}$) for all years in the SPR model is $\bar{\lambda}$=1.08 indicating the population is increasing. However, this rate of increase is less than what was reported in the Theodore Roosevelt National Park South Unit in the period after reintroduction from 1985-2005 ($\bar{\lambda}$=1.20-1.36; Sargeant and Oehler 2007). If we isolate the average growth rate from the last 4 years ($\bar{\lambda}$=1.03), we see that recent growth is comparable to what has been observed in Montana elk herds ($\bar{\lambda}$=1.01; Hansen et al. 2024). High natural survival of badland elk suggest that harvest is the main tool managers can use to manage elk populations in this area. survival is relatively high while elk abundance has been increasing. If greater elk abundance is desirable, the current harvest allowances are sufficient. However, if landowner tolerance of elk is surpassed, managers may need to increase harvest. Harvest of females will have the greatest effect on abundance.

The survival estimates produced by our SPR model were similar to survival estimates produced by the Kaplan-Meier Estimate confirming that SPR models to produce survival estimates is a viable alternative to conducting expensive collaring efforts to get survival estimates using Kaplan-Meier in the future. Survival estimates from the SPR are comparable to what has been recorded in Montana elk populations. Our adult female survival estimate ranged from 0.88-0.93 while adult female elk survival in Montana was 0.90. Montana reported male survival for males available for harvest, which are brow tined bulls only resulting in bulls typically 2-years-old or more. Our 2+ year old male survival ranged from 0.50-0.75, while adult male elk survival in Montana was 0.60 (Hansen et al. 2024).

Our SPR model will produce reliable estimates of population demographics that can be used to manage elk in western North Dakota into the foreseeable future. The SPR model will retain its utility if harvest regulations and predation rates do not change drastically for the badlands elk. The SPR model relies on the harvest vulnerability coefficient to produce reliable estimates. Major changes in harvest regulations such as significant changes in season length or large increases or decreases in license allocations that significantly change the harvest rates will affect the harvest vulnerability coefficient and may reduce the reliability of the current SPR model. If major changes did occur, additional telemetry auxiliary data may be required to calibrate the model.

Management Implications

The establishment of regular optimized aerial survey transects will allow managers to produce reliable counts and population trends for elk in the badlands. This data can be used as an auxiliary data source in place of the telemetry data in the SPR model moving forward. The count data will also allow managers to identify herd level changes in elk numbers, information the SPR model does not provide at the current harvest levels.

Age-at-harvest and hunter effort data is essential for the SPR model to perform well and produce reliable estimates. Therefore, it is important for hunters to report this information to NDGF. It is already mandatory for hunters to report this information to NDGF if they receive an elk license. But it may be beneficial to educate hunters about how this information is used to better manage the elk population and potentially increase their opportunity to draw a license. This information may incentivize hunters to report and increase the reporting rates for age-at-harvest and hunter effort data leading to improvements to the SPR model estimates.

Since survival is high and the population continues to grow, it is important for managers to work with private landowners to allow access to elk hunters to increase antlerless elk harvest in areas where conflicts exist. The information from the SPR may also be used to promote the Private Land Open To Sportsman (PLOTS) program in areas where elk numbers are above landowner tolerance.

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Figures

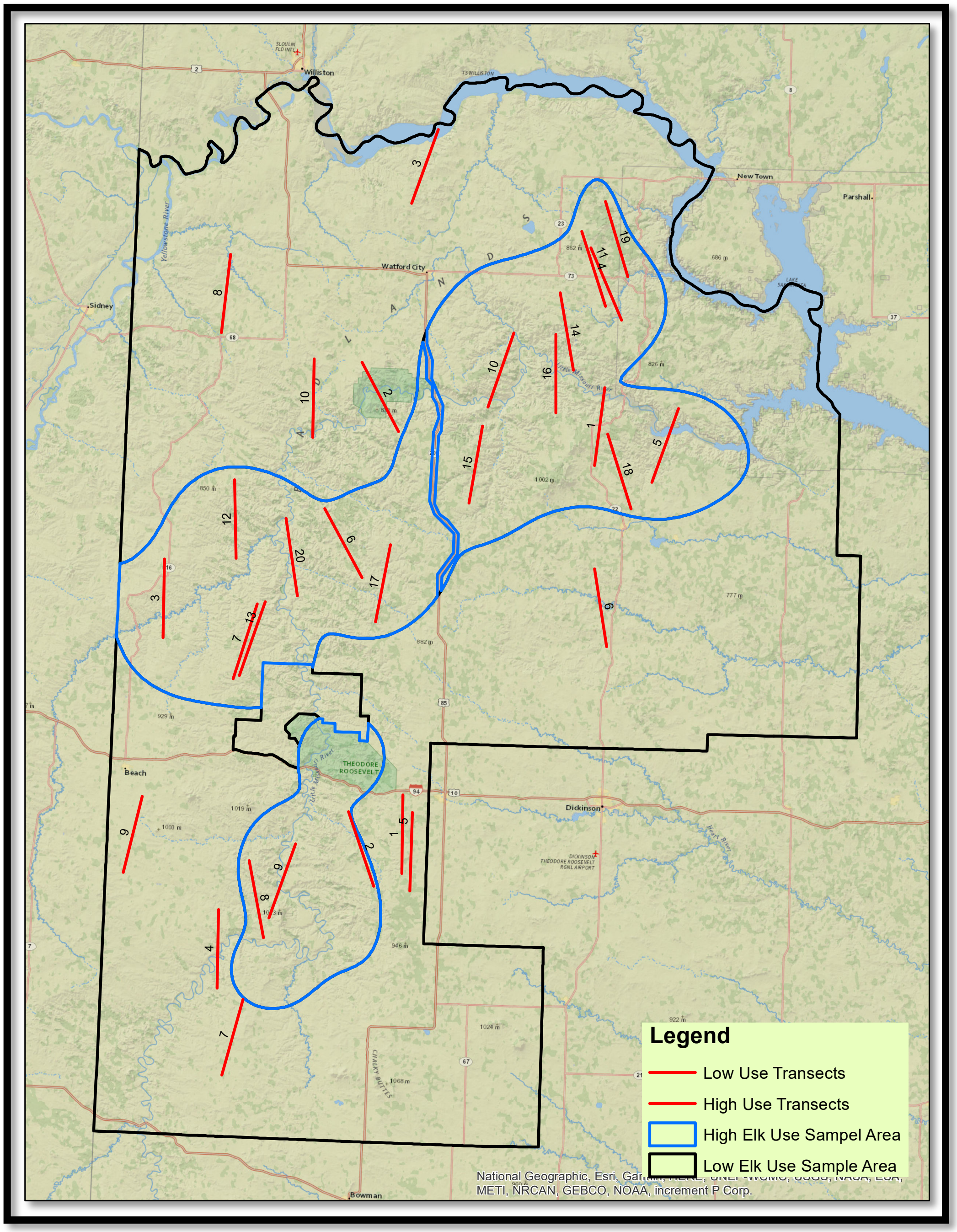


Figure 31. 2021 annual elk aerial survey transect map.

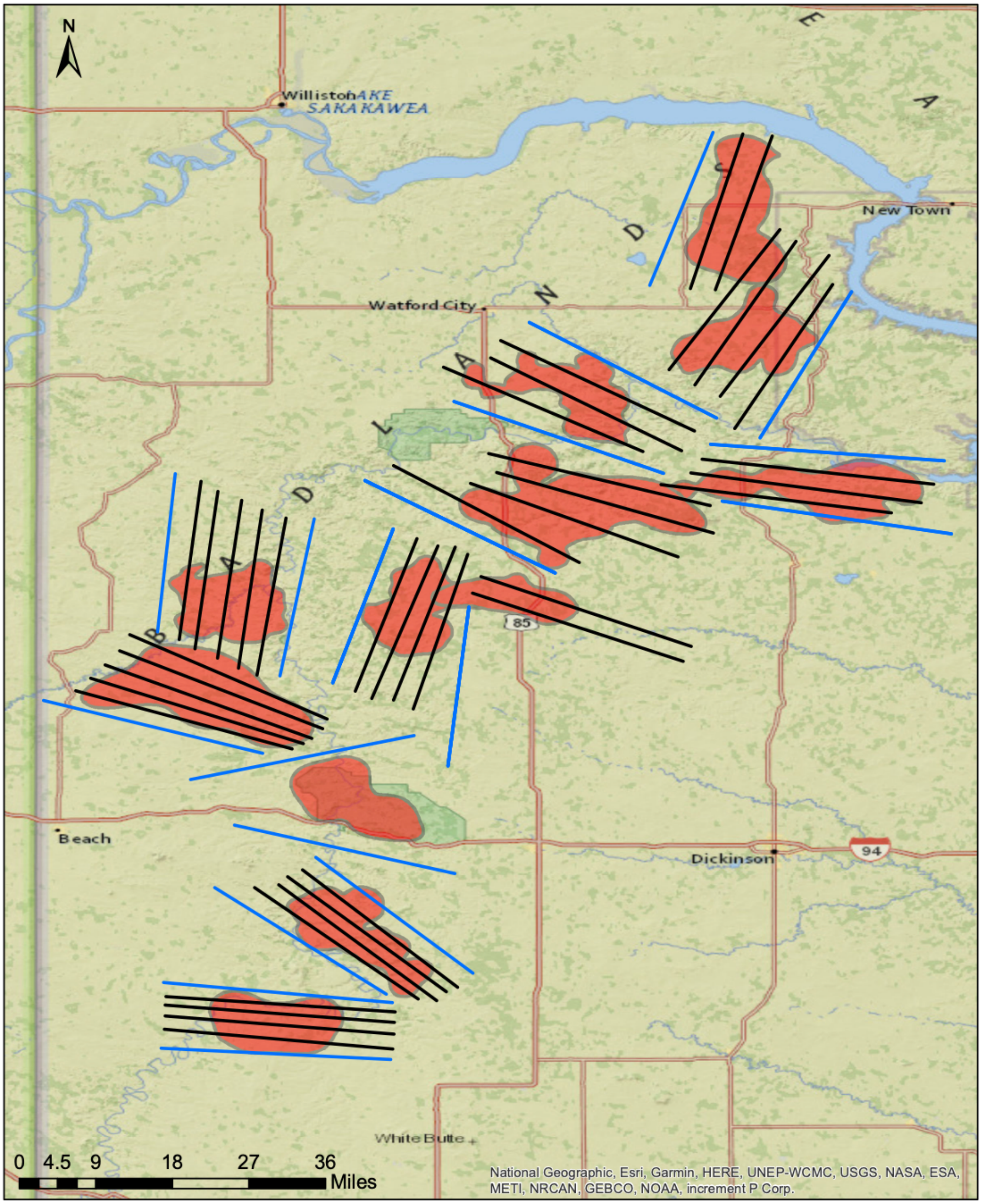


Figure 32. 2022 annual elk aerial survey transect map.

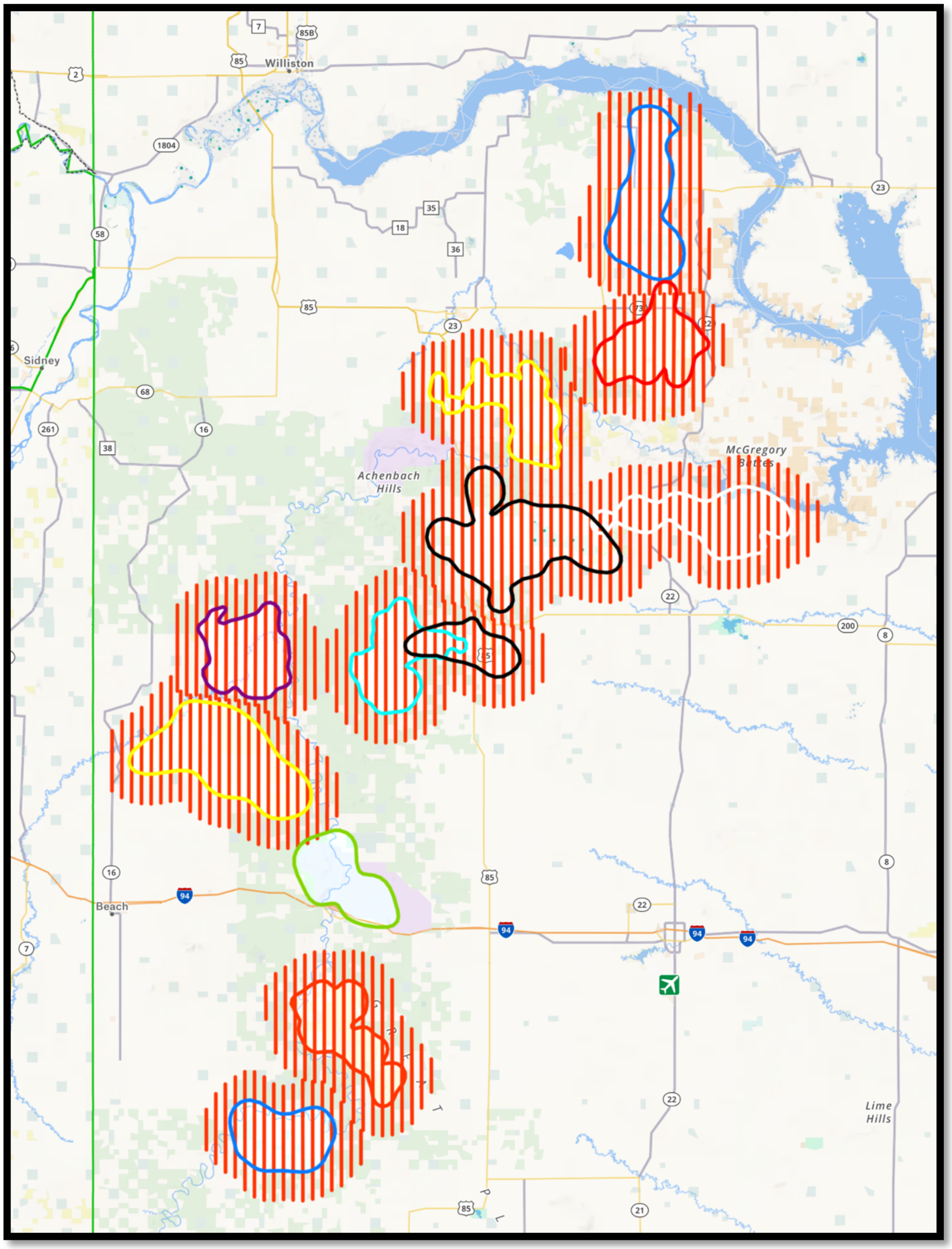


Figure 33. 2023+ annual elk aerial survey transect map.

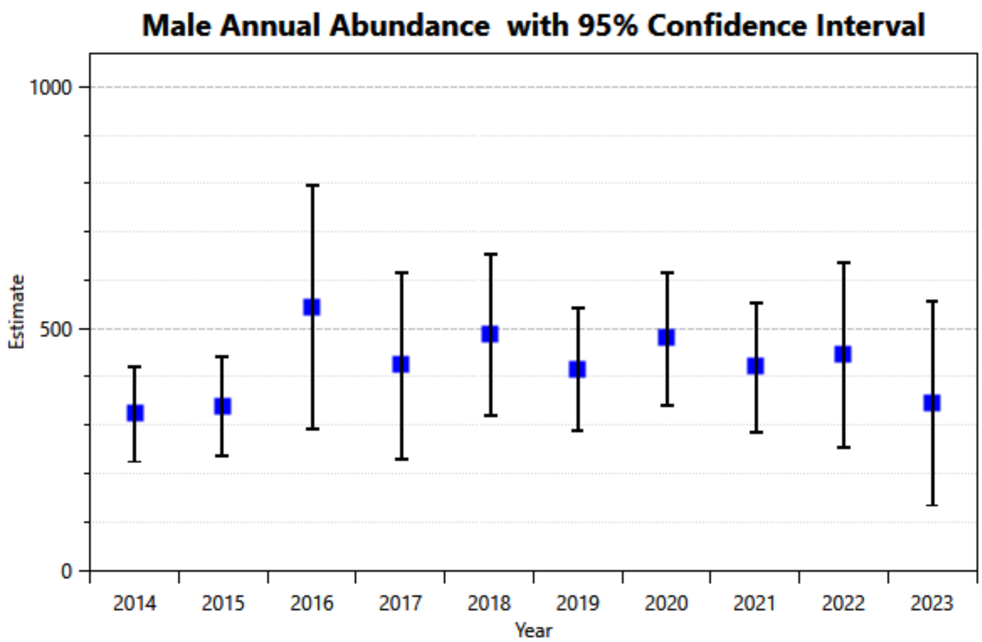


Figure 34. Estimates of male abundance per year.

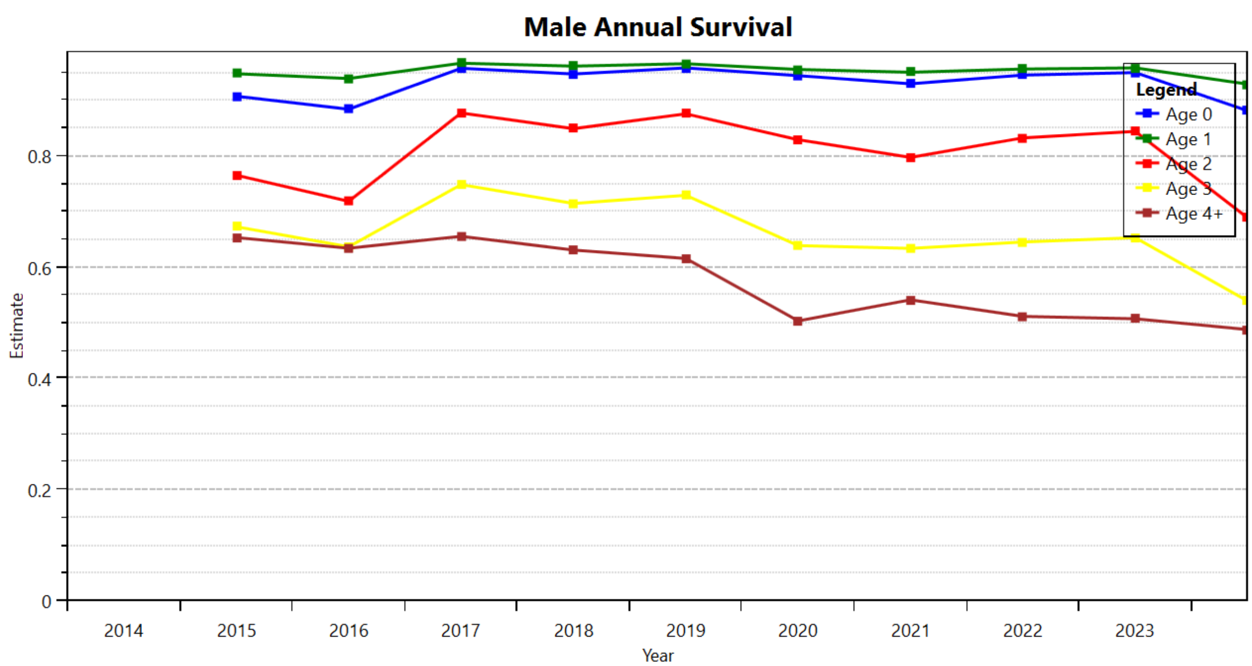


Figure 35. Estimates of male survival rates per year.

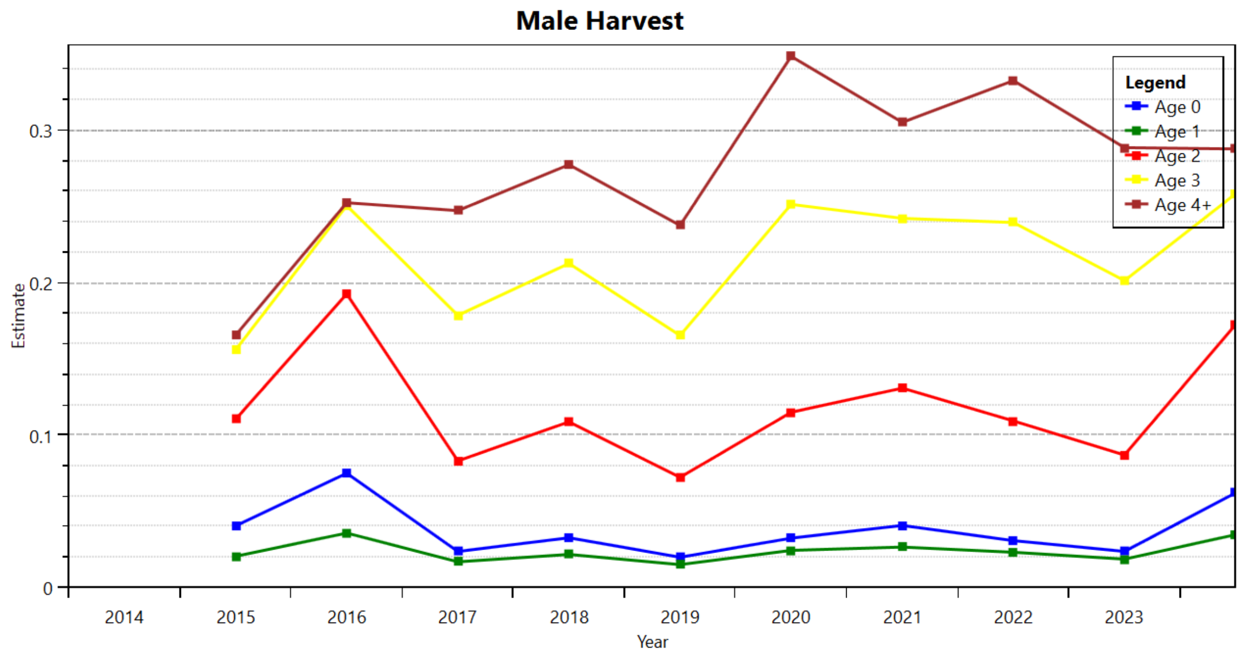


Figure 36. Estimate of male harvest rates per year.

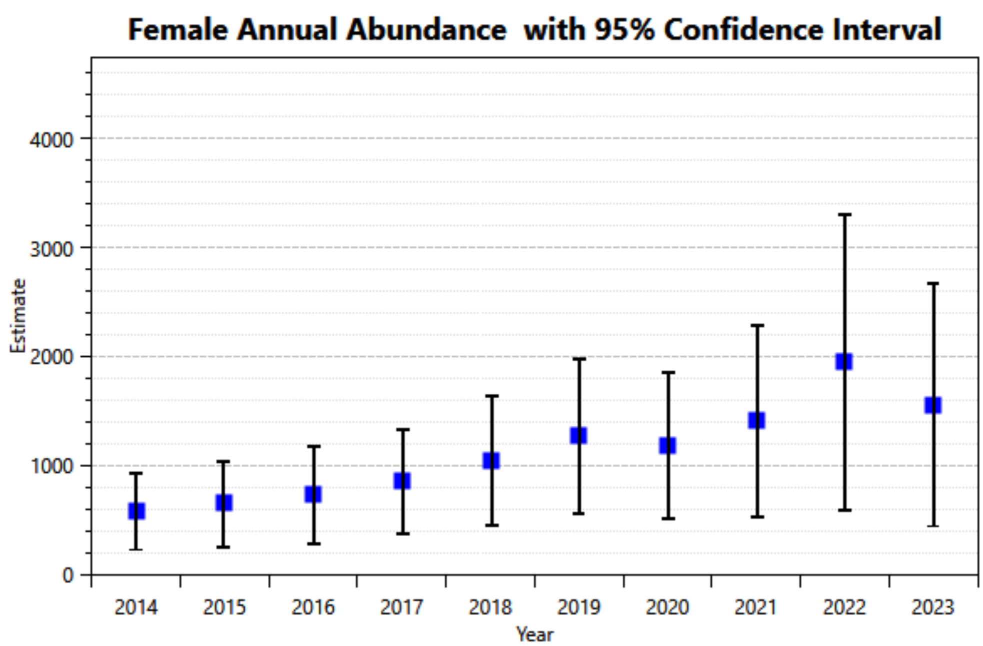


Figure 37. Estimates of female abundance per year.

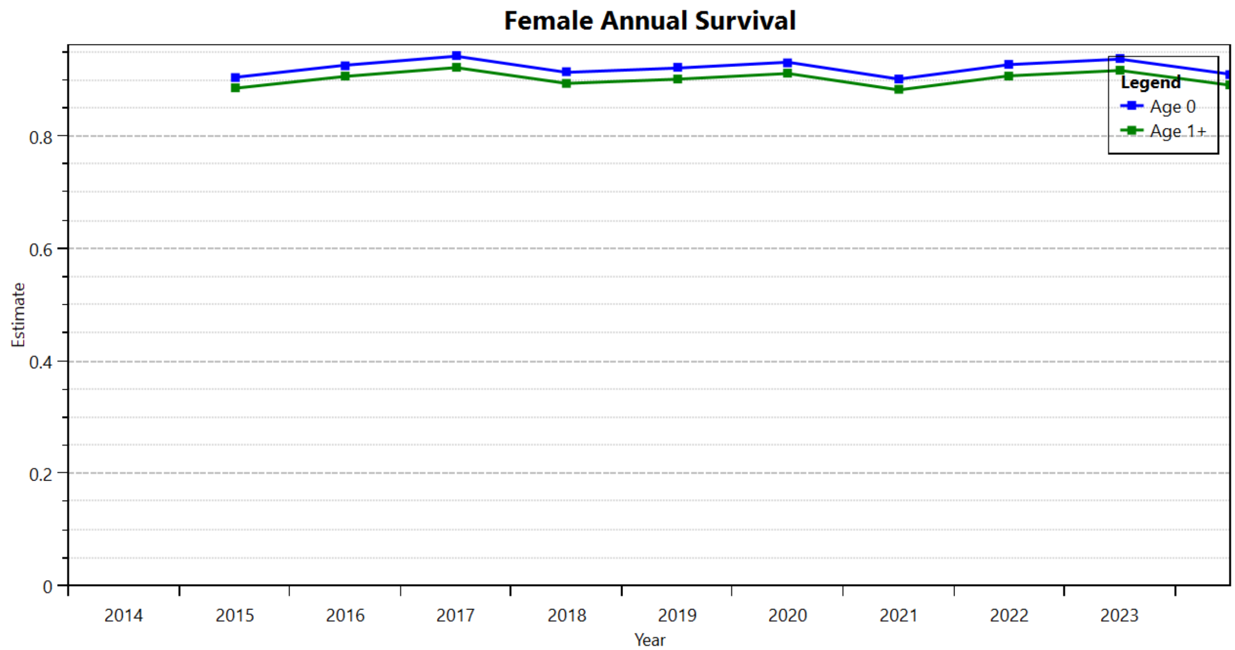


Figure 38. Estimates of female survival rates per year.

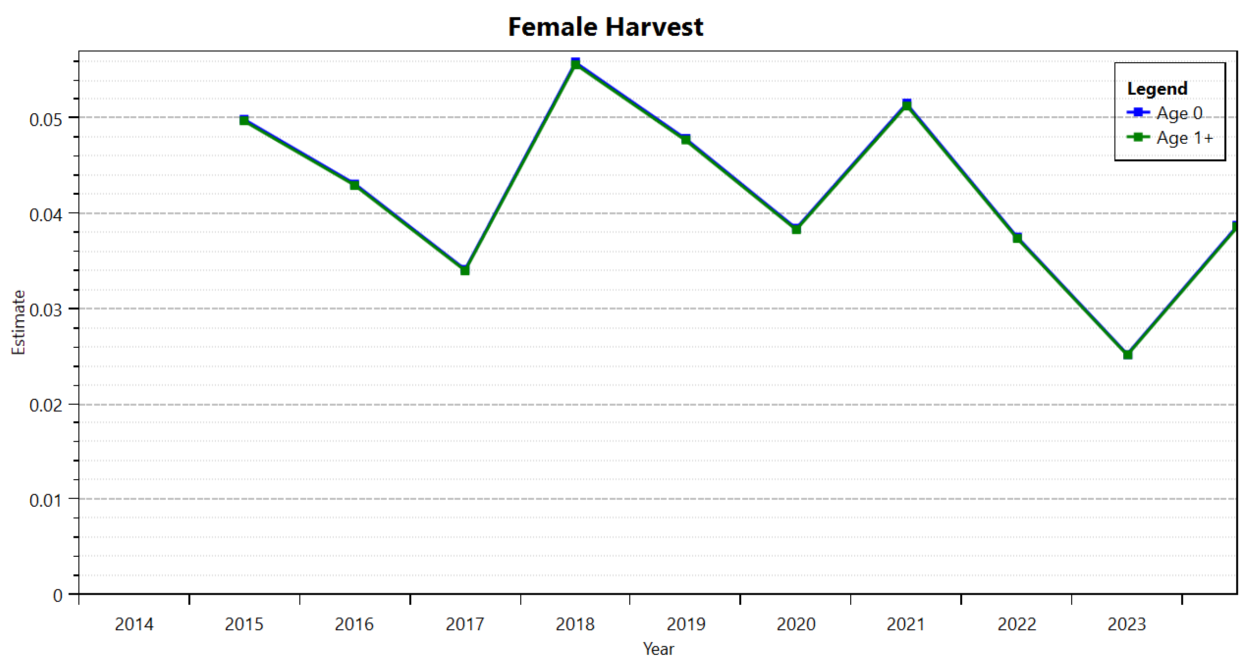


Figure 39. Estimate of female harvest rates per year.

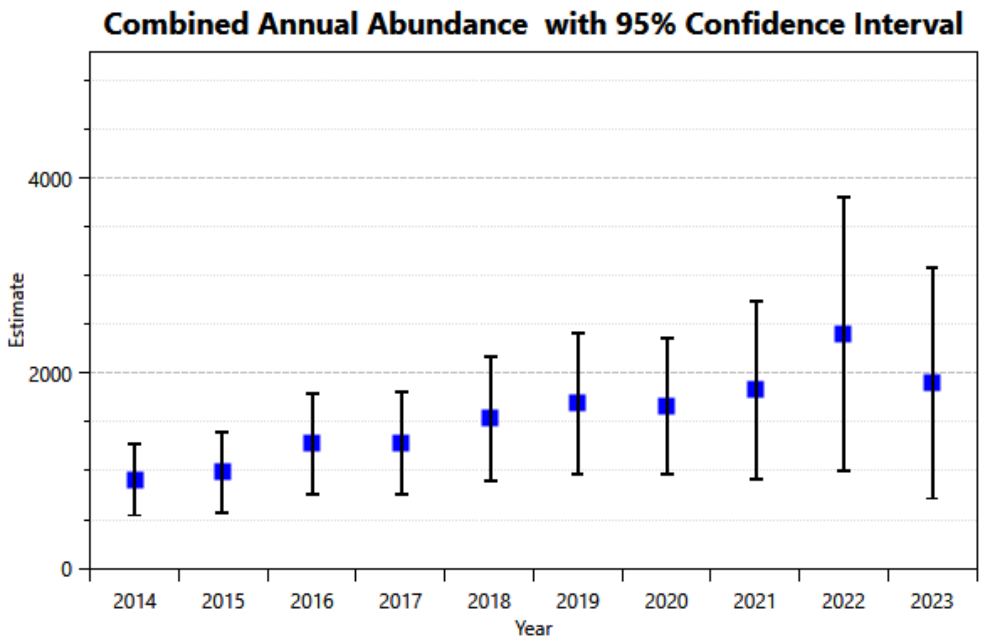


Figure 40. Estimates of total elk abundance per year.

Tables

Table 16. Annual Elk Aerial Survey Counts.

Hunting Unit E3			
Herd	**2022**	**2023**	**2024**
Elkhorn	270	525	415
Bell Lake	185	290	275
Scairt Woman	50	65	60
Devils Slide	35	80	90
Devils Slide South	65	65	110
Total	605	1025	950
Hunting Unit E2			
Herd	**2022**	**2023**	**2024**
Burnt Creek	130	140	135
Ranch Creek	140	175	270
Chimney Butte	70	100	165
Mormon Butte	65	90	50
Total	405	505	620
All Elk Total	**1010**	**1530**	**1570**

Table 17. Male GPS auxiliary data.

Hunting Season									
	1 Year Old			**2 Years Old**			**3 Years Old**		
Year	**At Risk**	**Harvested**	**Died**	**At Risk**	**Harvested**	**Died**	**At Risk**	**Harvested**	**Died**
2019	13	1	0	4	2	0	0	0	0
2020	0	0	0	7	3	0	1	0	0
2021	6	1	0	2	0	0	0	0	0

Non-Hunting Season						
	1 Year Old		**2 Years Old**		**3 Years Old**	
Year	**At Risk**	**Died**	**At Risk**	**Died**	**At Risk**	**Died**
2019	16	0	4	0	0	0
2020	0	0	7	0	1	0
2021	13	0	2	0	0	0

Table 18. Female GPS auxiliary data.

Hunting Season

	1 Year Old			2 Years Old			3 Years Old		
Year	**At Risk**	**Harvested**	**Died**	**At Risk**	**Harvested**	**Died**	**At Risk**	**Harvested**	**Died**
2019	5	1	0	44	3	0	18	0	0
2020	0	0	0	4	1	0	42	7	1
2021	3	0	0	19	0	0	17	1	1

Non-Hunting Season

	1 Year Old		2 Years Old		3 Years Old	
Year	**At Risk**	**Died**	**At Risk**	**Died**	**At Risk**	**Died**
2019	5	0	44	0	18	0
2020	0	0	4	0	48	1
2021	3	0	22	0	19	0

Table 19. Male abundance estimates for each age class by year. (One standard error).

Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9+	Annual
2014	0.0 (0.00)	48.5 (24.19)	90.6 (22.61)	70.5 (11.91)	60.4 (7.50)	12.1 (1.50)	30.2 (3.75)	6.0 (0.75)	6.0 (0.75)	0.0 (0.00)	324.3 (50.54)
2015	0.0 (0.00)	55.8 (33.24)	93.4 (18.10)	59.8 (10.69)	51.5 (6.25)	23.8 (2.88)	35.6 (4.33)	11.9 (1.44)	4.0 (0.48)	4.0 (0.48)	339.7 (52.40)
2016	84.3 (32.61)	118.0 (45.95)	168.3 (55.11)	61.6 (10.24)	36.4 (3.94)	24.3 (2.63)	4.0 (0.44)	32.3 (3.50)	12.1 (1.31)	4.0 (0.44)	545.4 (127.85)
2017	0.0 (0.00)	91.7 (35.36)	91.9 (36.49)	122.2 (26.42)	54.0 (5.80)	18.0 (1.93)	14.4 (1.55)	7.2 (0.77)	10.8 (1.16)	14.4 (1.55)	424.7 (98.23)
2018	100.3 (38.83)	0.0 (0.00)	96.7 (25.83)	139.0 (25.42)	58.9 (7.19)	42.1 (5.14)	16.8 (2.05)	21.0 (2.57)	4.2 (0.51)	8.4 (1.03)	487.4 (85.16)
2019	61.6 (22.69)	40.9 (15.67)	78.2 (23.53)	115.3 (14.52)	45.9 (4.91)	34.4 (3.69)	11.5 (1.23)	2.9 (0.31)	8.6 (0.92)	17.2 (1.84)	416.4 (64.59)
2020	49.0 (16.08)	75.1 (23.57)	114.6 (23.56)	90.8 (13.10)	62.2 (5.94)	59.0 (5.62)	13.1 (1.25)	6.6 (0.62)	3.3 (0.31)	6.6 (0.62)	480.1 (69.97)
2021	64.8 (25.79)	43.0 (16.53)	91.4 (22.96)	83.5 (12.18)	66.1 (7.39)	36.1 (4.03)	18.0 (2.01)	9.0 (1.01)	0.0 (0.00)	9.0 (1.01)	421.0 (67.92)
2022	42.1 (21.55)	106.8 (48.23)	80.4 (27.62)	74.5 (13.84)	48.5 (6.05)	41.6 (5.19)	20.8 (2.59)	6.9 (0.86)	3.5 (0.43)	20.8 (2.59)	445.8 (97.81)
2023	48.2 (33.97)	57.5 (35.43)	17.4 (8.15)	73.5 (18.93)	83.4 (12.53)	20.8 (3.13)	20.8 (3.13)	13.9 (2.09)	3.5 (0.52)	6.9 (1.04)	346.0 (108.12)

Table 20. Male survival estimates for each age class per year. (One standard error).

Year	Age 0	Age 1	Age 2	Age 3	Age 4+
2014	0.9076 (0.0392)	0.9481 (0.0216)	0.7655 (0.0604)	0.6728 (0.0545)	0.6534 (0.0378)
2015	0.8843 (0.0535)	0.9395 (0.0302)	0.7185 (0.0543)	0.6369 (0.0640)	0.6342 (0.0425)
2016	0.9579 (0.0127)	0.9671 (0.0091)	0.8776 (0.0377)	0.7485 (0.0409)	0.6556 (0.0341)
2017	0.9476 (0.0222)	0.9618 (0.0110)	0.8493 (0.0567)	0.7147 (0.0601)	0.6309 (0.0364)
2018	0.9586 (0.0124)	0.9662 (0.0101)	0.8760 (0.0313)	0.7294 (0.0473)	0.6157 (0.0410)
2019	0.9447 (0.0170)	0.9558 (0.0132)	0.8294 (0.0490)	0.6390 (0.0440)	0.5035 (0.0464)
2020	0.9300 (0.0201)	0.9508 (0.0125)	0.7976 (0.0405)	0.6339 (0.0505)	0.5413 (0.0369)
2021	0.9456 (0.0178)	0.9566 (0.0129)	0.8327 (0.0403)	0.6454 (0.0497)	0.5115 (0.0476)
2022	0.9503 (0.0206)	0.9587 (0.0141)	0.8445 (0.0507)	0.6532 (0.0625)	0.5074 (0.0525)
2023	0.8815 (0.0765)	0.9294 (0.0373)	0.6889 (0.1416)	0.5392 (0.1145)	0.4879 (0.0690)

Table 21. Female abundance estimates for each age class by year. (One standard error).

Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9+	Annual
2014	100.3 (30.96)	20.1 (6.23)	201.2 (62.34)	80.5 (24.94)	20.1 (6.23)	20.1 (6.23)	0.0 (0.00)	80.5 (24.94)	20.1 (6.23)	40.2 (12.47)	583.2 (180.58)
2015	46.4 (14.06)	93.1 (28.31)	93.1 (28.31)	162.9 (49.55)	93.1 (28.31)	93.1 (28.31)	46.5 (14.16)	0.0 (0.00)	0.0 (0.00)	23.3 (7.08)	651.4 (198.09)
2016	58.6 (18.22)	88.2 (27.49)	58.8 (18.33)	117.6 (36.65)	205.8 (64.14)	0.0 (0.00)	88.2 (27.49)	29.4 (9.16)	29.4 (9.16)	58.8 (18.33)	734.8 (228.95)
2017	125.3 (35.40)	89.8 (25.44)	125.7 (35.62)	161.7 (45.79)	53.9 (15.27)	125.7 (35.62)	18.0 (5.09)	53.9 (15.27)	53.9 (15.27)	53.9 (15.27)	861.7 (244.02)
2018	167.2 (48.64)	83.9 (24.45)	167.8 (48.90)	272.7 (79.47)	188.8 (55.01)	62.9 (18.34)	0.0 (0.00)	42.0 (12.23)	62.9 (18.34)	0.0 (0.00)	1,048.2 (305.37)
2019	104.0 (29.44)	104.4 (29.58)	313.2 (88.74)	261.0 (73.95)	130.5 (36.97)	52.2 (14.79)	104.4 (29.58)	78.3 (22.19)	52.2 (14.79)	78.3 (22.19)	1,278.7 (362.20)
2020	97.0 (28.18)	97.3 (28.31)	311.5 (90.58)	194.7 (56.62)	97.3 (28.31)	155.8 (45.29)	58.4 (16.98)	116.8 (33.97)	19.5 (5.66)	38.9 (11.32)	1,187.3 (345.23)
2021	133.1 (42.42)	213.7 (68.12)	240.4 (76.64)	320.6 (102.19)	187.0 (59.61)	0.0 (0.00)	80.1 (25.55)	133.6 (42.58)	26.7 (8.52)	80.1 (25.55)	1,415.3 (451.16)
2022	198.1 (70.02)	397.6 (140.52)	318.1 (112.42)	318.1 (112.42)	238.6 (84.31)	198.8 (70.26)	39.8 (14.05)	119.3 (42.16)	79.5 (28.10)	39.8 (14.05)	1,947.6 (688.31)
2023	103.2 (37.92)	258.9 (95.09)	258.9 (95.09)	233.0 (85.58)	284.8 (104.60)	77.7 (28.53)	103.6 (38.04)	51.8 (19.02)	51.8 (19.02)	129.5 (47.55)	1,553.1 (570.44)

Table 22. Female survival estimates for each age class per year. (One standard error).

Year	Age 0	Age 1+
2014	0.9051 (0.0280)	0.8857 (0.0269)
2015	0.9268 (0.0201)	0.9069 (0.0219)
2016	0.9428 (0.0153)	0.9225 (0.0198)
2017	0.9140 (0.0221)	0.8944 (0.0241)
2018	0.9216 (0.0204)	0.9019 (0.0238)
2019	0.9320 (0.0165)	0.9120 (0.0220)
2020	0.9021 (0.0257)	0.8827 (0.0289)
2021	0.9278 (0.0200)	0.9079 (0.0255)
2022	0.9376 (0.0191)	0.9174 (0.0255)
2023	0.9106 (0.0298)	0.8911 (0.0344)

Table 23. Combined abundance estimates for both males and females per year. (One standard error).

Year	Combined Abundance
2014	907.5 (188.65)
2015	991.0 (207.19)
2016	1,280.1 (263.38)
2017	1,286.4 (268.28)
2018	1,535.7 (324.08)
2019	1,695.1 (370.63)
2020	1,667.3 (355.85)
2021	1,836.4 (467.73)
2022	2,393.4 (710.93)
2023	1,899.1 (608.03)

Appendix A – Dispersal, migration, and other interesting movement maps

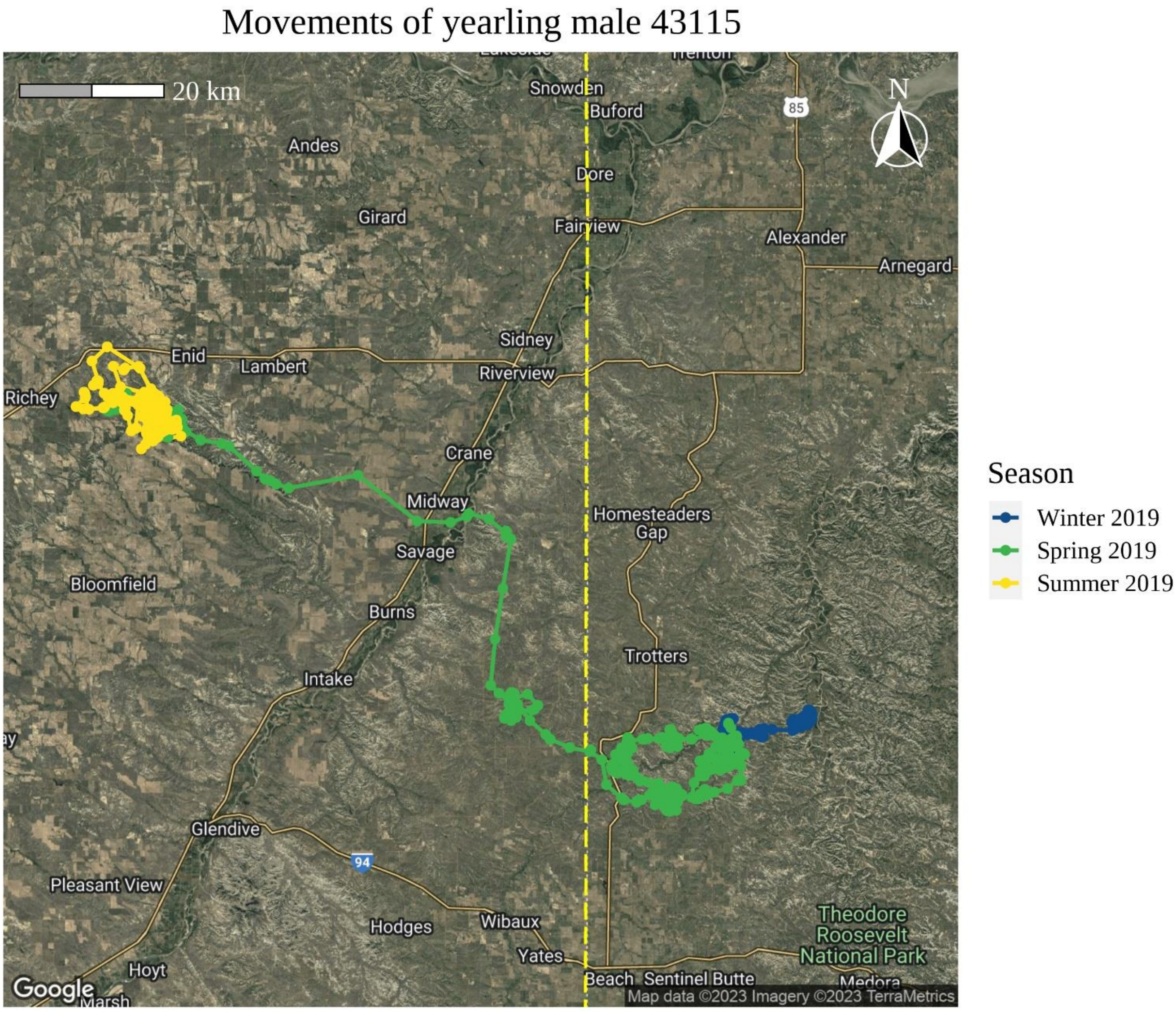


Figure A1. Movements of male 43115, collared as a yearling in 2019 within the Belle Lake/Tommy O herd. This elk spent all of winter 2019 in North Dakota and then moved into Montana on May 11, 2019. He remained in his new range until his collar stopped transmitting on July 20, 2019. It is possible this elk remained in Montana, because he was legally harvested in Montana in October 2022 as a 5-year-old.

Movements of yearling male 48841

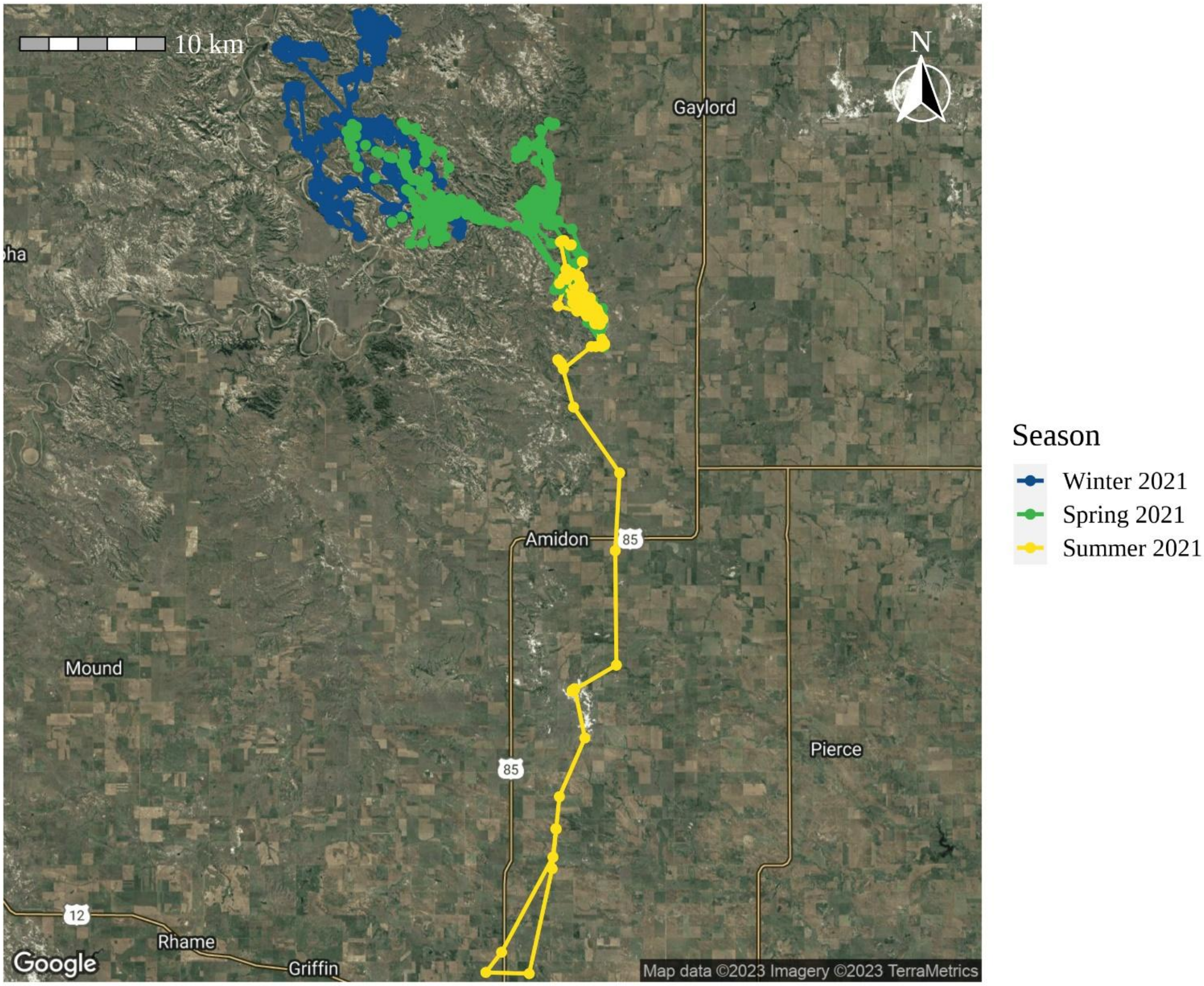


Figure A2. Movements of male 48841, collared as a yearling in 2021 within the Devil's Slide herd. This elk spent all of winter and spring 2021 within the Devil's Slide herd, then started making a dispersal movement on June 12, 2021. Unfortunately, his collar fell off prematurely on June 14, 2021, so there we do not know where this elk ended up post-dispersal.

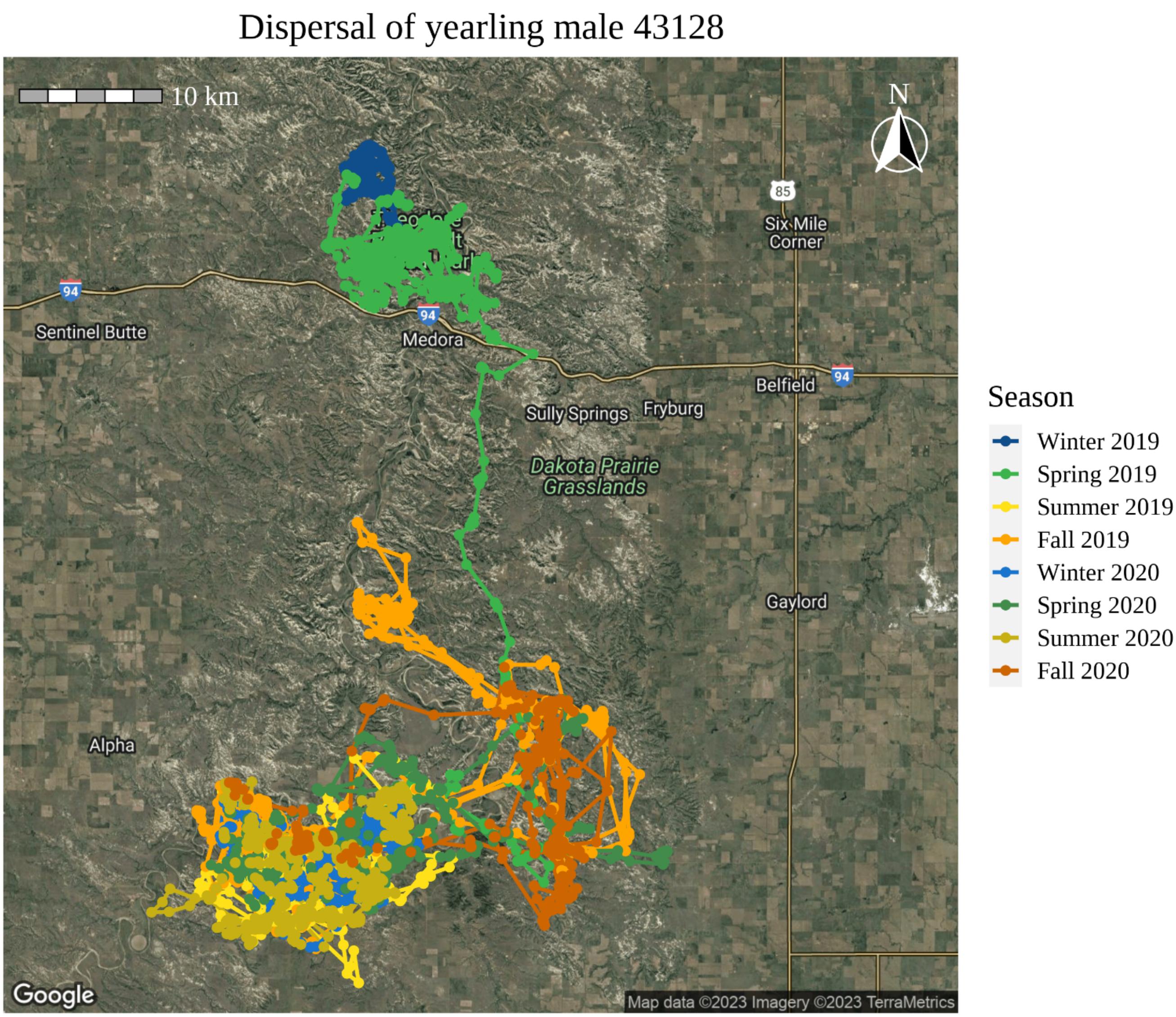


Figure A3. Dispersal of male 43128, caught as a yearling in 2019 within the SUTRNP herd. This elk started dispersing on May 19, 2019, and moved to the Devil's Slide herd, where he stayed until he was legally harvested on October 10, 2020.

Movements of yearling male 43111A

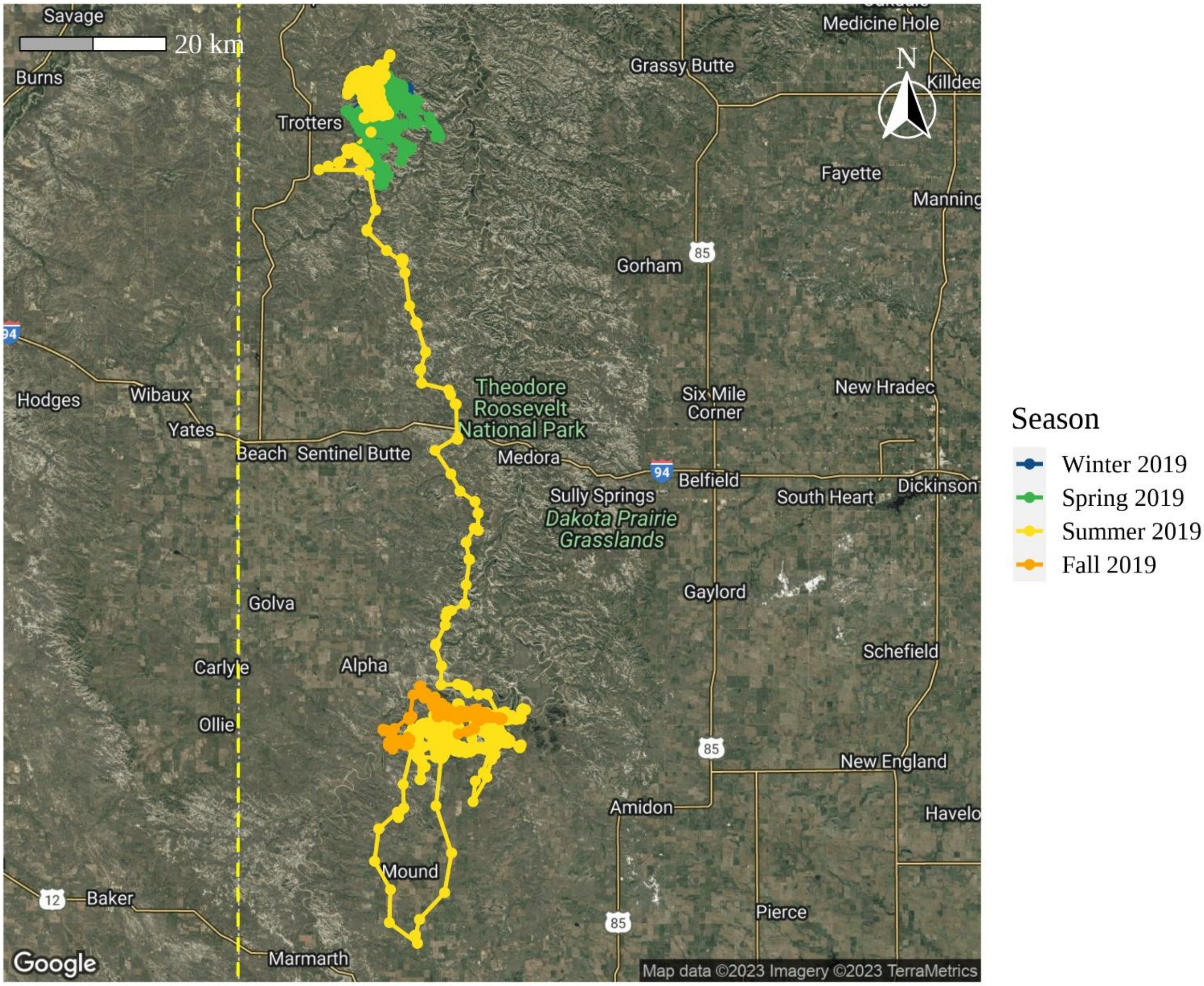


Figure A4. Movements of male 43111A, collared as a yearling in 2019 within the Elkhorn herd. This elk spent all of winter and spring 2019 within the Elkhorn herd before moving south on June 24, 2019. He remained in his new range until his collar was removed on September 27, 2019.

Movements of yearling male 43112A

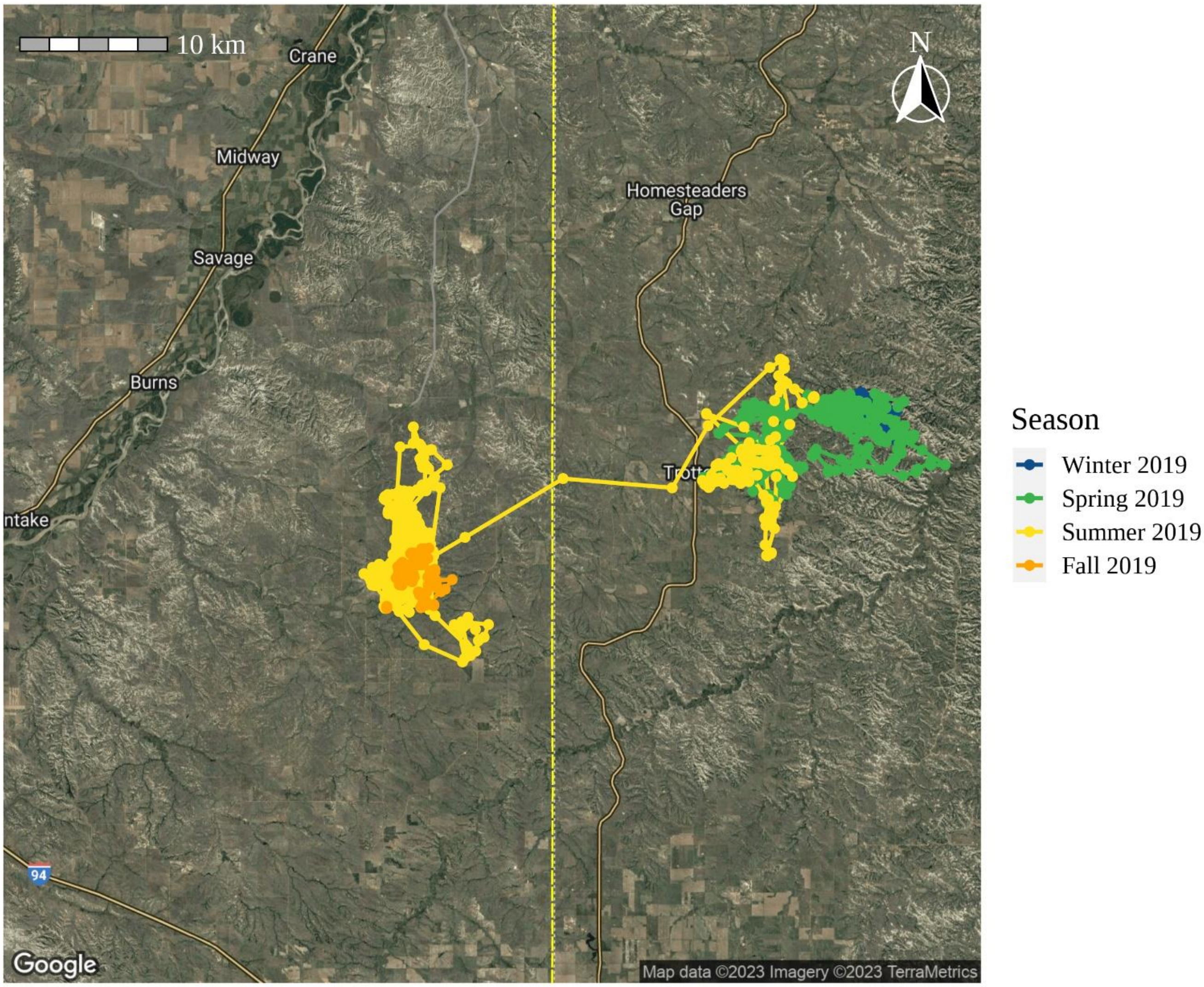


Figure A5. Movements of male 43112A, caught as a yearling in 2019 within the Elkhorn herd. This elk spent winter and spring 2019 in North Dakota, then moved west to Montana on June 17, 2019. He lived in Montana until his collar was removed on September 24, 2019.

Movements of male 43123

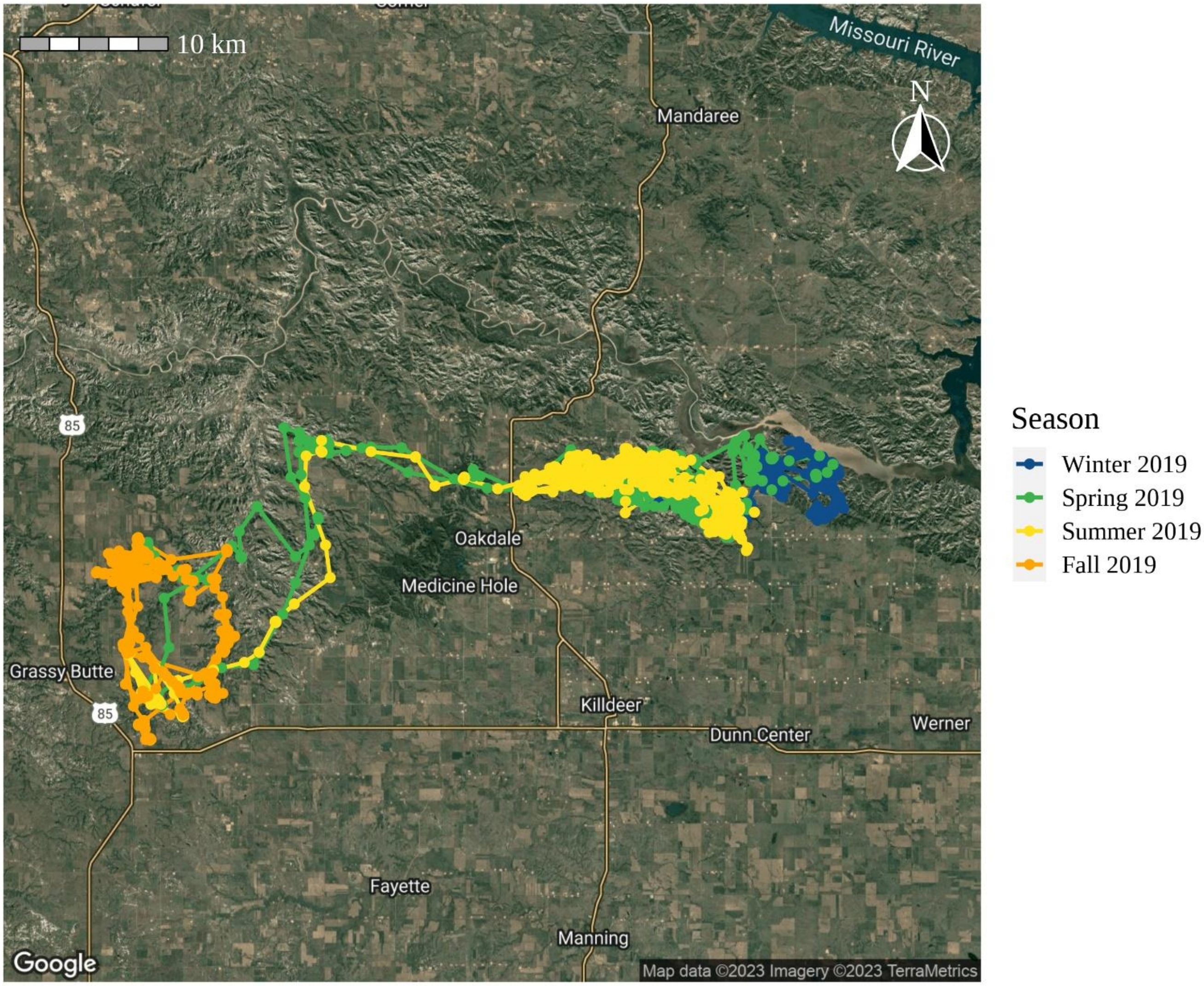


Figure A6. Movements of male 43123, caught as an adult in 2019. This elk spent winter 2019 where he was caught within the Chimney Butte herd, then moved back and forth between an area further west during spring and summer 2019. He spent fall 2019 near Grassy Butte until his collar stopped transmitting on October 7, 2019.

Movements of yearling male 43125

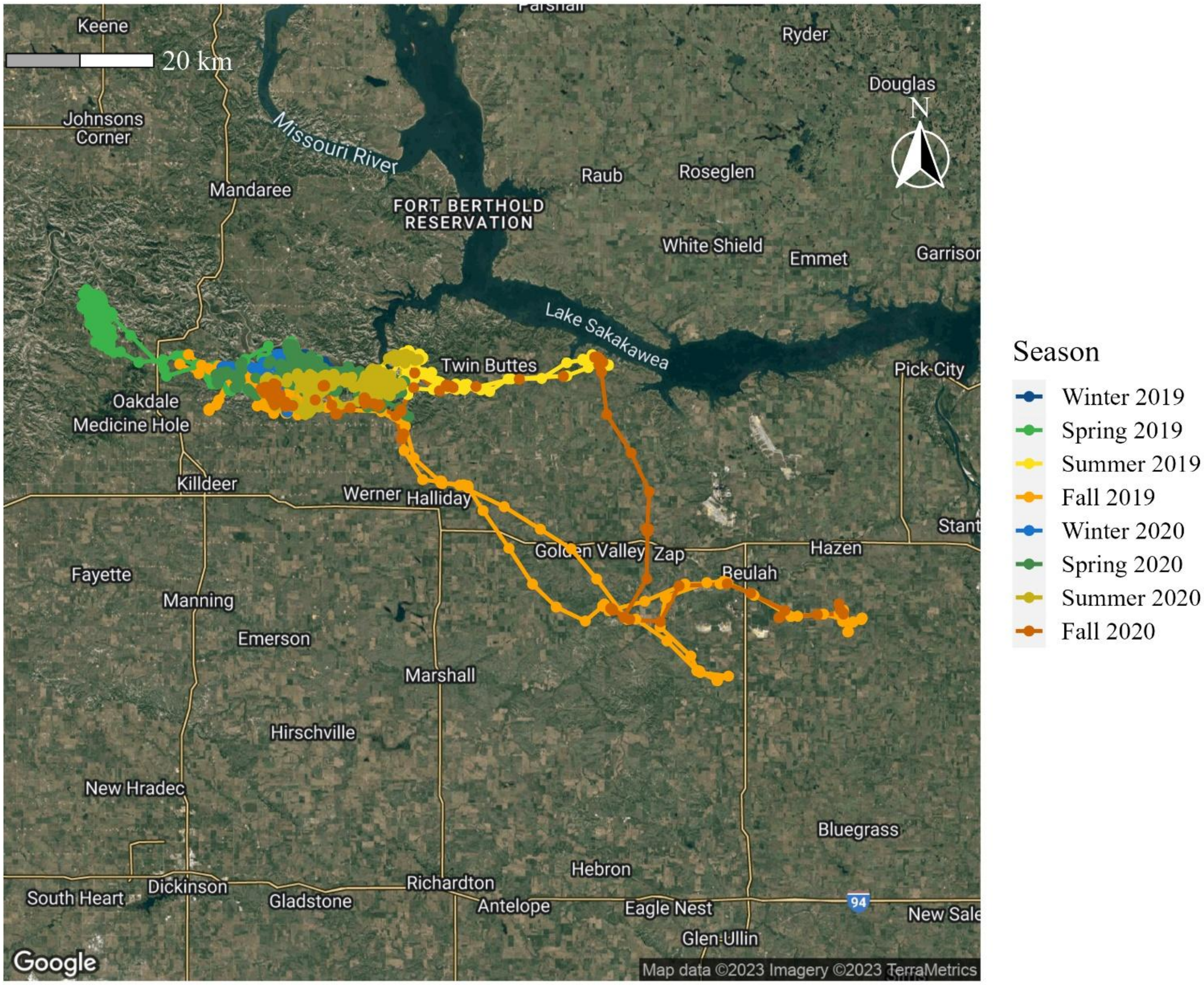


Figure A7. Movements of male 43125, caught as a yearling in 2019. This elk primarily remained within the State Park herd range, but in fall 2019 and fall 2020 he moved further east. In fall 2019, he left on September 14, 2019, and returned to the herd on October 1, 2019. In fall 2020, he left on September 8, 2020, and was harvested adjacent to the captive elk farm south of Hazen on September 16, 2020.

Dispersal of yearling male 43122

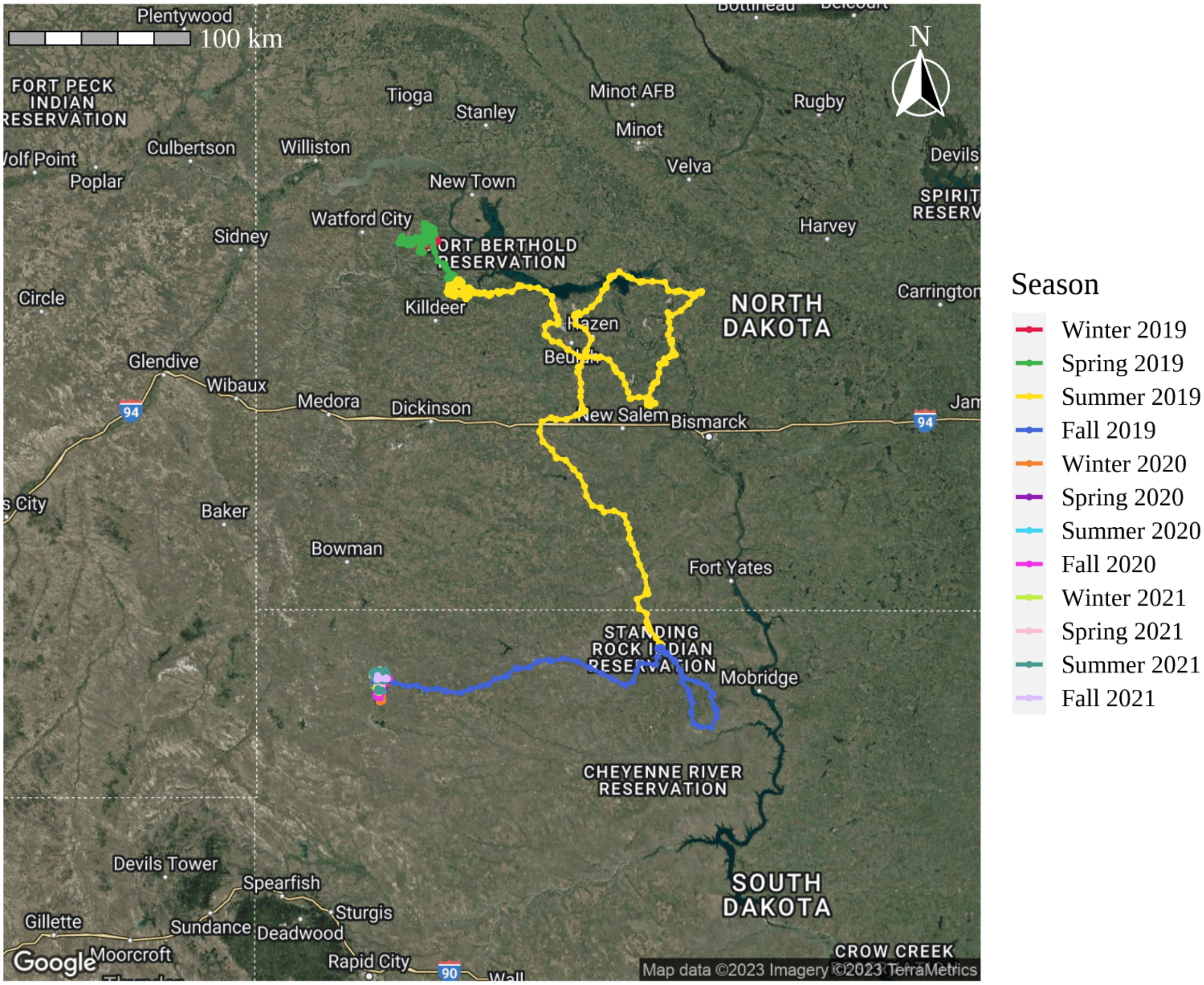


Figure A8. Dispersal of male 43122 caught as yearling in 2019 within the Reservation herd. On May 26, 2019, this elk moved to south of the Little Missouri River, where he remained until July 28, 2019. For the remainder of the summer, he moved further east and south until crossing into South Dakota on August 25, 2019, and then headed west. On September 25, 2019, he reached his new home range where a small herd of elk reside near Reva (Slim Buttes), South Dakota. He remained in this area until his collar fell off on September 1, 2021. This elk dispersed 150 miles (straight line distance) from his capture location and walked approximately 550 miles in 122 days.

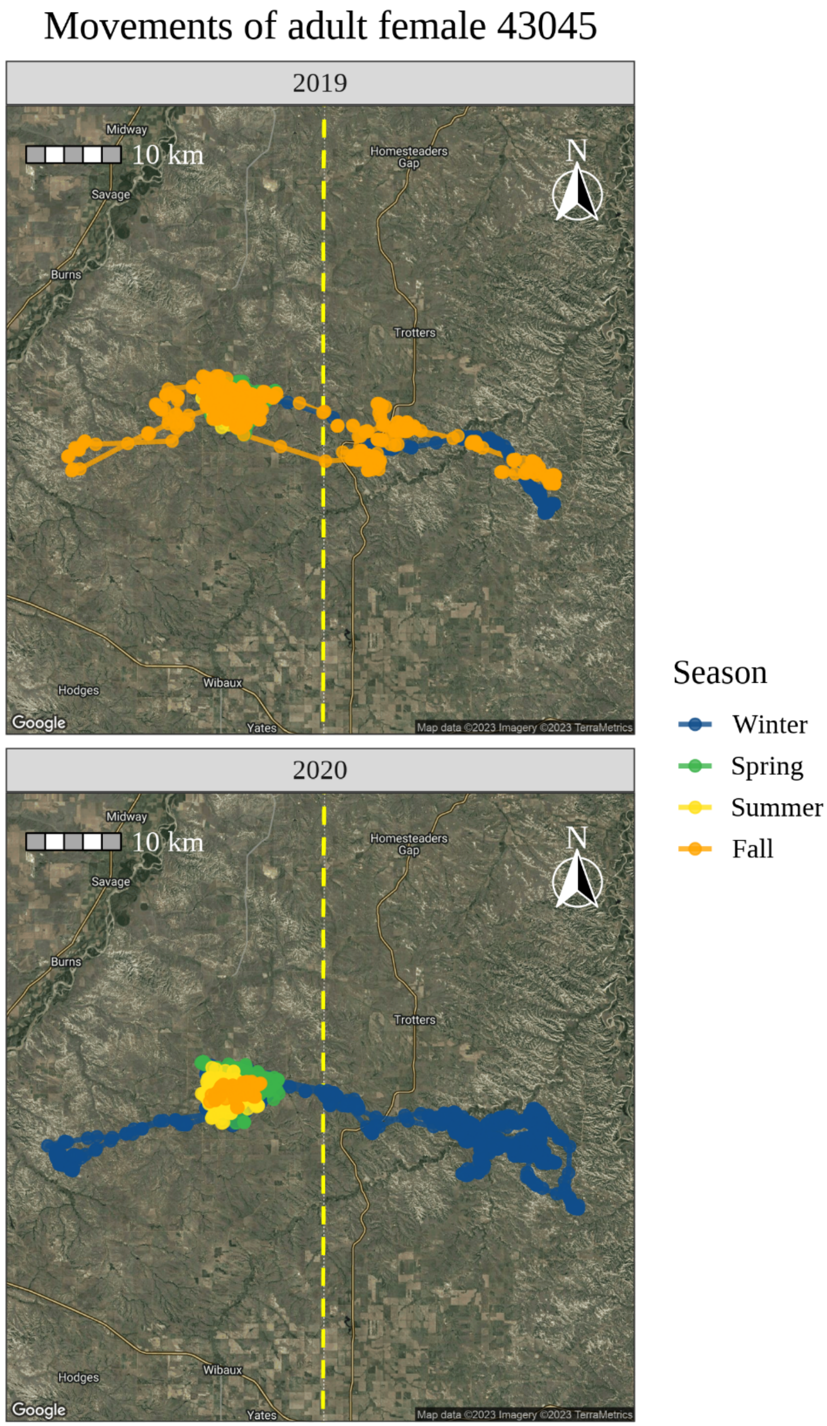


Figure A9. Movements of adult female elk 43045. This elk moved from North Dakota to Montana in winter 2019 and then spent spring and summer 20219 in Montana. She moved back and forth between Montana and North Dakota in fall 2019 and winter 2020, before spending spring, summer, and the start of fall 2020 in Montana. Her collar stopped transmitting on Sept 16, 2020, while in Montana.

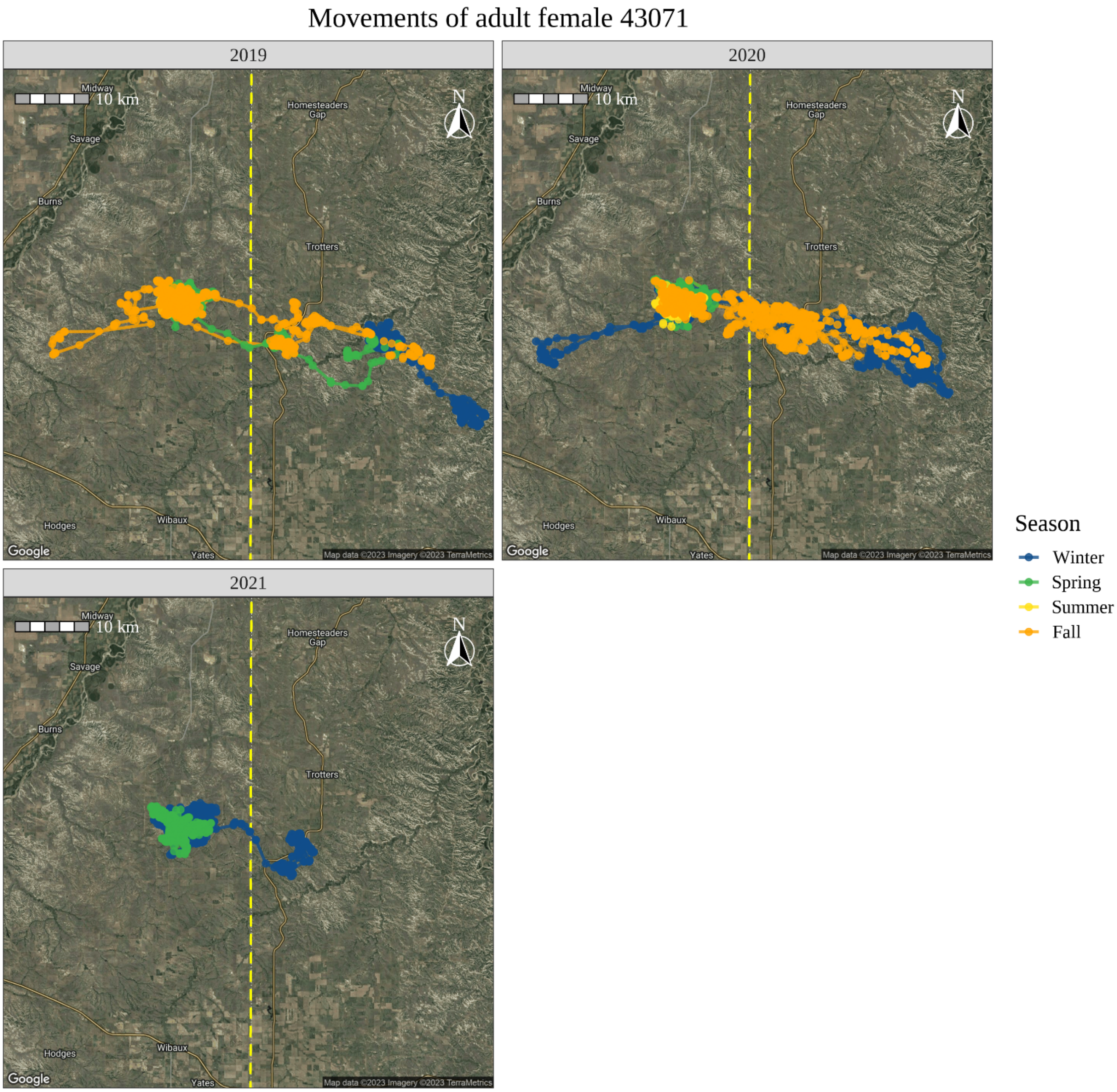


Figure A10. Movements of female elk 43071. This elk first moved from North Dakota to Montana in spring 2019, spent summer 2019 in Montana, then moved back and forth between North Dakota and Montana in fall 2019 and winter 2020. She spent spring and summer 2020 in Montana, then again spent fall 2020 and winter 2021 moving back and forth between Montana and North Dakota. Her collar stopped transmitting locations May 12, 2021, while in Montana.

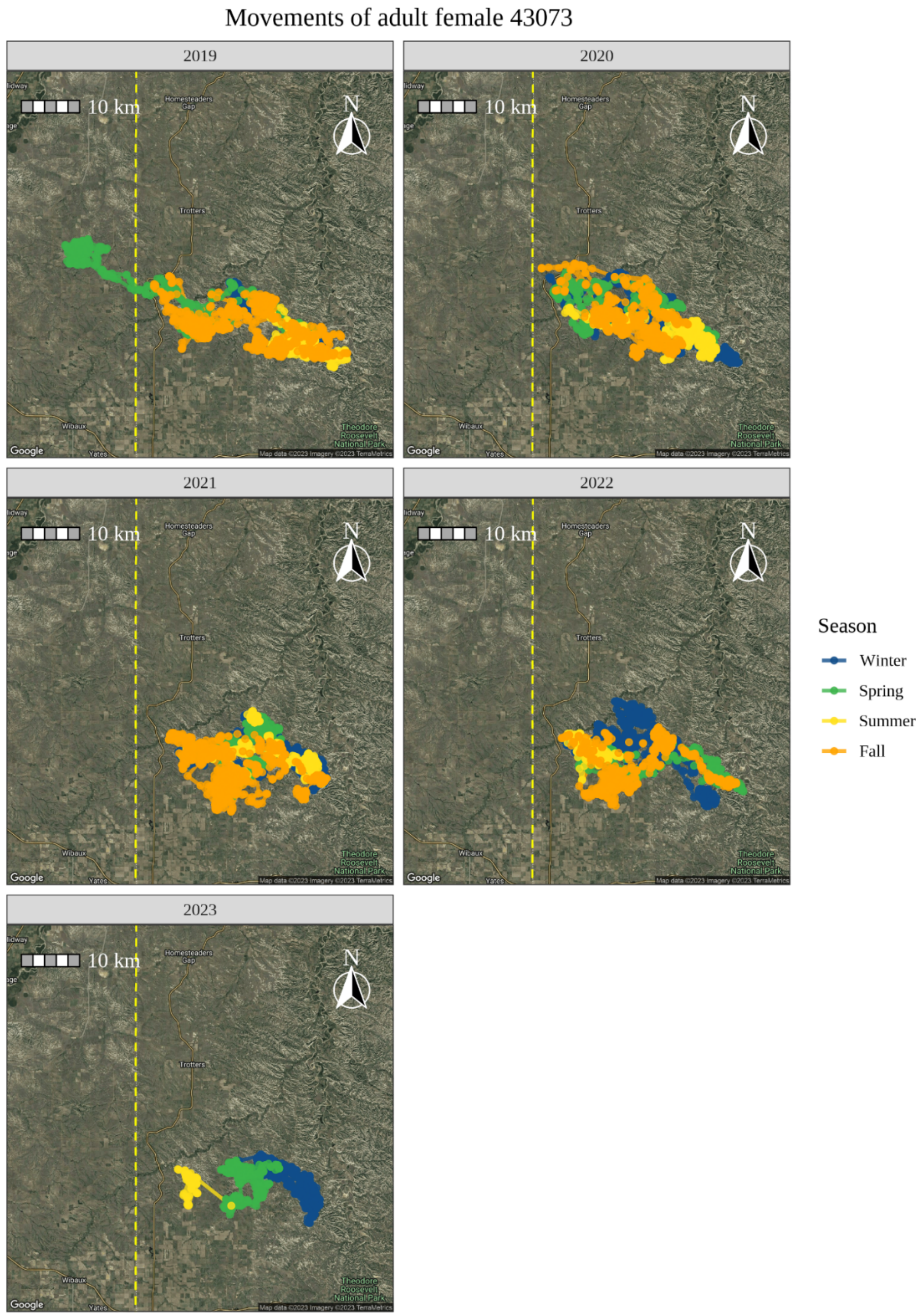


Figure A11. Movements of female elk 43073. This elk only moved into Montana during spring 2019, but otherwise spent the rest of the time it was collared in North Dakota.

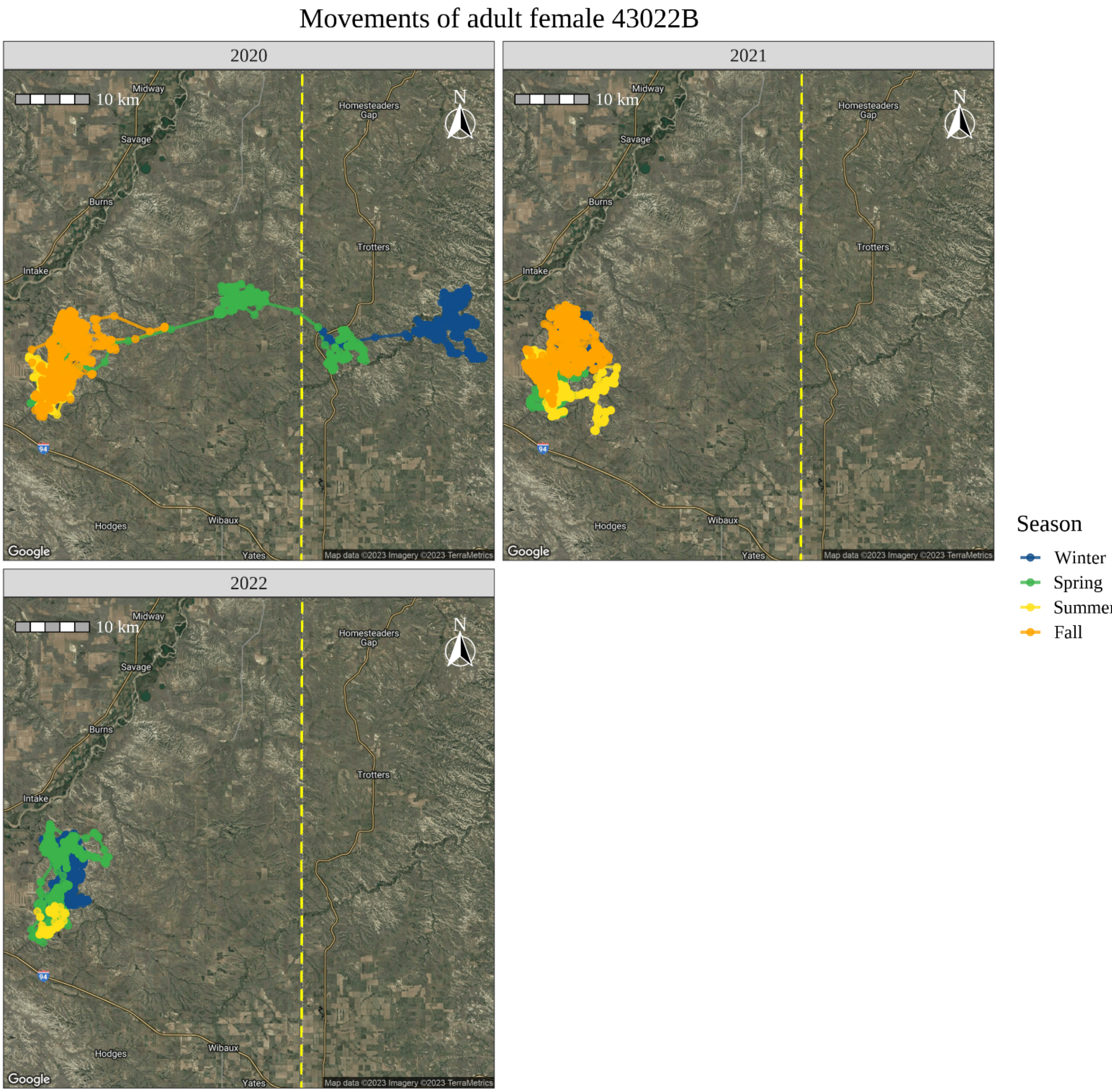


Figure A12. Movement of female elk 43022B. This elk spent winter 2020 in North Dakota, then moved to Montana in spring 2020 where she lived for the remaining time her collar was working (summer 2020 – summer 2022).

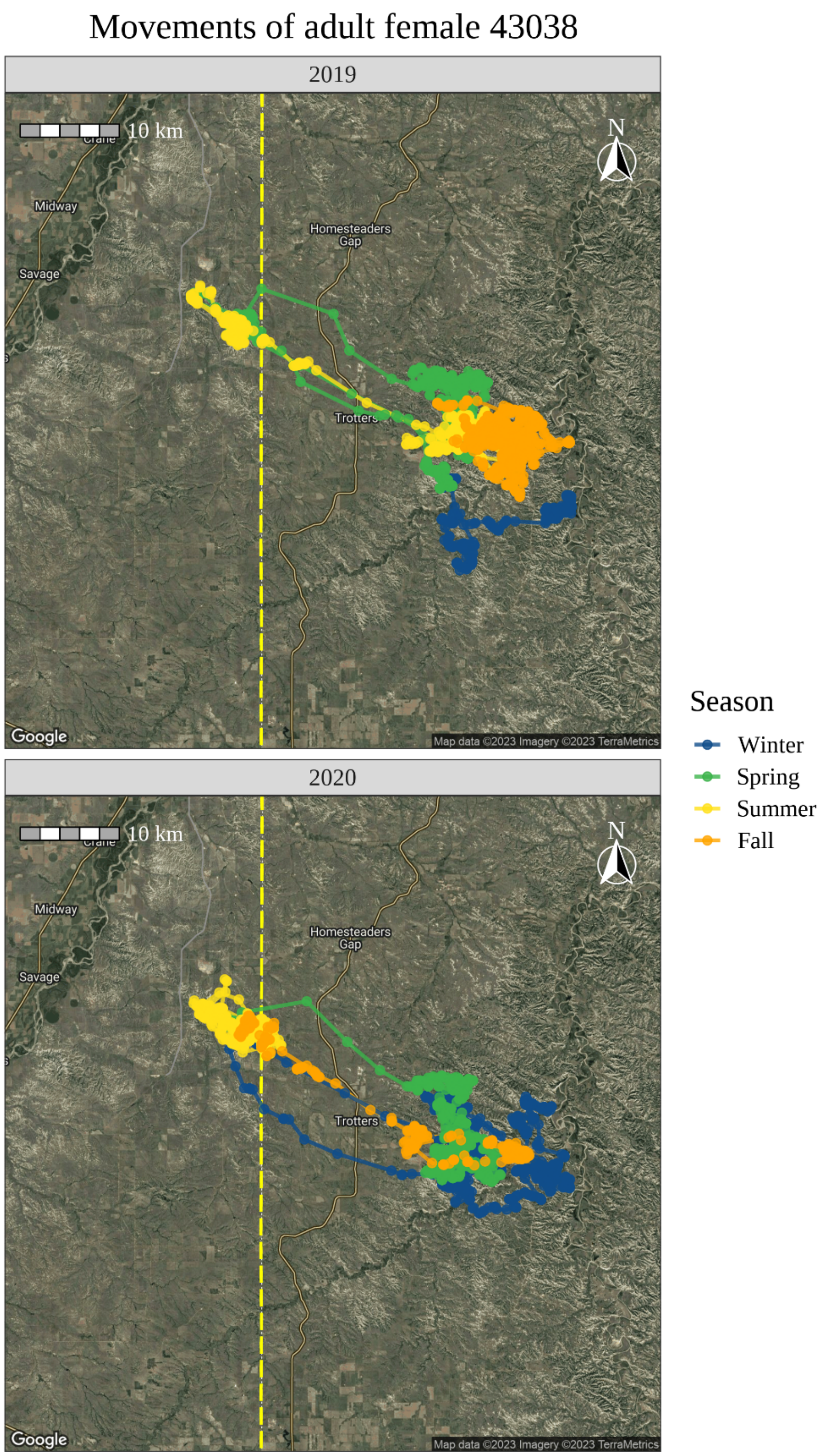


Figure A13. Movements of female elk 43038. This elk spent winter 2019 in North Dakota, then moved back and forth between North Dakota and Montana in spring and summer 2019. She spent the fall 2019 in North Dakota and then moved back and forth between North Dakota and Montana during all of 2020 until she died on October 16, 2020, from an unknown cause of mortality.

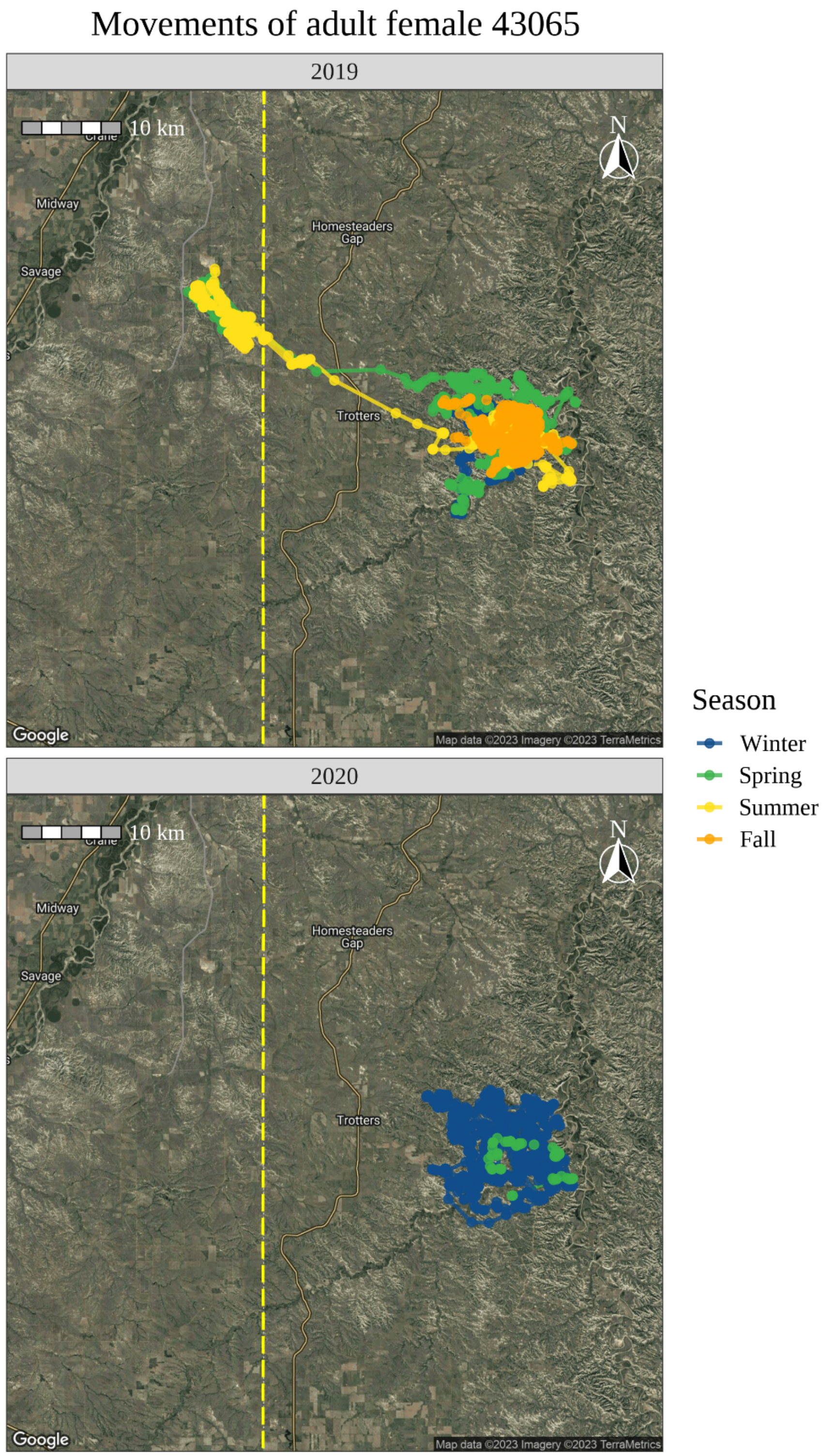


Figure A14. Movements of female elk 43065. This elk spent winter 2019 in North Dakota before moving to Montana in spring 2019 and returning to North Dakota during summer 2019. She then spent the rest of the time her collar was transmitting locations in North Dakota (September 1, 2019 – April 6, 2020).

Movements of adult female 43026

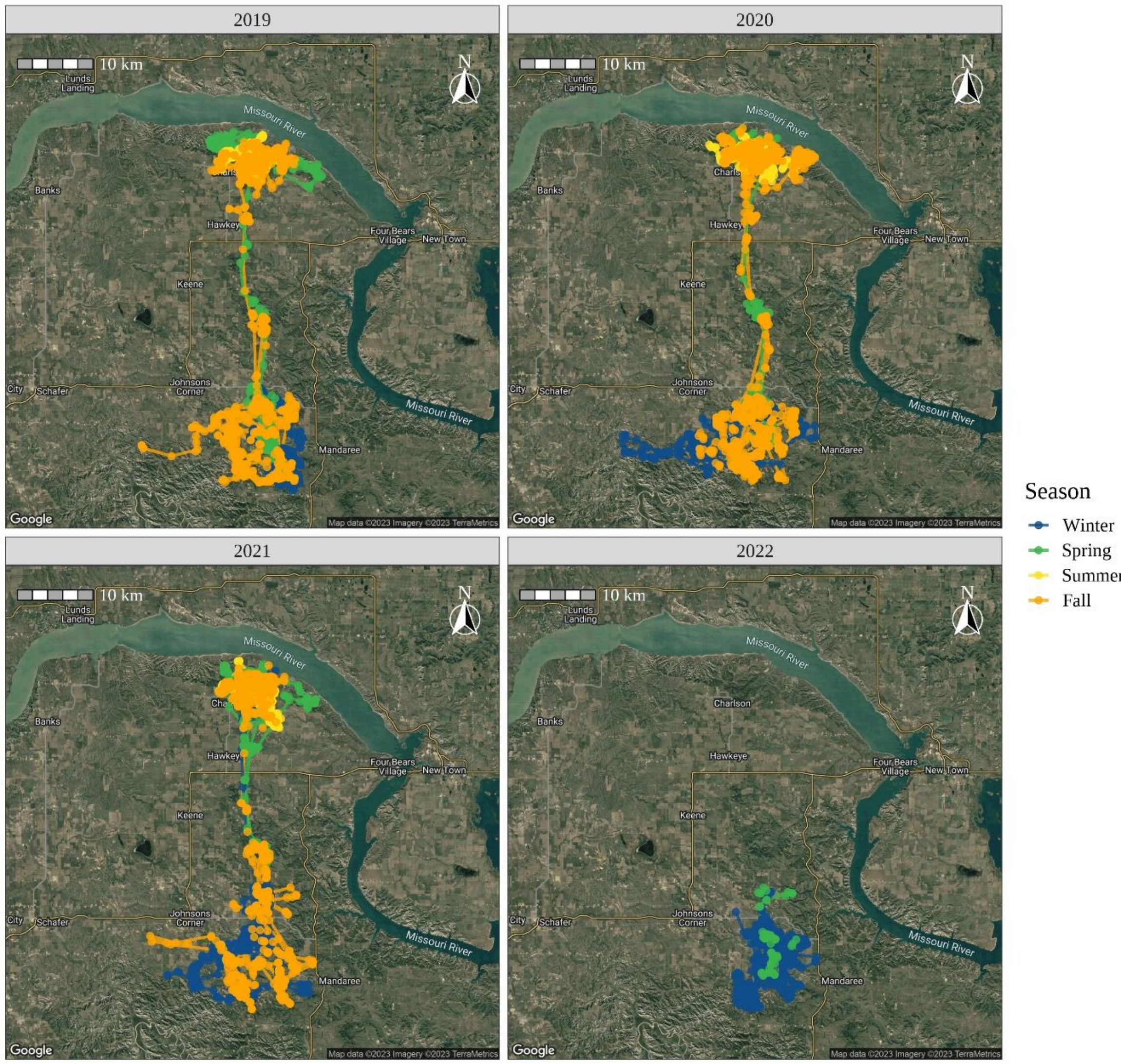


Figure A15. Movements of female elk 43026. This elk appears to be migratory, with distinct summer and winter ranges. She migrates north to an area close to the Missouri River in early April, then returns to her winter range in late October/early November each year.

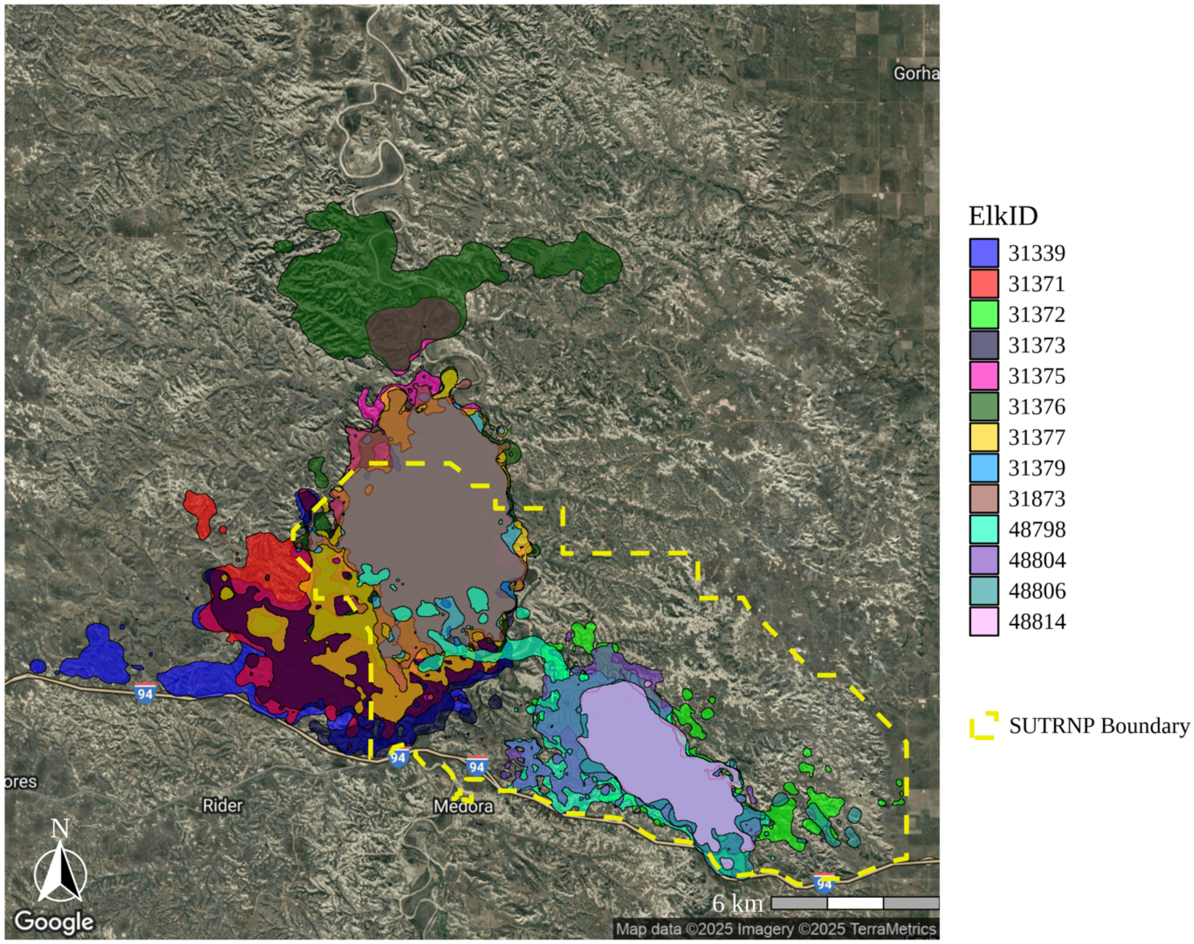


Figure A16. Annual home ranges of female elk in the SUTRNP herd. There is no overlap between elk in the west and east side of the herd, except for elk 48798.

Appendix B – Seasonal locations of elk caught within South Unit Theodore Roosevelt National Park

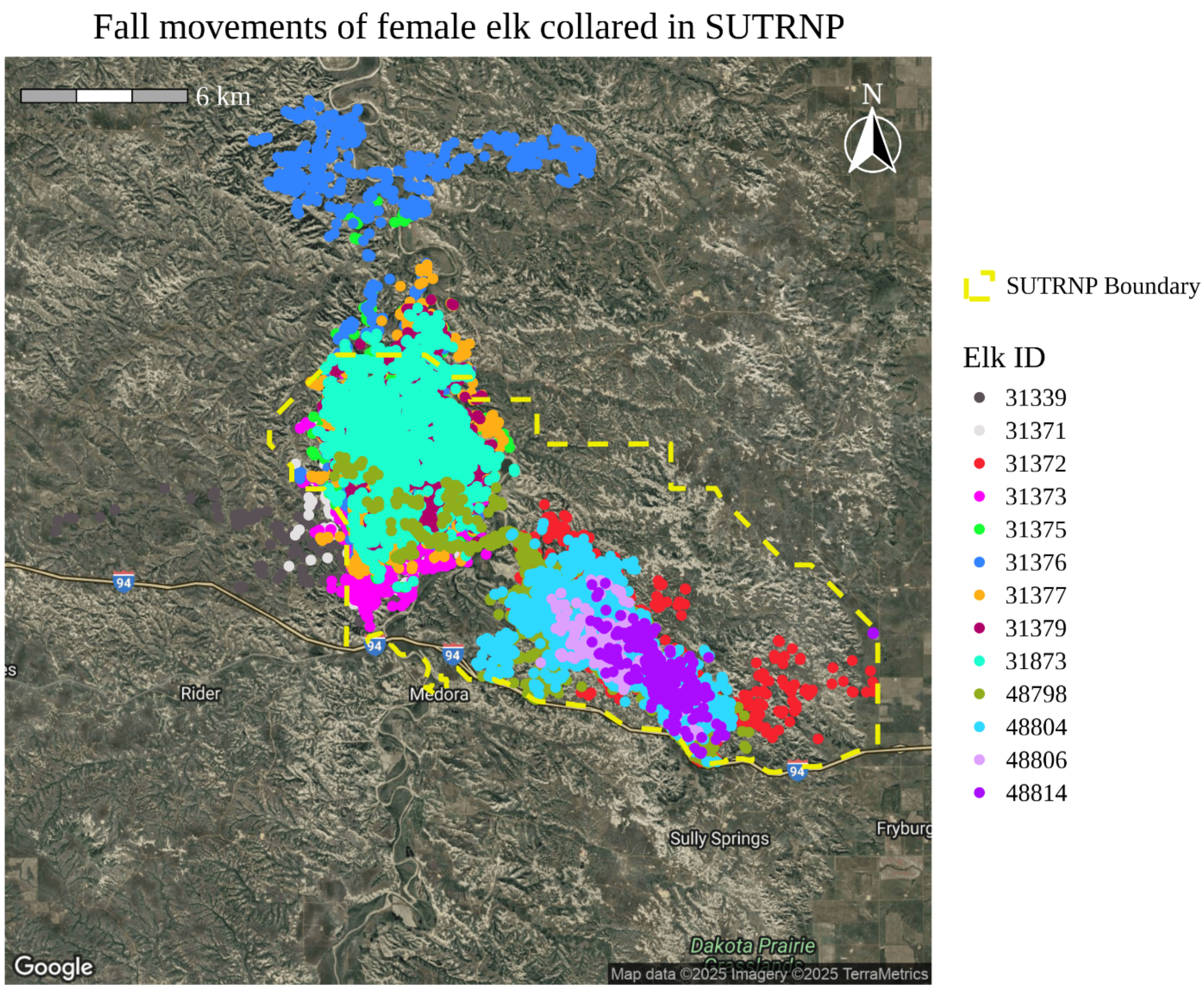


Figure B1. GPS collar locations of all female elk captured within the South Unit Theodore Roosevelt National Park during fall (September 1 – December 31) across all years (2019 – 2023).

Fall movements of male elk collared in SUTRNP

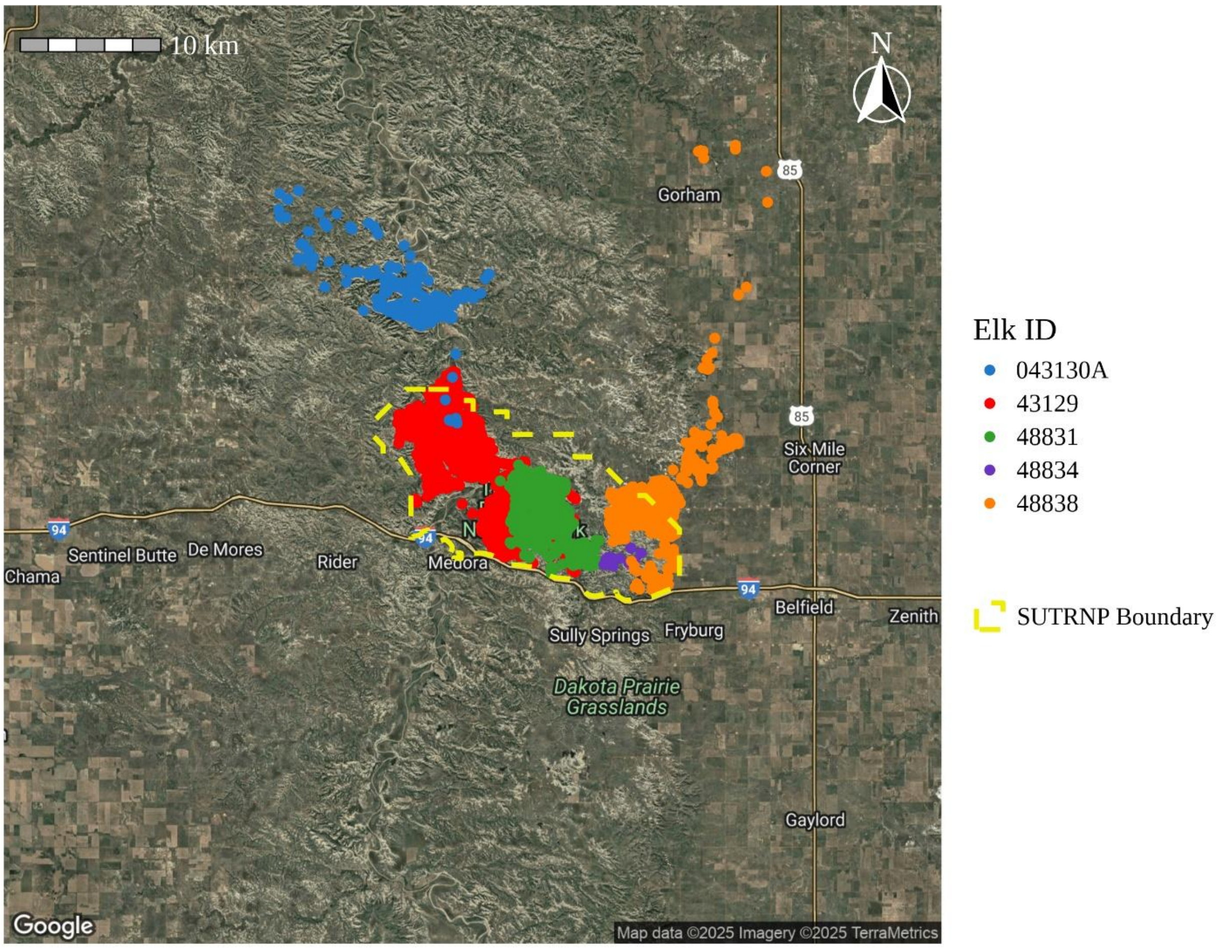


Figure B2. GPS collar locations of all male elk captured within South Unit Theodore Roosevelt National Park during fall (September 1 – December 31) across all years (2019 – 2023).

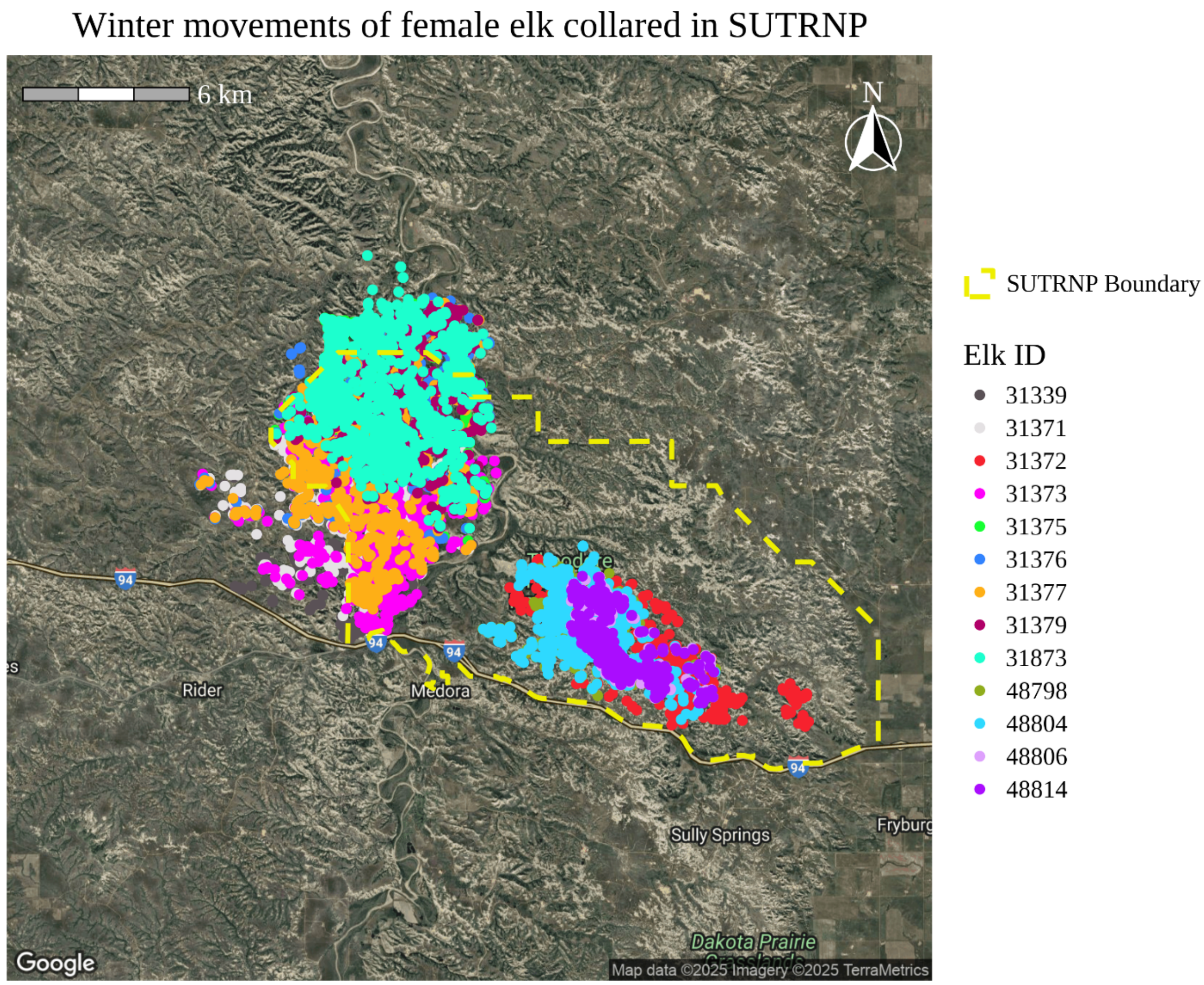


Figure B3. GPS collar locations of all female elk captured within South Unit Theodore Roosevelt National Park during winter (January 1 – March 31) across all years (2019 – 2023).

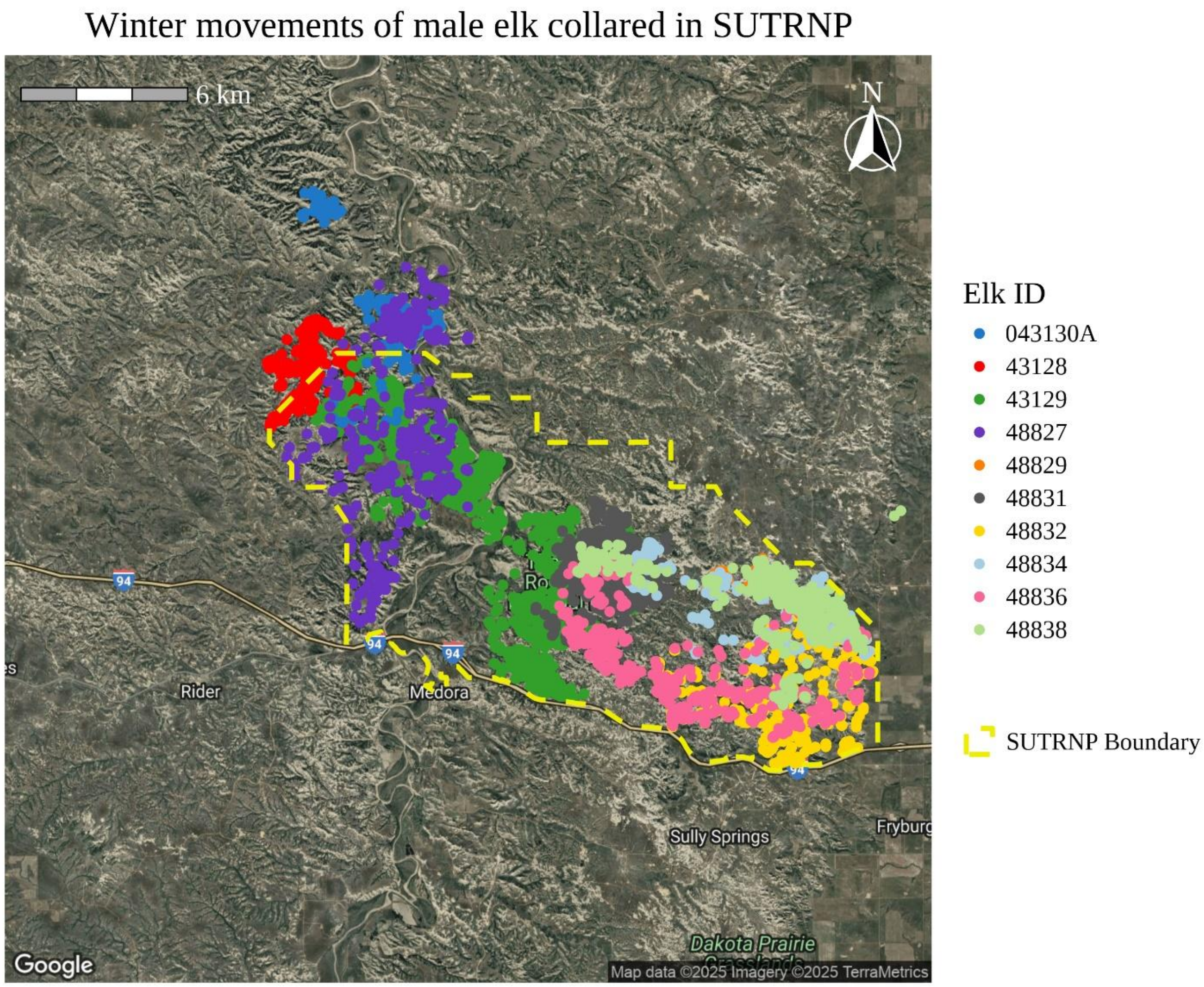


Figure B4. GPS collar locations of all male elk captured within South Unit Theodore Roosevelt National Park during winter (January 1 – March 31) across all years (2019 – 2023).

Spring movements of female elk collared in SUTRNP

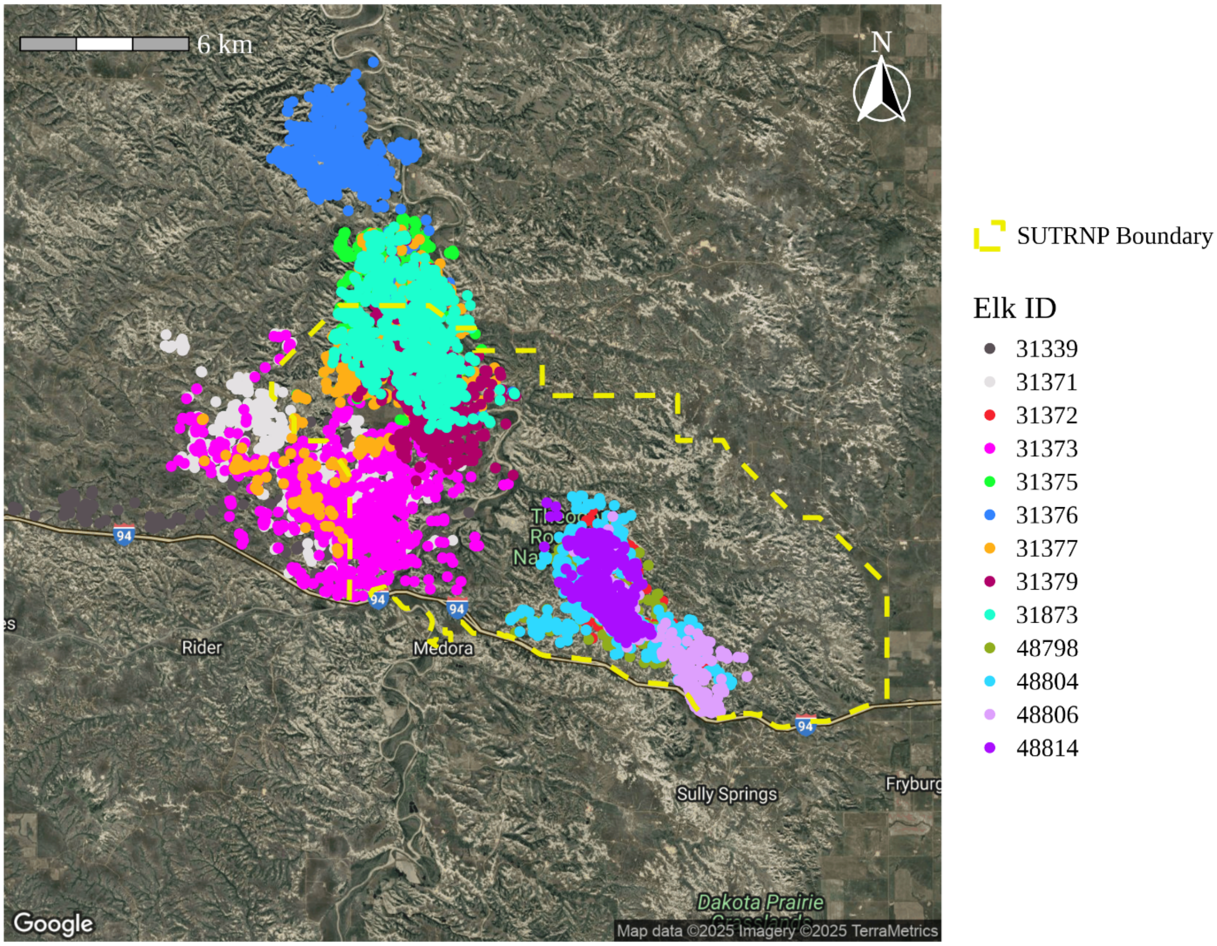


Figure B5. GPS collar locations of all female elk captured within South Unit Theodore Roosevelt National Park during spring (April 1 – May 31) across all years (2019 – 2023).

Spring movements of male elk collared in SUTRNP

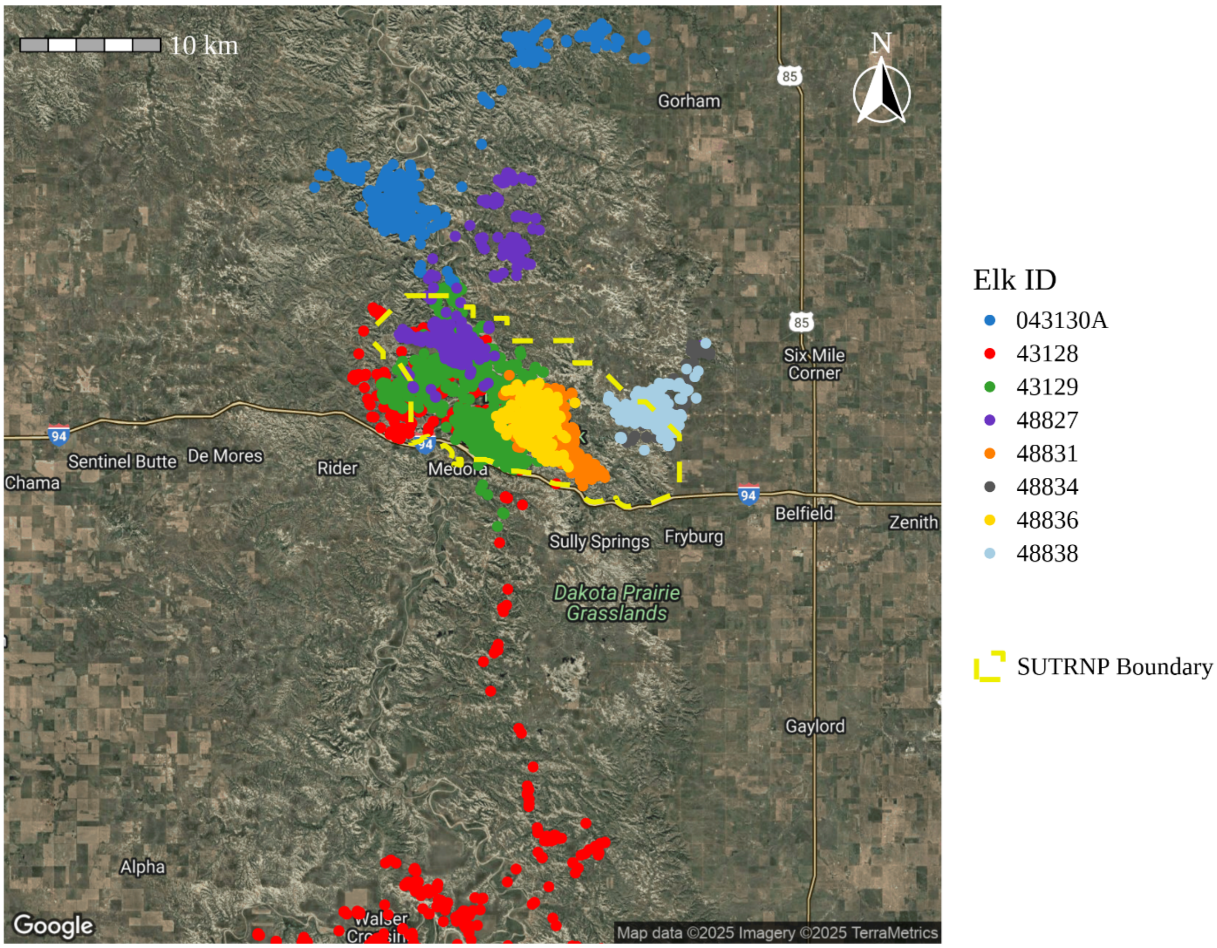


Figure B6. GPS collar locations of all male elk captured within South Unit Theodore Roosevelt National Park during spring (April 1 – May 31) across all years (2019 – 2023).

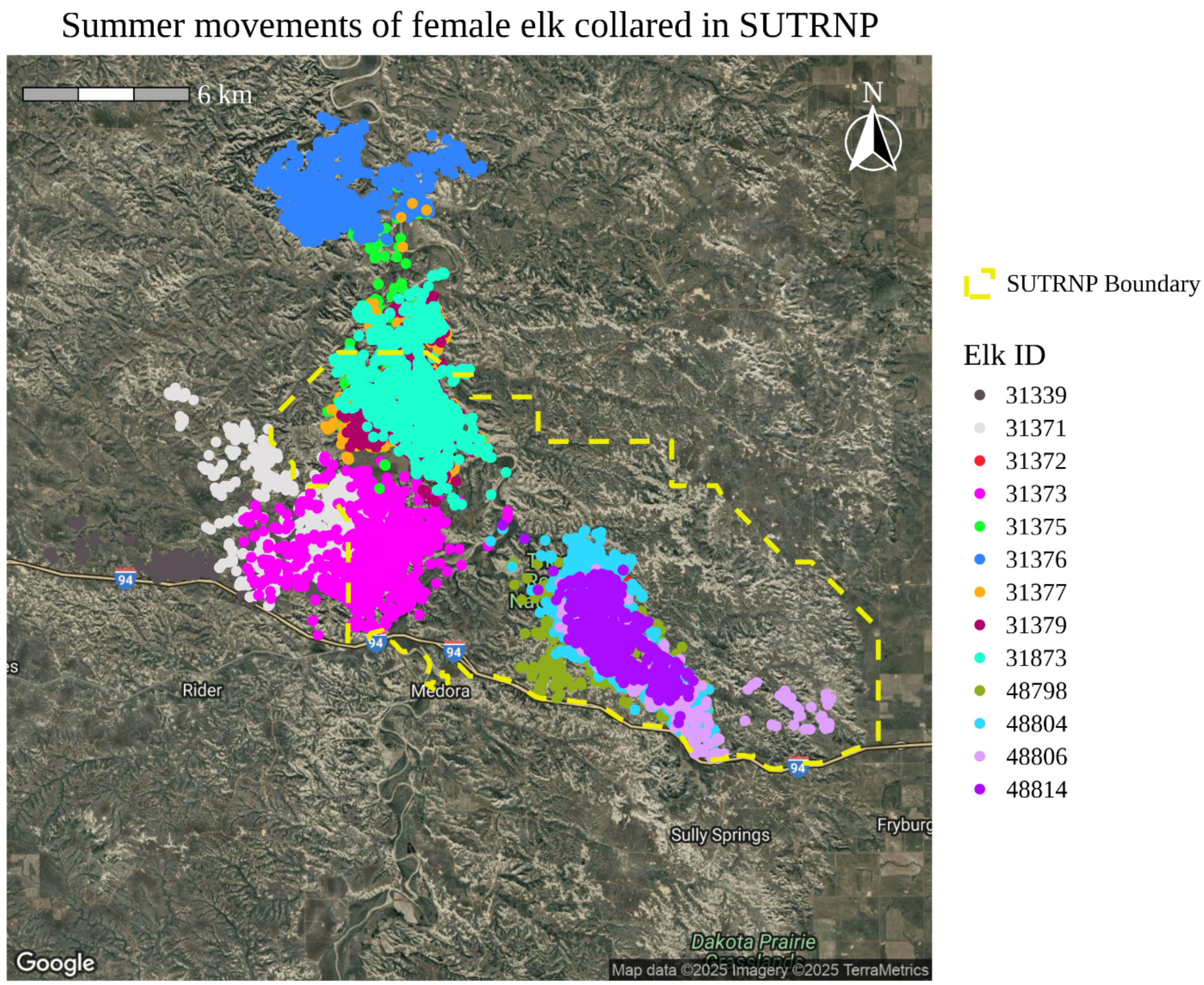


Figure B7. GPS collar locations of all female elk captured within South Unit Theodore Roosevelt National Park during summer (June 1 – August 31) across all years (2019 – 2023).

Summer movements of male elk collared in SUTRNP

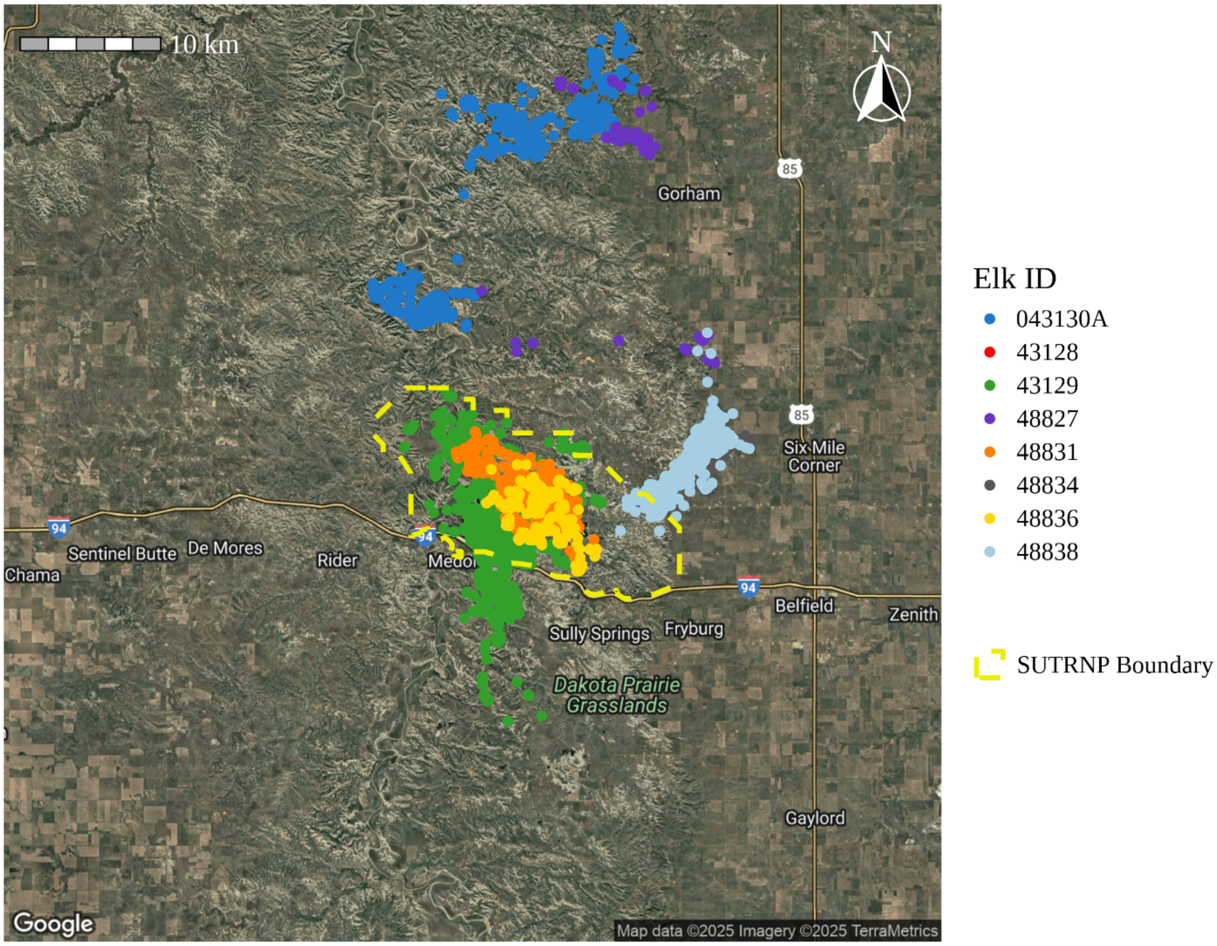


Figure B8. GPS collar locations of all male elk captured within South Unit Theodore Roosevelt National Park during summer (June 1 – August 31) across all years (2019 – 2023).

Appendix C – Herd range maps

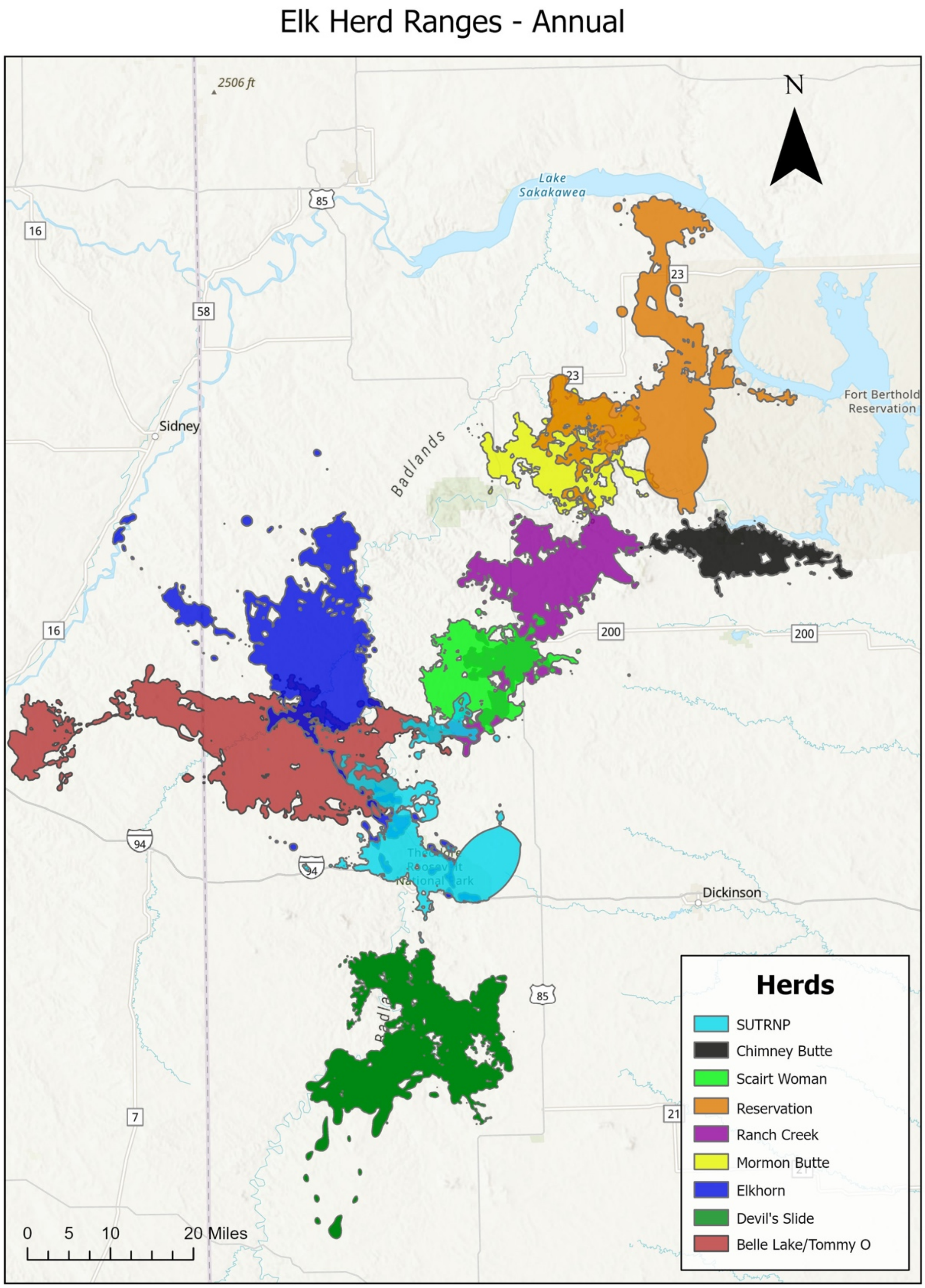


Figure C1. Annual herd ranges created using all GPS collared elk within each herd.

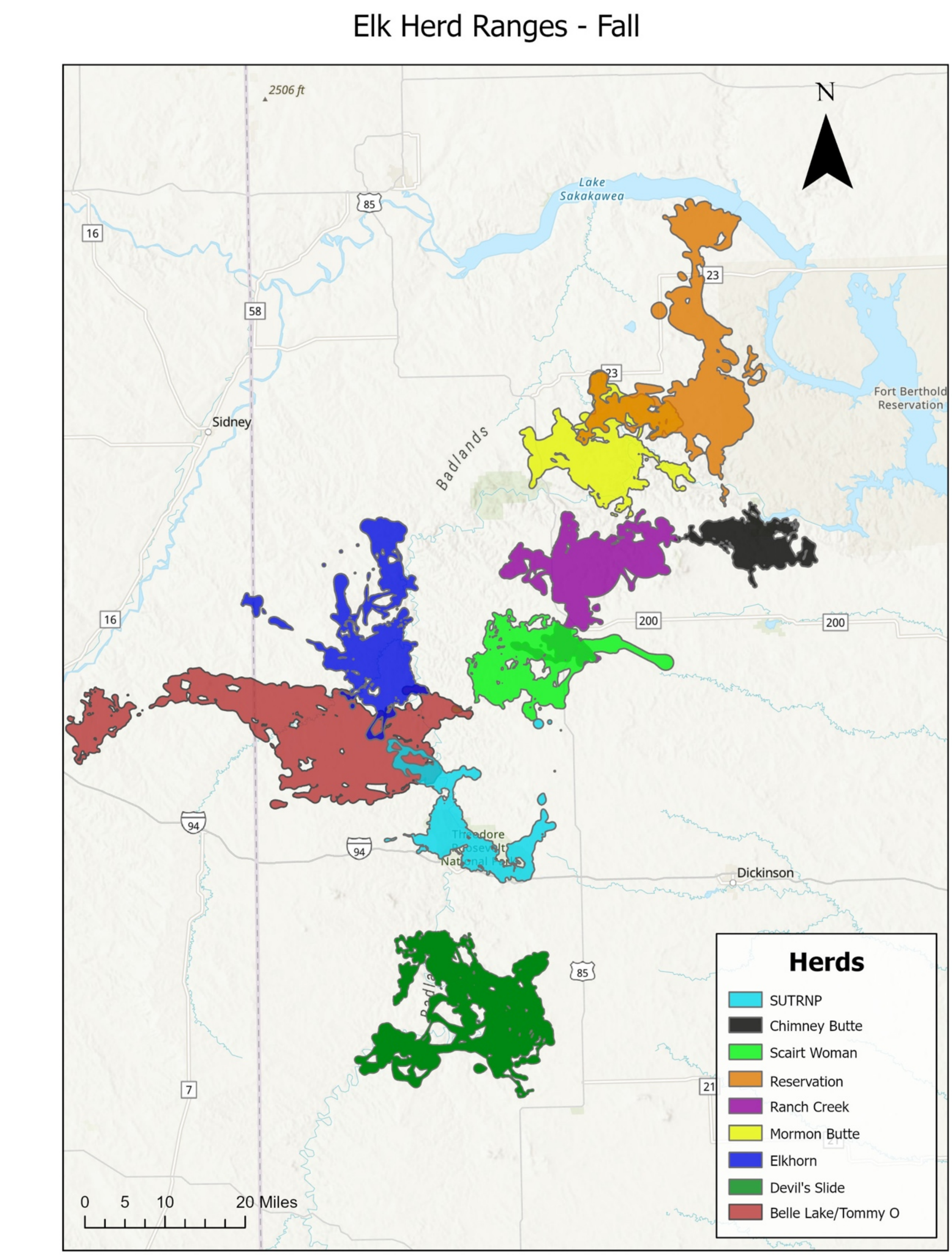


Figure C2. Herd ranges during the fall created using all GPS collared elk within each herd.

Elk Herd Ranges - Winter

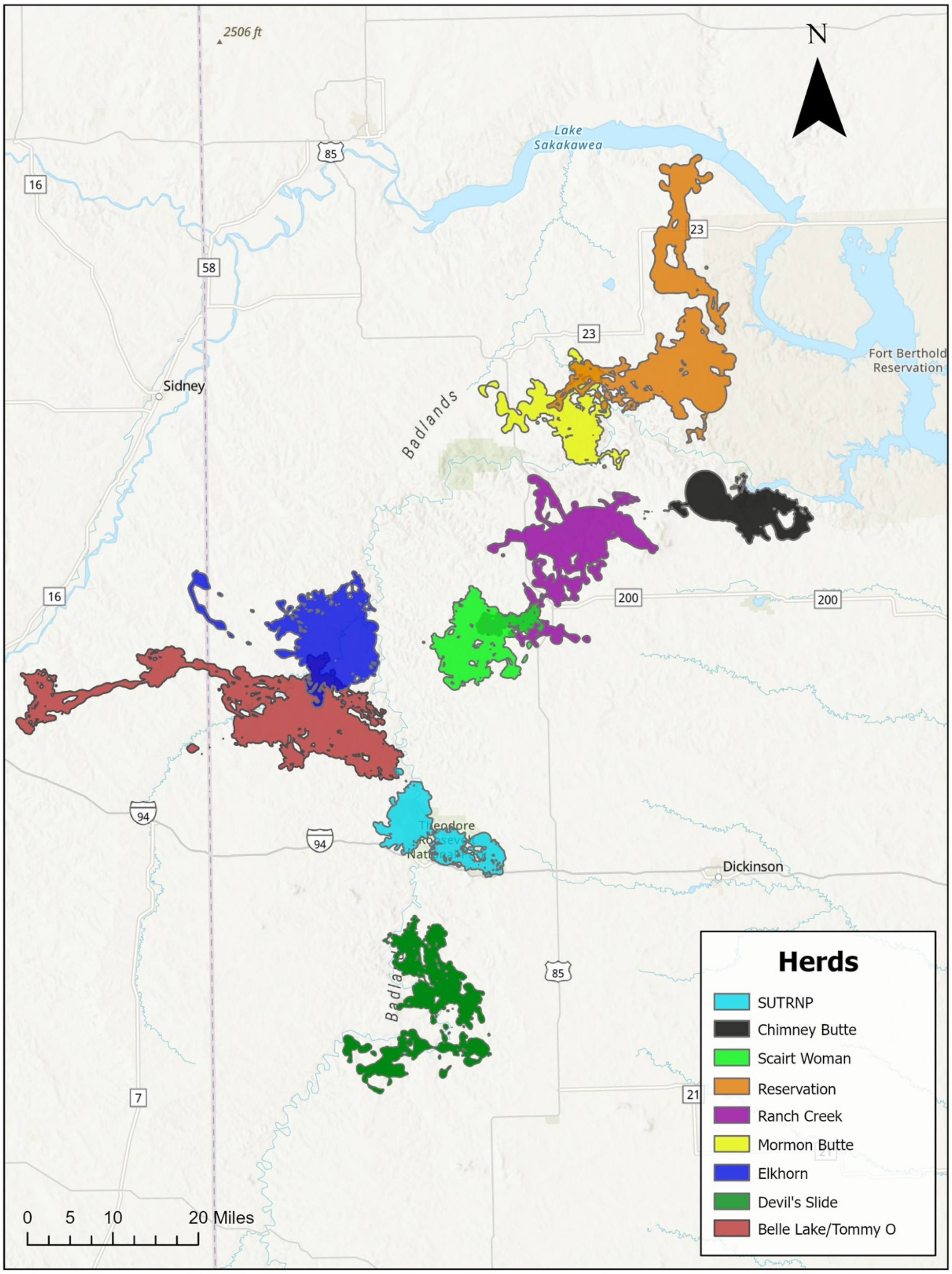


Figure C3. Herd ranges during the winter created using all GPS collared elk within each herd.

Elk Herd Ranges - Spring

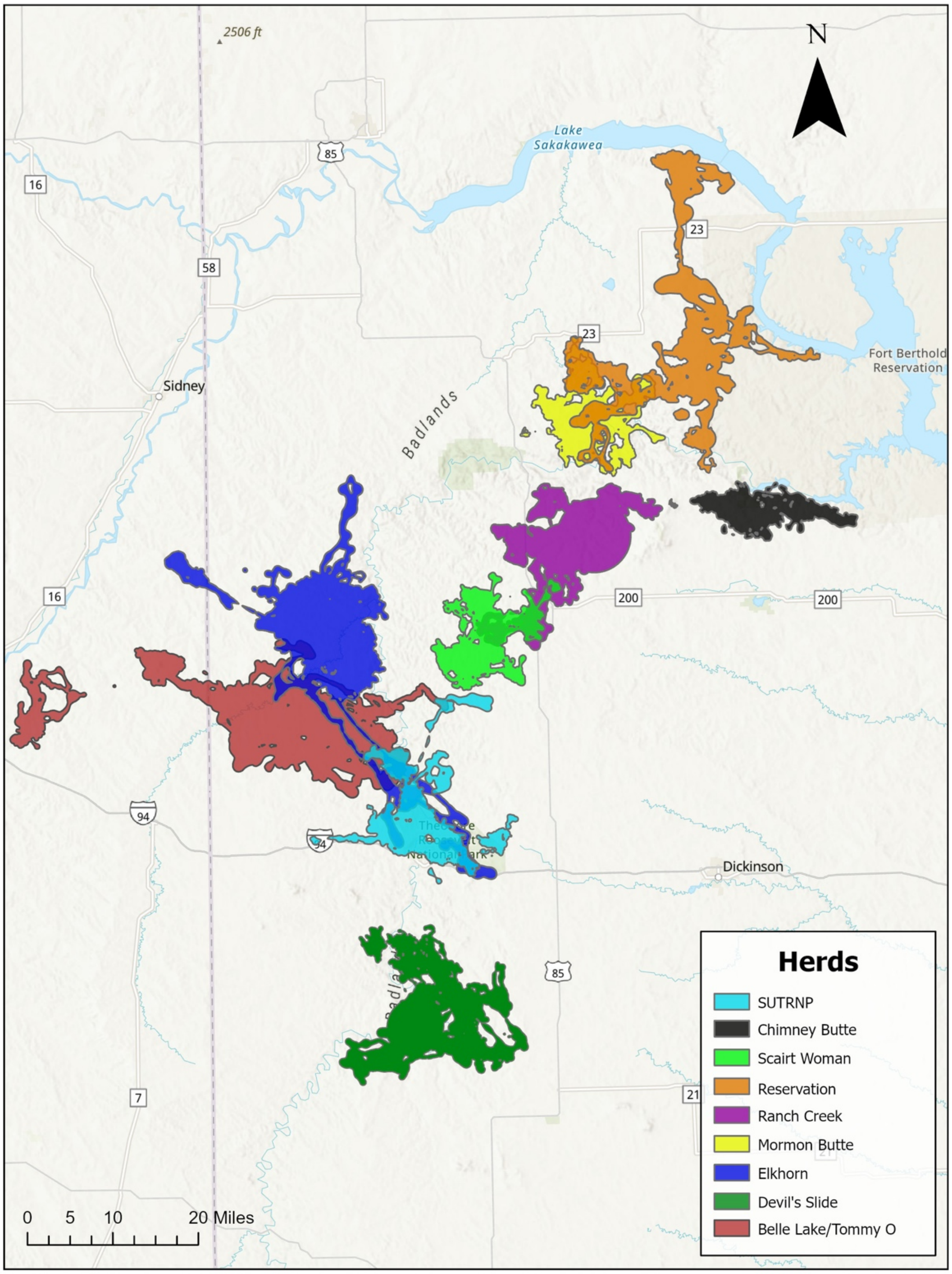


Figure C4. Herd ranges during the winter created using all GPS collared elk within each herd.

Elk Herd Ranges - Summer

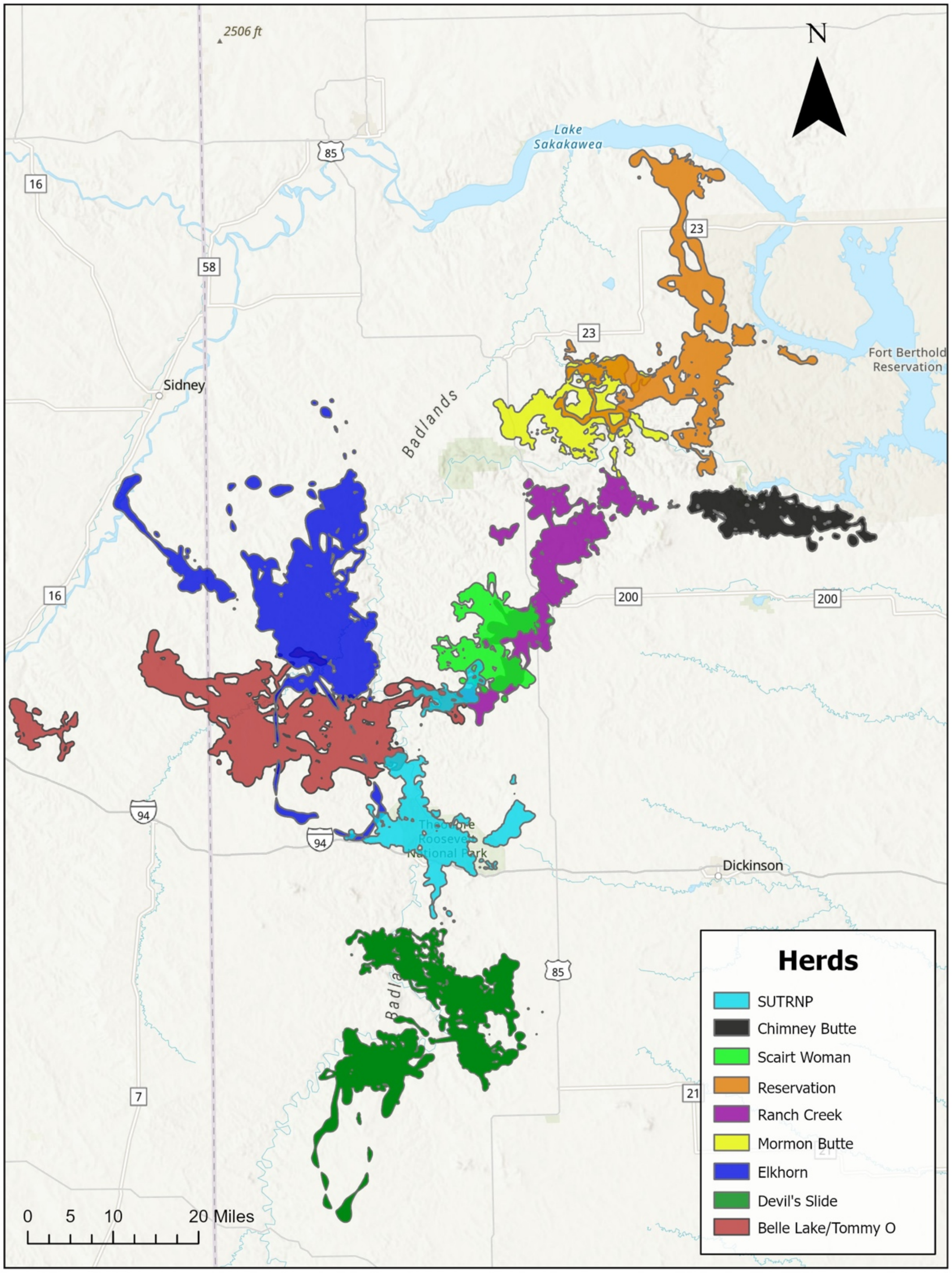


Figure C5. Herd ranges during the summer created using all GPS collared elk within each herd.

Appendix D – Model output from seasonal home range level RSFs

Table D1. Output from models quantifying female elk resource selection during early fall in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-14.88	0.08	-193.42	<0.001
North	0.17	0.00	54.88	<0.001
Topographic Wetness Index	0.38	0.00	80.55	<0.001
Topographic Wetness Index^2	-0.08	0.00	-53.92	<0.001
Woodland	0.34	0.01	25.63	<0.001
Grassland	-1.20	0.01	-89.07	<0.001
Other	-0.92	0.03	-26.76	<0.001
Shrub	-0.83	0.01	-67.84	<0.001
Public	-1.19	0.01	-171.79	<0.001
Reservation	-0.69	0.02	-34.17	<0.001
Distance to Unimproved Road - 5km	1.62	0.01	109.24	<0.001
Distance to Improved Road - 5km	0.84	0.01	73.15	<0.001
Distance to Active Well - 5km	1.08	0.02	55.78	<0.001
Distance to Paved Road - 5km	2.06	0.02	87.34	<0.001
Elevation	-0.12	0.00	-28.18	<0.001
Elevation^2	-0.11	0.00	-44.36	<0.001
log(Slope)	-0.08	0.00	-18.31	<0.001
Distance to Inactive Well - 5km	1.83	0.04	43.09	<0.001
Distance to Drilling Well - 5km	0.56	0.06	10.14	<0.001
East	0.13	0.00	46.42	<0.001
Random Intercept	0.26			

Table D2. Output from models quantifying female elk resource selection during late fall in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-16.30	0.16	-104.80	<0.001
Distance to Active Well - 5km	1.56	0.02	72.62	<0.001
Public	-0.70	0.01	-102.56	<0.001
Reservation	-0.82	0.02	-33.48	<0.001
Distance to Unimproved Road - 5km	0.88	0.01	65.27	<0.001
Distance to Paved Road - 10km	1.53	0.02	87.33	<0.001
Distance to Inactive Well - 5km	3.06	0.05	56.29	<0.001
Elevation	-0.07	0.00	-14.79	<0.001
$Elevation^2$	-0.15	0.00	-58.53	<0.001
Woodland	-0.24	0.01	-16.40	<0.001
Grassland	-0.67	0.01	-52.21	<0.001
Other	-1.19	0.04	-30.38	<0.001
Shrub	-0.73	0.01	-58.92	<0.001
East	0.14	0.00	46.97	<0.001
log(Slope)	-0.30	0.00	-60.81	<0.001
Distance to Improved Road - 5km	0.58	0.01	50.02	<0.001
Distance to Drilling Well - 2.5km	1.97	0.14	13.79	<0.001
Topographic Wetness Index	-0.02	0.01	-3.89	<0.001
Topographic Wetness $Index^2$	-0.02	0.00	-10.37	<0.001
Random Intercept	0.27			

Table D3. Output from models quantifying female elk resource selection during winter in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-16.21	0.14	-115.76	<0.001
Public	-0.32	0.01	-63.48	<0.001
Reservation	-1.13	0.02	-51.54	<0.001
Slope	0.13	0.00	29.63	<0.001
$Slope^2$	-0.09	0.00	-46.60	<0.001
Distance to Improved Road - 5km	0.94	0.01	99.21	<0.001
Distance to Paved Road - 10km	2.24	0.02	134.59	<0.001
Elevation	0.17	0.00	45.13	<0.001
$Elevation^2$	-0.19	0.00	-87.58	<0.001
Distance to Unimproved Road - 5km	0.81	0.01	75.82	<0.001
East	0.16	0.00	70.50	<0.001
North	-0.11	0.00	-50.63	<0.001
Distance to Active Well - 3.5km	1.18	0.02	59.86	<0.001
Distance to Inactive Well - 2.5km	1.45	0.06	22.81	<0.001
log(Topographic Wetness Index)	-0.28	0.01	-21.84	<0.001
Distance to Drilling Well - 2.5km	2.26	0.11	19.79	<0.001
Random Intercept	0.45			

Table D4. Output from models quantifying female elk resource selection during spring in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-18.28	0.51	-35.52	<0.001
Public	-0.31	0.01	-54.15	<0.001
Reservation	-0.88	0.02	-39.98	<0.001
Distance to Improved Road - 5km	1.10	0.01	100.18	<0.001
Distance to Active Well - 5km	0.77	0.02	43.90	<0.001
Distance to Drilling Well - 1km	5.20	0.51	10.14	<0.001
Distance to Inactive Well - 5km	0.05	0.03	1.76	0.08
Topographic Wetness Index	0.58	0.00	131.55	<0.001
Topographic Wetness Index^2	-0.11	0.00	-69.39	<0.001
North	0.23	0.00	90.12	<0.001
East	0.16	0.00	63.67	<0.001
Elevation	0.02	0.00	4.23	<0.001
Elevation^2	-0.15	0.00	-62.40	<0.001
Slope	0.62	0.00	127.66	<0.001
Slope^2	-0.18	0.00	-85.78	<0.001
Distance to Paved Road - 10km	2.48	0.02	125.61	<0.001
Distance to Unimproved Road - 5km	0.92	0.01	74.67	<0.001
Random Intercept	0.40			

Table D5. Output from models quantifying female elk resource selection during summer in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-15.61	0.13	-122.57	<0.001
North	0.21	0.00	83.32	<0.001
Distance to Improved Road - 3.5km	1.15	0.01	116.97	<0.001
Distance to Paved Road - 10km	2.40	0.02	149.68	<0.001
Topographic Wetness Index	0.57	0.00	156.16	<0.001
Topographic Wetness Index^2	-0.10	0.00	-80.42	<0.001
Forest	0.26	0.01	22.07	<0.001
Grassland	-1.64	0.01	-127.60	<0.001
Other	-0.96	0.03	-30.69	<0.001
Shrub	-0.88	0.01	-79.67	<0.001
Elevation	0.04	0.00	10.60	<0.001
Elevation^2	-0.22	0.00	-100.62	<0.001
Public	-0.58	0.00	-118.67	<0.001
Reservation	-0.32	0.02	-20.56	<0.001
Distance to Unimproved Road - 5km	1.24	0.01	111.22	<0.001
East	0.14	0.00	61.68	<0.001
Distance to Inactive Well – 5km	0.06	0.02	2.45	0.01
Distance to Active Well - 3.5km	0.80	0.02	44.37	<0.001
Slope	0.37	0.00	81.11	<0.001
Slope^2	-0.15	0.00	-77.46	<0.001
Distance to Drilling Well - 2.5km	2.95	0.12	24.51	<0.001
Random Intercept	0.31			

Table D6. Output from models quantifying male elk resource selection during early fall in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-19.38	0.62	-31.50	<0.001
Woodland	0.08	0.03	2.78	0.01
Grassland	-1.51	0.03	-51.68	<0.001
Other	-1.47	0.09	-15.95	<0.001
Shrub	-1.16	0.03	-43.64	<0.001
Distance to Unimproved Road - 5km	1.76	0.04	50.26	<0.001
Public	-0.67	0.02	-43.84	<0.001
Reservation	-2.07	0.07	-31.06	<0.001
Distance to Improved Road - 2.5km	1.27	0.03	39.40	<0.001
Distance to Paved Road - 10km	0.91	0.03	28.57	<0.001
Distance to Active Well - 2.5km	1.97	0.08	23.99	<0.001
East	0.18	0.01	26.43	<0.001
Elevation	-0.12	0.01	-12.16	<0.001
$Elevation^2$	-0.10	0.01	-16.97	<0.001
Topographic Wetness Index	0.19	0.01	26.98	<0.001
North	0.16	0.01	20.95	<0.001
Distance to Inactive Well - 3.5km	1.44	0.13	11.51	<0.001
Slope	0.20	0.01	14.65	<0.001
$Slope^2$	-0.07	0.01	-13.78	<0.001
Distance to Drilling Well - 2.5km	5.01	0.60	8.32	<0.001
Random Intercept	0.19			

Table D7. Output from models quantifying male elk resource selection during late fall in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-59.69	9.56	-6.24	<0.001
Woodland	-0.45	0.09	-5.06	<0.001
Grassland	-1.60	0.08	-20.42	<0.001
Other	-1.40	0.19	-7.25	<0.001
Shrub	-1.61	0.07	-22.26	<0.001
Distance to Improved Road - 5km	-0.57	0.15	-3.89	<0.001
Public	-0.75	0.02	-38.25	<0.001
Reservation	-1.59	0.07	-24.21	<0.001
Topographic Wetness Index	0.09	0.02	5.91	<0.001
Topographic Wetness Index^2	0.00	0.00	0.51	0.61
North	0.00	0.01	-0.36	0.72
Elevation	0.16	0.01	12.45	<0.001
Elevation^2	-0.20	0.01	-25.74	<0.001
East	0.20	0.01	24.47	<0.001
Distance to Active Well - 5km	1.87	0.06	29.68	<0.001
Distance to Drilling Well - 1km	45.79	9.56	4.79	<0.001
Distance to Inactive Well - 2.5km	1.09	0.22	4.94	<0.001
Slope	0.38	0.02	22.11	<0.001
Slope^2	-0.13	0.01	-18.94	<0.001
Distance to Unimproved Road - 500m	0.57	0.09	6.08	<0.001
Distance to Paved Road - 1km	2.25	0.12	18.29	<0.001
Woodland × Distance to Improved Road - 5km	1.88	0.17	11.29	<0.001

Covariate	Estimate	Standard Error	z value	p value
Grassland × Distance to Improved Road - 5km	2.46	0.16	15.27	<0.001
Other × Distance to Improved Road - 5km	1.11	0.42	2.64	0.01
Shrub × Distance to Improved Road - 5km	2.55	0.15	16.52	<0.001
Random Intercept	0.33			

Table D8. Output from models quantifying male elk resource selection during winter in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-27.85	0.95	-29.31	<0.001
Woodland	-0.10	0.09	-1.14	0.25
Grassland	-1.08	0.09	-12.72	<0.001
Other	-0.97	0.19	-5.24	<0.001
Shrub	-1.11	0.08	-13.77	<0.001
Distance to Improved Road - 5km	0.55	0.16	3.37	<0.001
Public	0.05	0.01	4.55	<0.001
Reservation	-1.48	0.05	-29.49	<0.001
Slope	0.39	0.01	36.06	<0.001
Slope^2	-0.14	0.00	-33.44	<0.001
Distance to Paved Road - 3.5km	3.22	0.05	61.36	<0.001
Distance to Unimproved Road - 5km	0.61	0.02	25.45	<0.001
Elevation	0.15	0.01	18.51	<0.001
Elevation^2	-0.18	0.00	-38.63	<0.001
North	-0.13	0.01	-22.26	<0.001
East	0.20	0.01	39.03	<0.001
Topographic Wetness Index	-0.10	0.01	-10.63	<0.001
Topographic Wetness Index^2	0.02	0.00	4.50	<0.001

Covariate	Estimate	Standard Error	z value	p value
Distance to Active Well - 3.5km	1.74	0.06	30.44	<0.001
Distance to Inactive Well - 5km	0.68	0.08	9.07	<0.001
Distance to Drilling Well - 2.5km	12.13	0.94	12.85	<0.001
Woodland × Distance to Improved Road - 5km	1.74	0.17	10.09	<0.001
Grassland × Distance to Improved Road - 5km	1.86	0.17	10.87	<0.001
Other × Distance to Improved Road - 5km	0.76	0.33	2.31	0.02
Shrub ×Distance to Improved Road - 5km	2.16	0.17	12.91	<0.001
Random Intercept	0.35			

Table D9. Output from models quantifying male elk resource selection during spring in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-20.84	0.47	-44.31	<0.001
Distance to Improved Road - 5km	2.02	0.03	75.99	<0.001
Distance to Paved Road - 3.5km	1.65	0.04	38.51	<0.001
Distance to Active Well - 5km	1.75	0.05	37.46	<0.001
Woodland	1.60	0.04	35.48	<0.001
Grassland	-0.13	0.04	-2.82	0
Other	0.18	0.09	1.90	0.06
Shrub	0.42	0.04	9.62	<0.001
Slope	0.58	0.01	51.54	<0.001
Slope^2	-0.15	0.00	-34.90	<0.001
East	0.18	0.01	33.33	<0.001
Topographic Wetness Index	0.45	0.01	48.51	<0.001
Topographic Wetness Index^2	-0.07	0.00	-22.54	<0.001

Covariate	Estimate	Standard Error	z value	p value
Distance to Drilling Well - 3.5km	5.80	0.46	12.58	<0.001
Elevation	0.09	0.01	11.40	<0.001
$Elevation^2$	-0.10	0.00	-23.62	<0.001
North	0.07	0.01	10.91	<0.001
Distance to Inactive Well - 5km	1.06	0.09	12.21	<0.001
Distance to Unimproved Road - 5km	0.01	0.02	0.38	0.7
Random Intercept	0.24			

Table D10. Output from models quantifying male elk resource selection during spring in western North Dakota during 2019 – 2023. The reference level includes crop and private land.

Covariate	Estimate	Standard Error	z value	p value
Intercept	-13.82	0.27	-51.59	<0.001
Distance to Improved Road - 5km	1.21	0.02	57.85	<0.001
Distance to Paved Road - 3.5km	0.82	0.03	25.87	<0.001
Distance to Active Well - 5km	2.07	0.04	52.64	<0.001
Woodland	0.71	0.02	31.09	<0.001
Grassland	-1.50	0.02	-65.04	<0.001
Other	-0.75	0.06	-12.82	<0.001
Shrub	-0.85	0.02	-41.37	<0.001
Slope	0.48	0.01	47.96	<0.001
$Slope^2$	-0.14	0.00	-34.07	<0.001
East	0.16	0.00	33.73	<0.001
Topographic Wetness Index	0.64	0.01	77.84	<0.001
Topographic Wetness $Index^2$	-0.11	0.00	-37.64	<0.001
Distance to Drilling Well - 3.5km	2.67	0.26	10.30	<0.001
Elevation	0.38	0.01	58.79	<0.001
$Elevation^2$	-0.03	0.00	-10.89	<0.001
North	0.17	0.01	30.62	<0.001
Distance to Inactive Well - 5km	-0.87	0.05	-17.93	<0.001
Distance to Unimproved Road - 5km	0.15	0.02	7.42	<0.001
Random Intercept	0.30			

Appendix E – Additional plots created for seasonal home range level RSFs

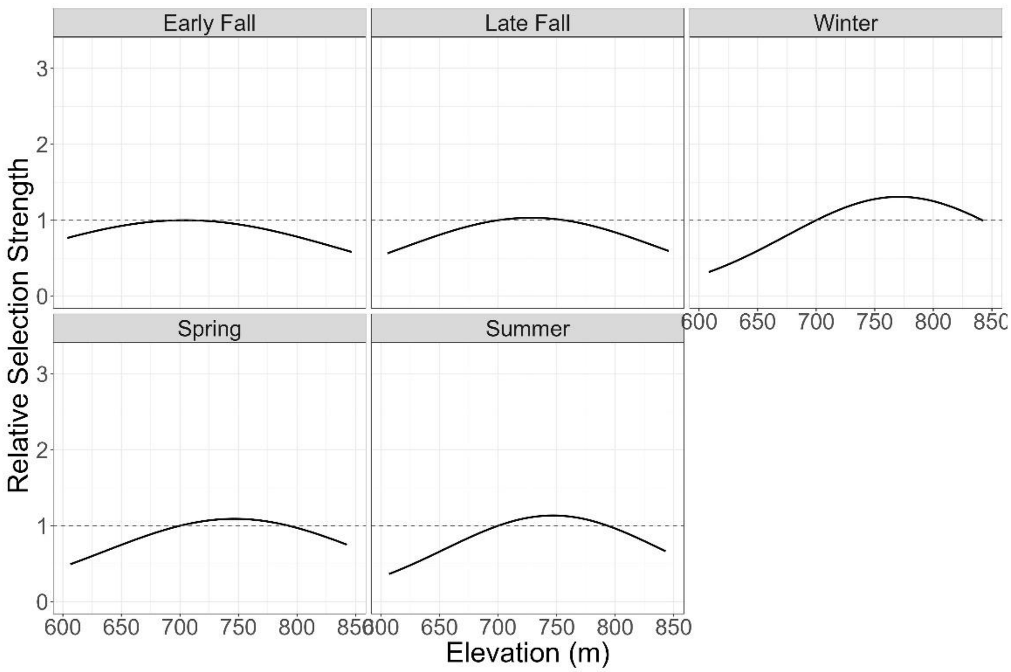


Figure E1. Female elk relative selection strength at different elevations compared to being at an elevation of 700 m, with values above 1 indicating selection and values below 1 indicating avoidance. The relative selection strength shows how much more likely an elk is to select a location relative to another location. Therefore, this plot generally shows that elk prefer areas with intermediate elevations in all seasons.

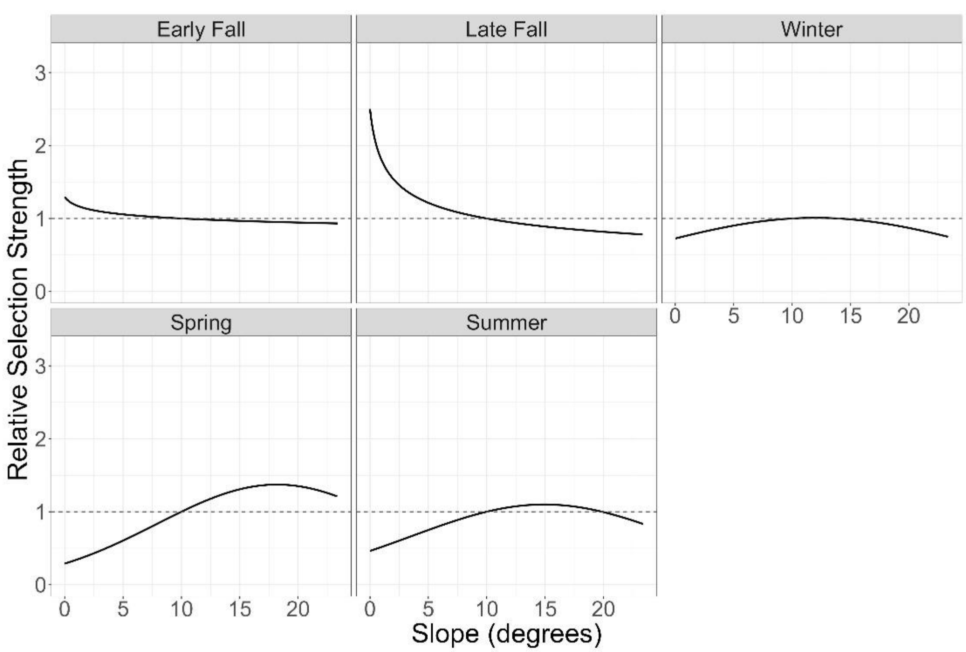


Figure E2. Female elk relative selection strength at varying slopes compared to being on a 10-degree slope.

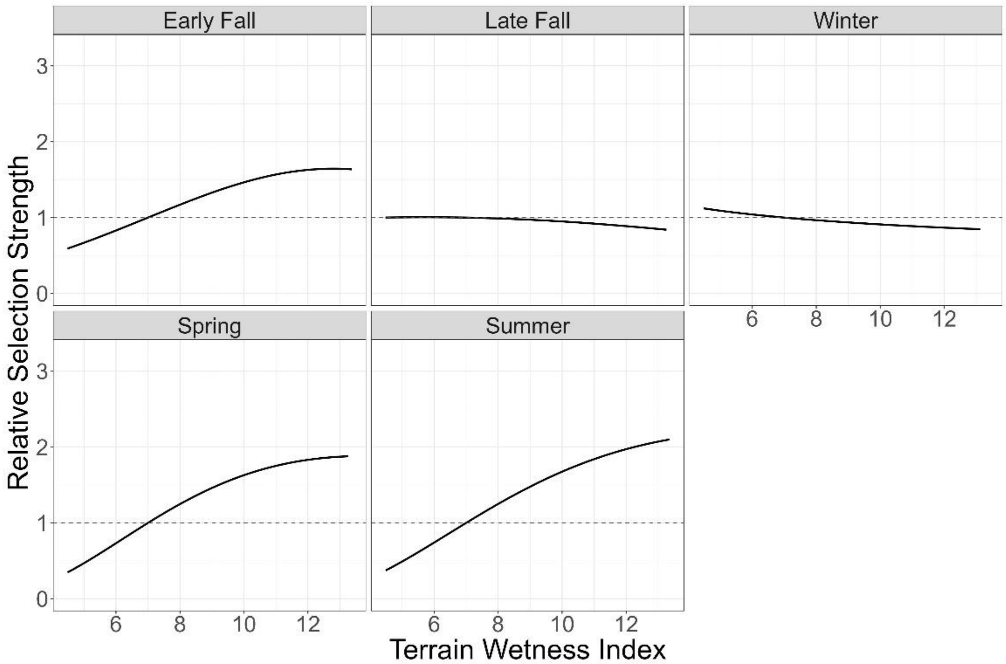


Figure E3. Female elk relative selection strength at different terrain wetness indices compared to being at a TWI value of 7 (higher values indicate wetter sites).

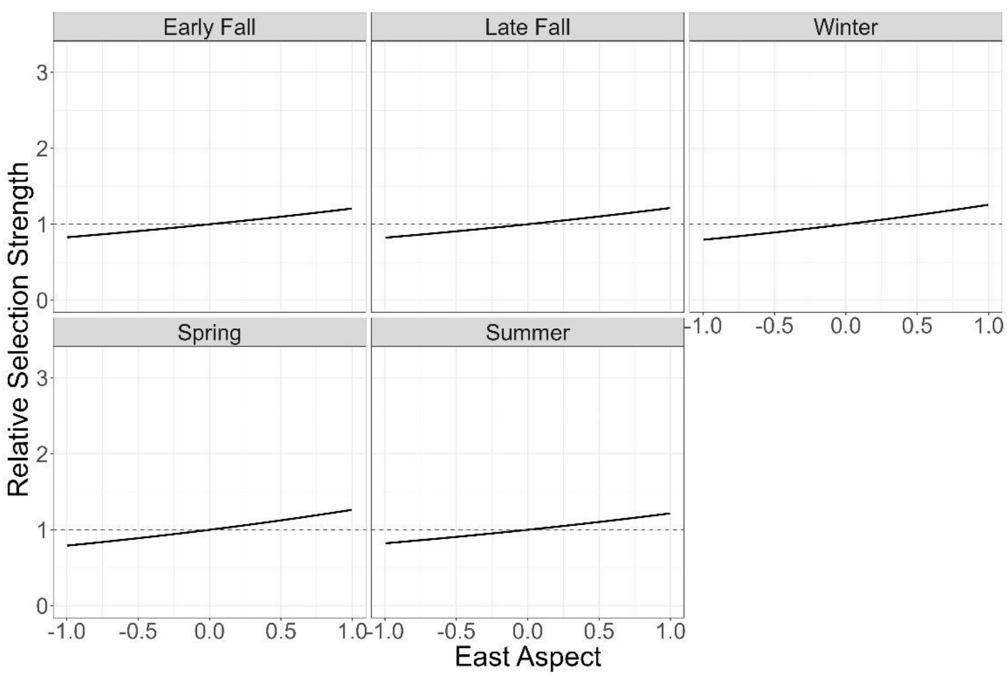


Figure E4. Female elk relative selection strength at different east-facing aspects (-1 = completely west facing, +1 = completely east facing).

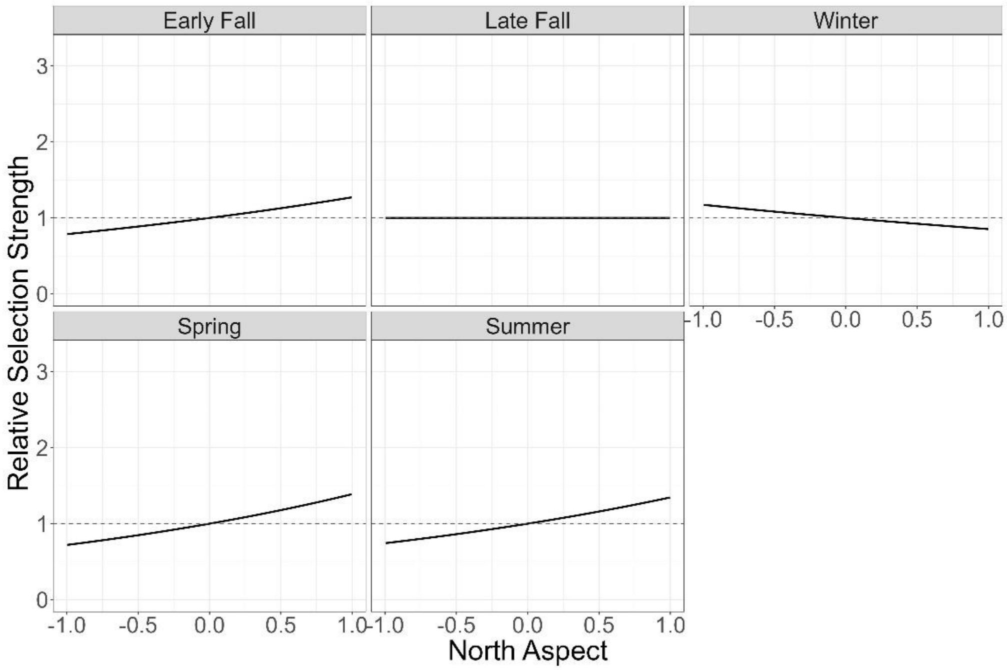


Figure E5. Female elk relative selection strength at different north-facing aspects (-1 = completely south facing, +1 = completely north facing).

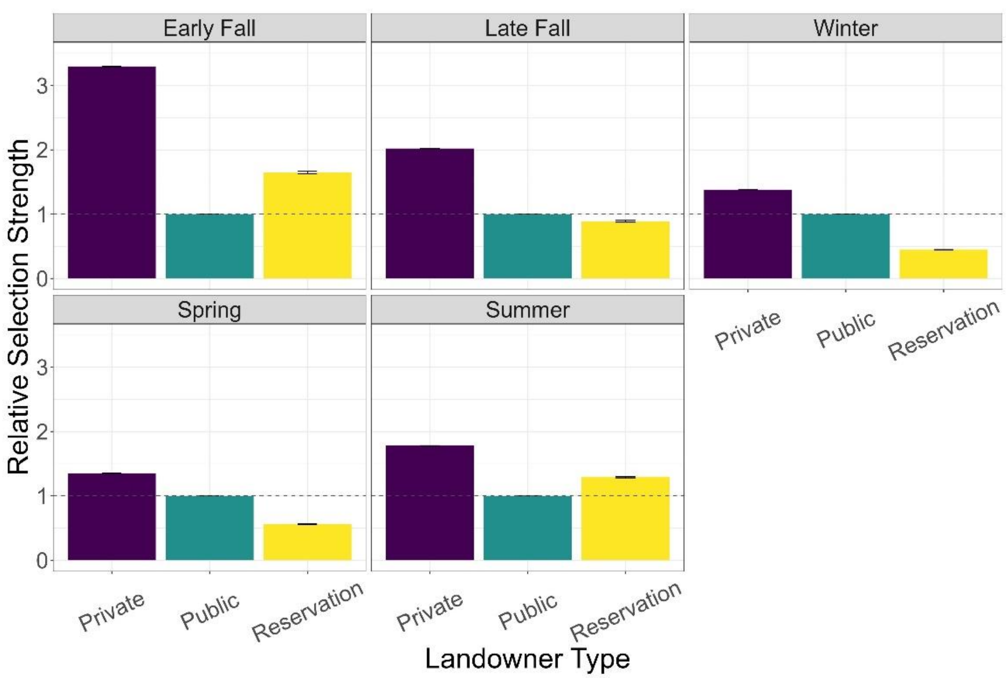


Figure E6. Female elk relative selection strength of different landowner types compared to being on public land.

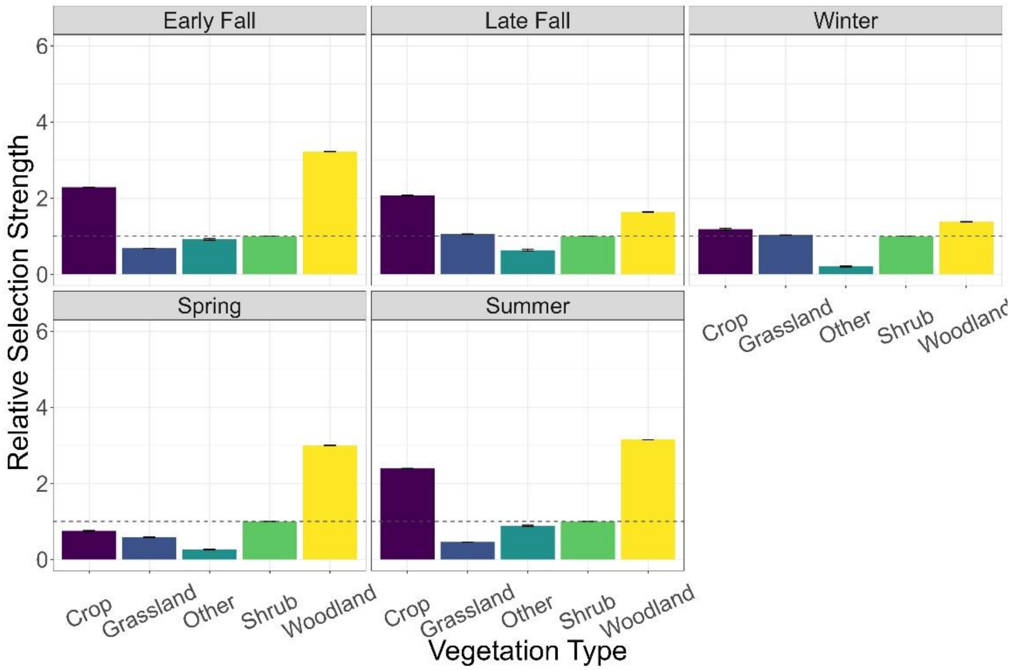


Figure E7. Female elk relative selection strength of different vegetation types compared to being in shrub.

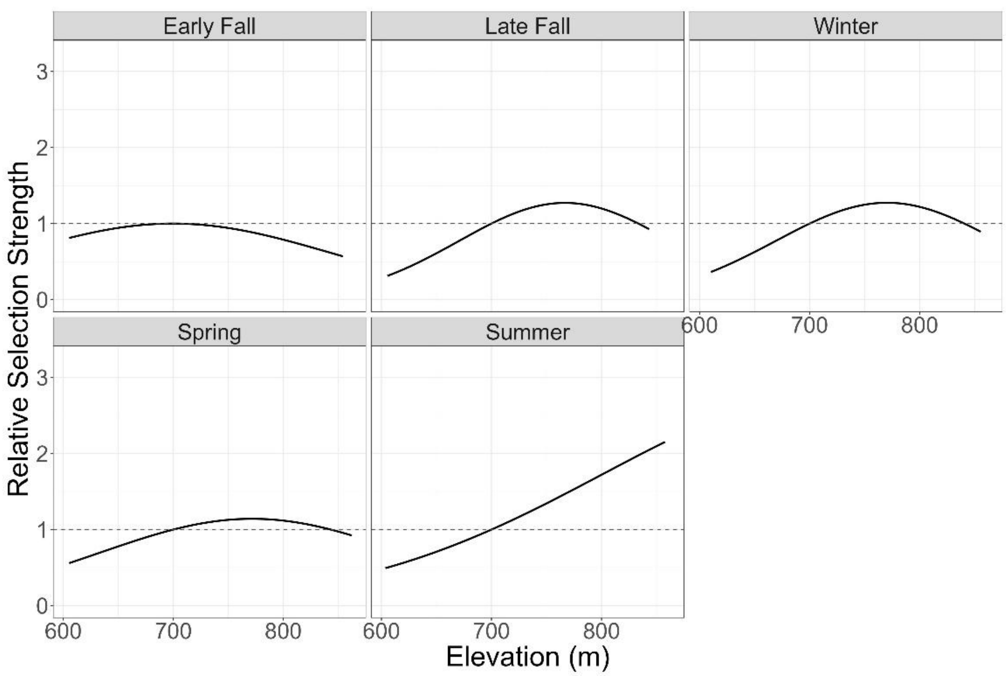


Figure E8. Male elk relative selection strength at different elevations compared to being at an elevation of 700 m.

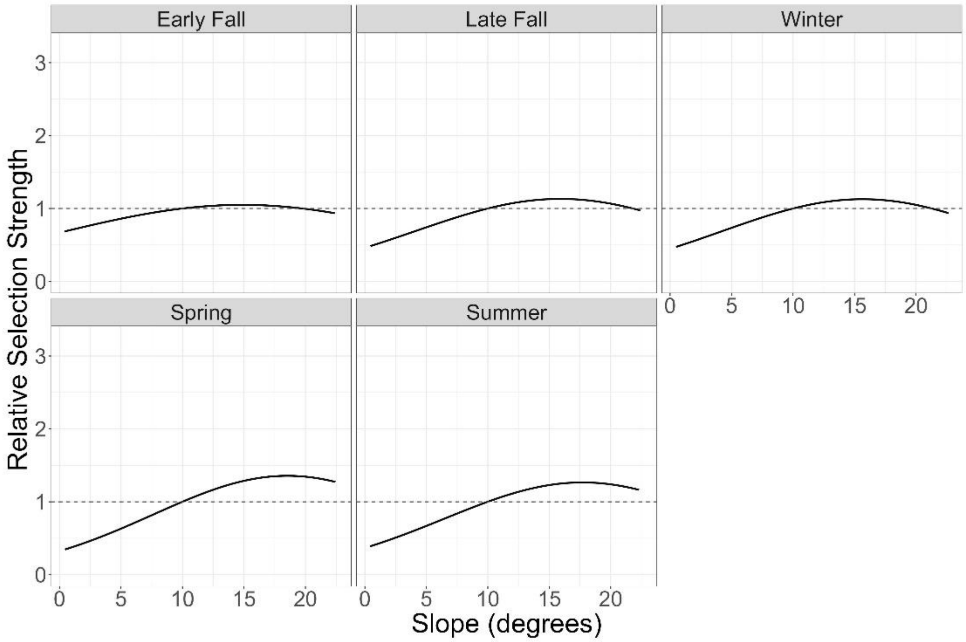


Figure E9. Male elk relative selection strength at varying slopes compared to being on a 10-degree slope.

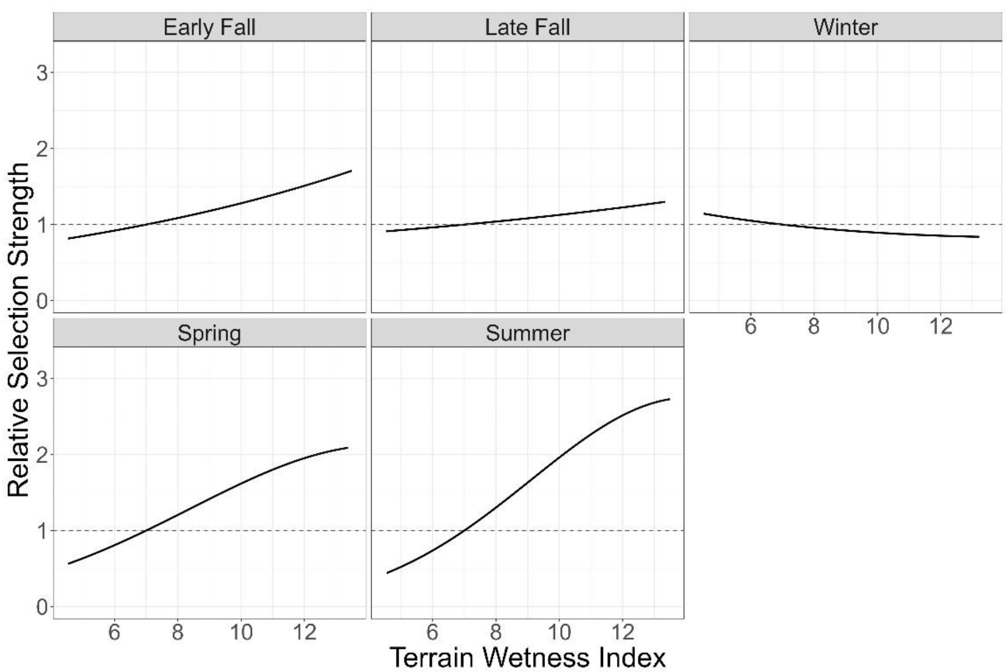


Figure E10. Male elk relative selection strength at different terrain wetness indices compared to being at a TWI value of 7 (higher values indicate wetter sites).

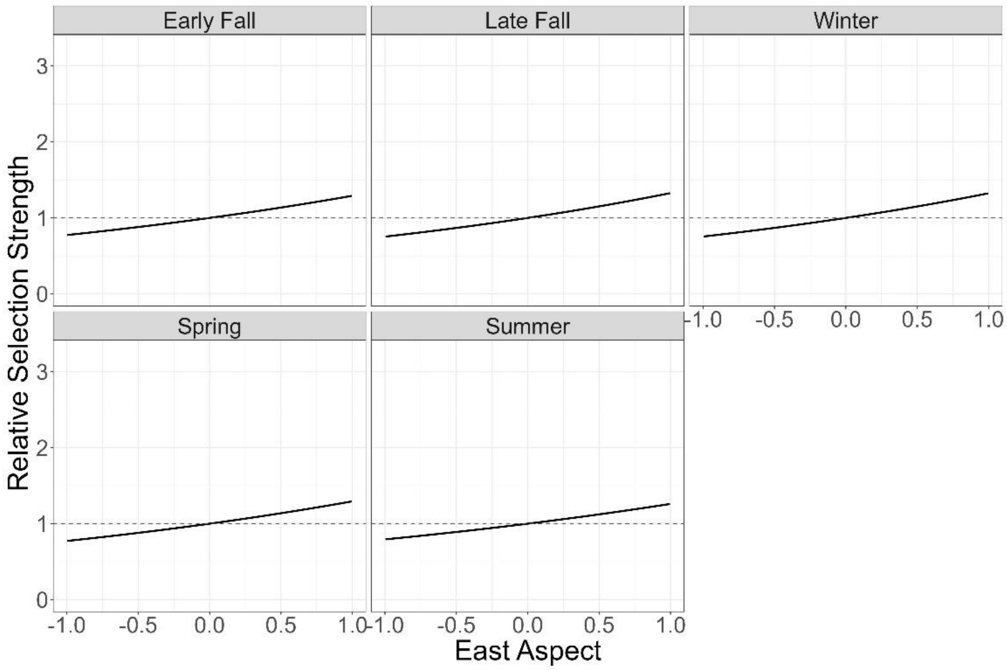


Figure E11. Male elk relative selection strength at different east-facing aspects (-1 = completely west facing, +1 = completely east facing).

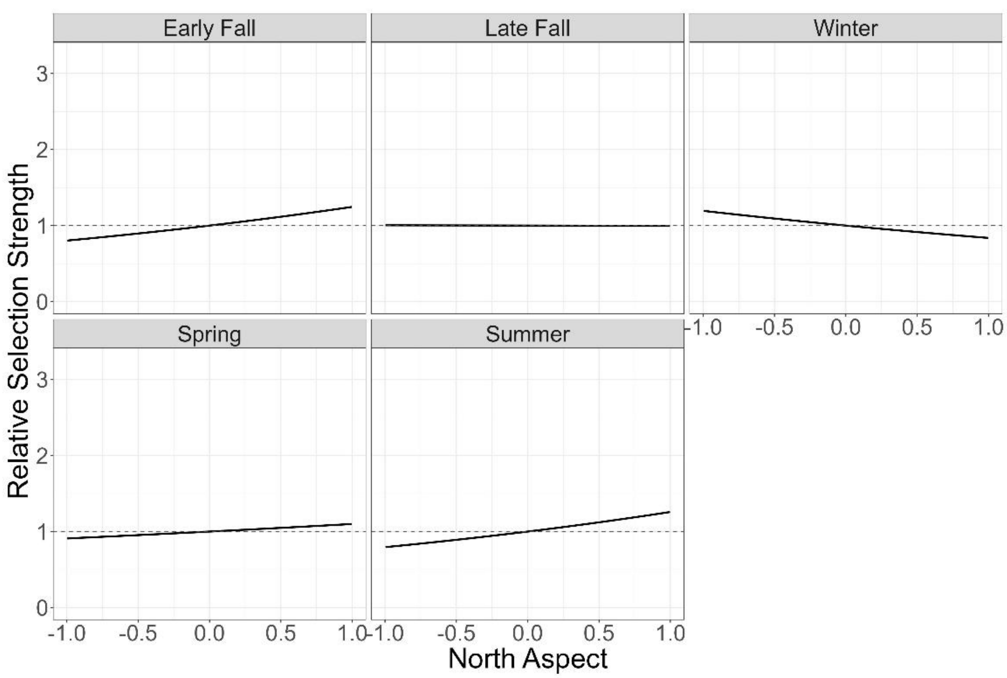


Figure E12. Male elk relative selection strength at different north-facing aspects (-1 = completely south facing, +1 = completely north facing).

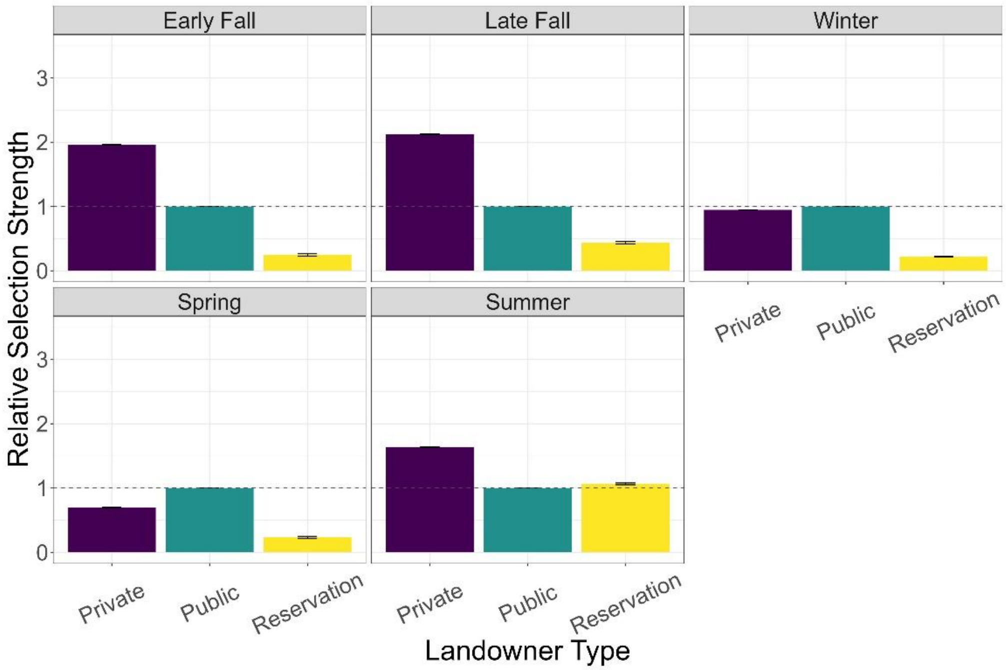


Figure E13. Male elk relative selection strength of different landowner types compared to being on public land.

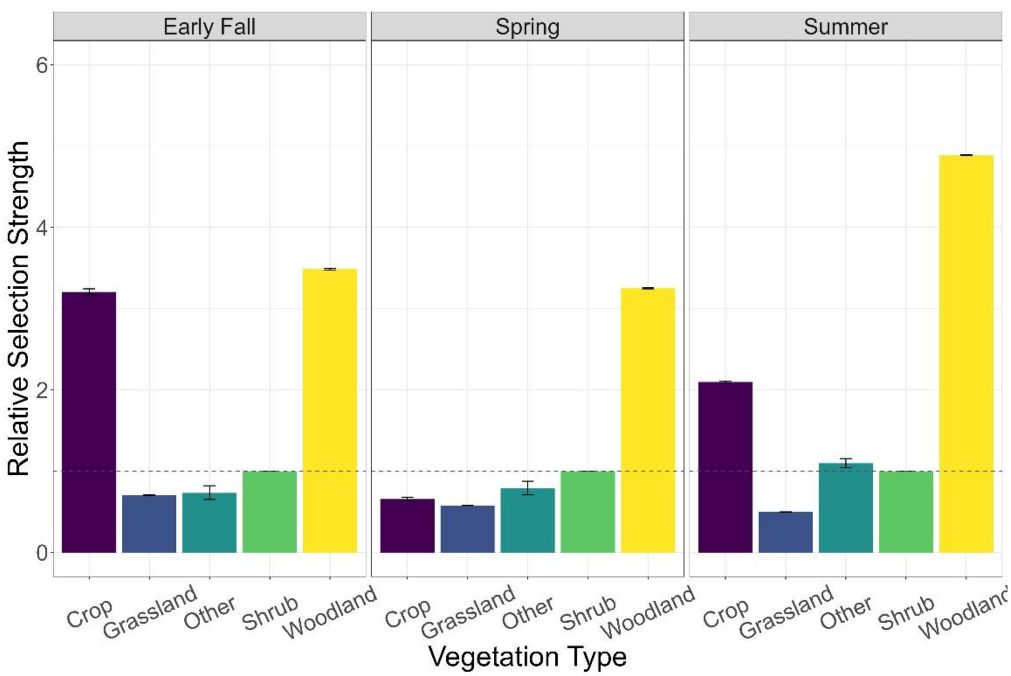


Figure E14. Male elk relative selection strength of different vegetation types compared to being in shrub.

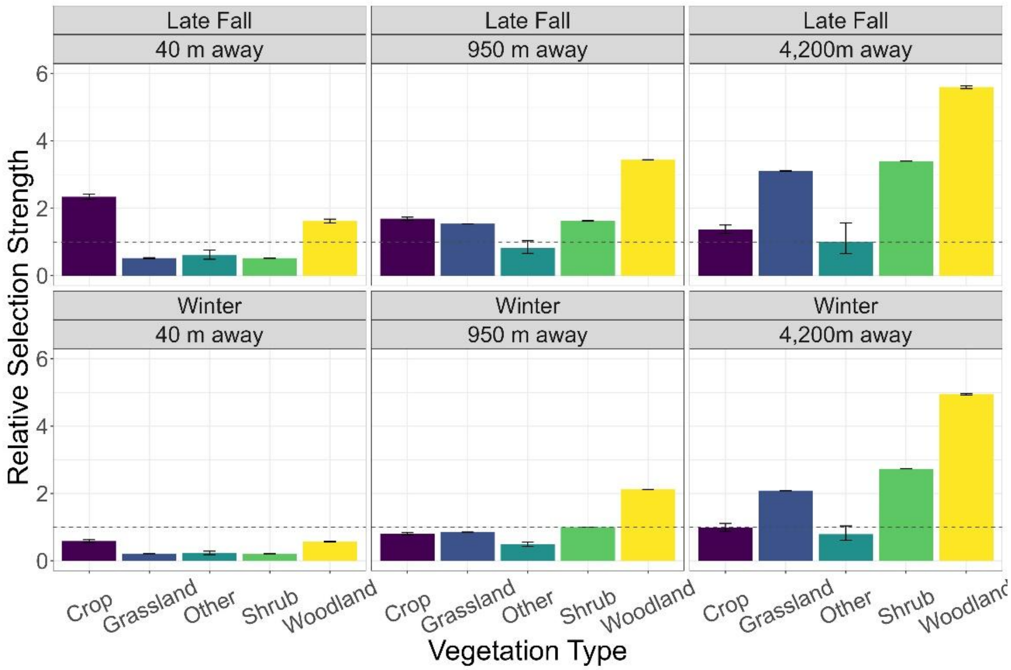


Figure E15. Male elk relative selection strength of different vegetation types and distances to improved roads compared to being in shrub vegetation and 950 m away from an improved road.

Appendix C - Predictive Resource Selection Surface Maps

For all maps below, we predicted the top RSF model for each sex and season over all spatial covariates included within that model. We divided the continuous selection probabilities into 100 equal area divisions with 1 representing low selection probability areas and 100 representing high selection probability areas. We clipped the prediction surfaces to the spatial extent of the available area to avoid making predictions beyond where we collected data.

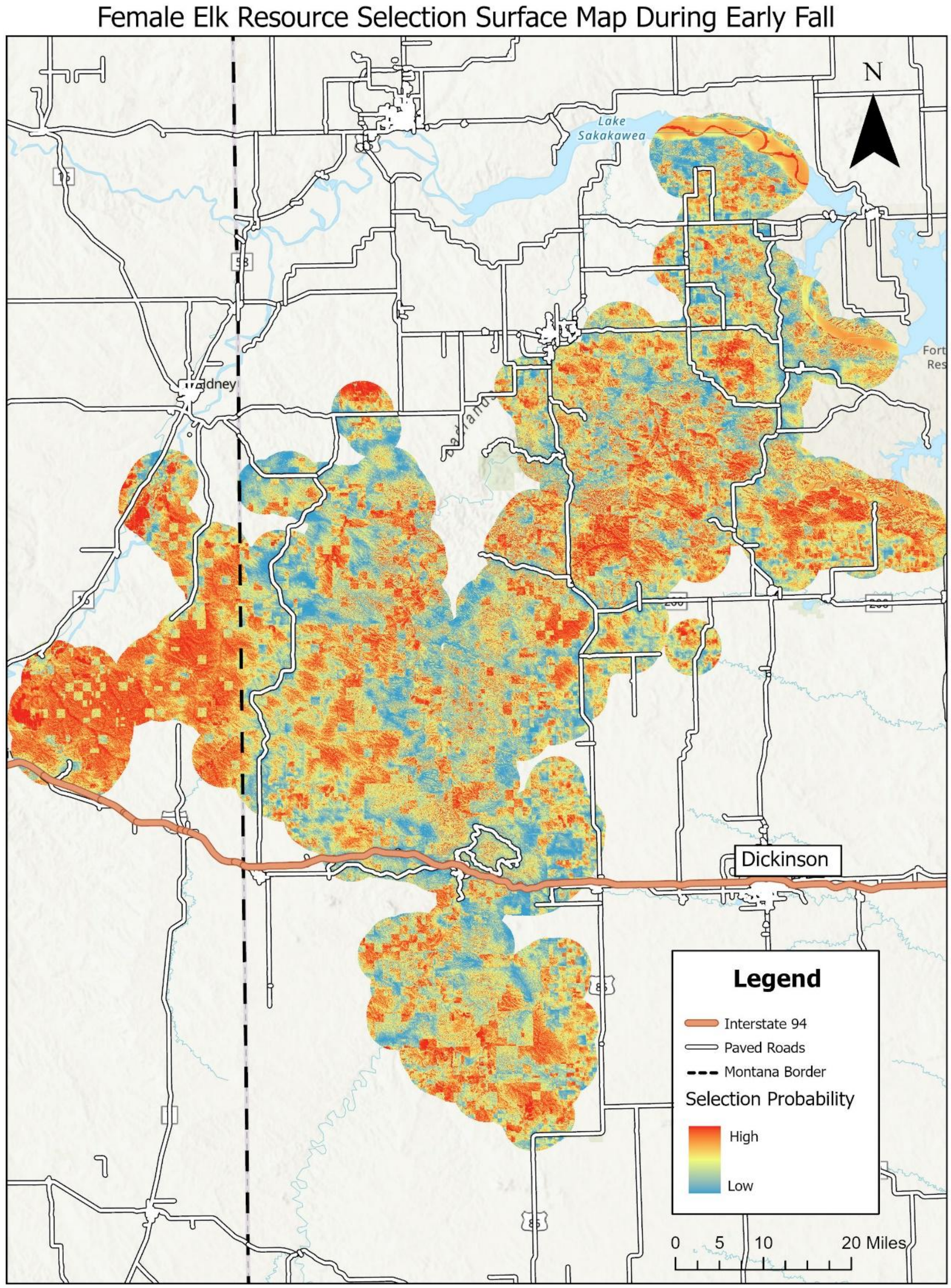


Figure F1. Predicted selection map for female elk in the early fall.

Male Elk Resource Selection Surface Map During Early Fall

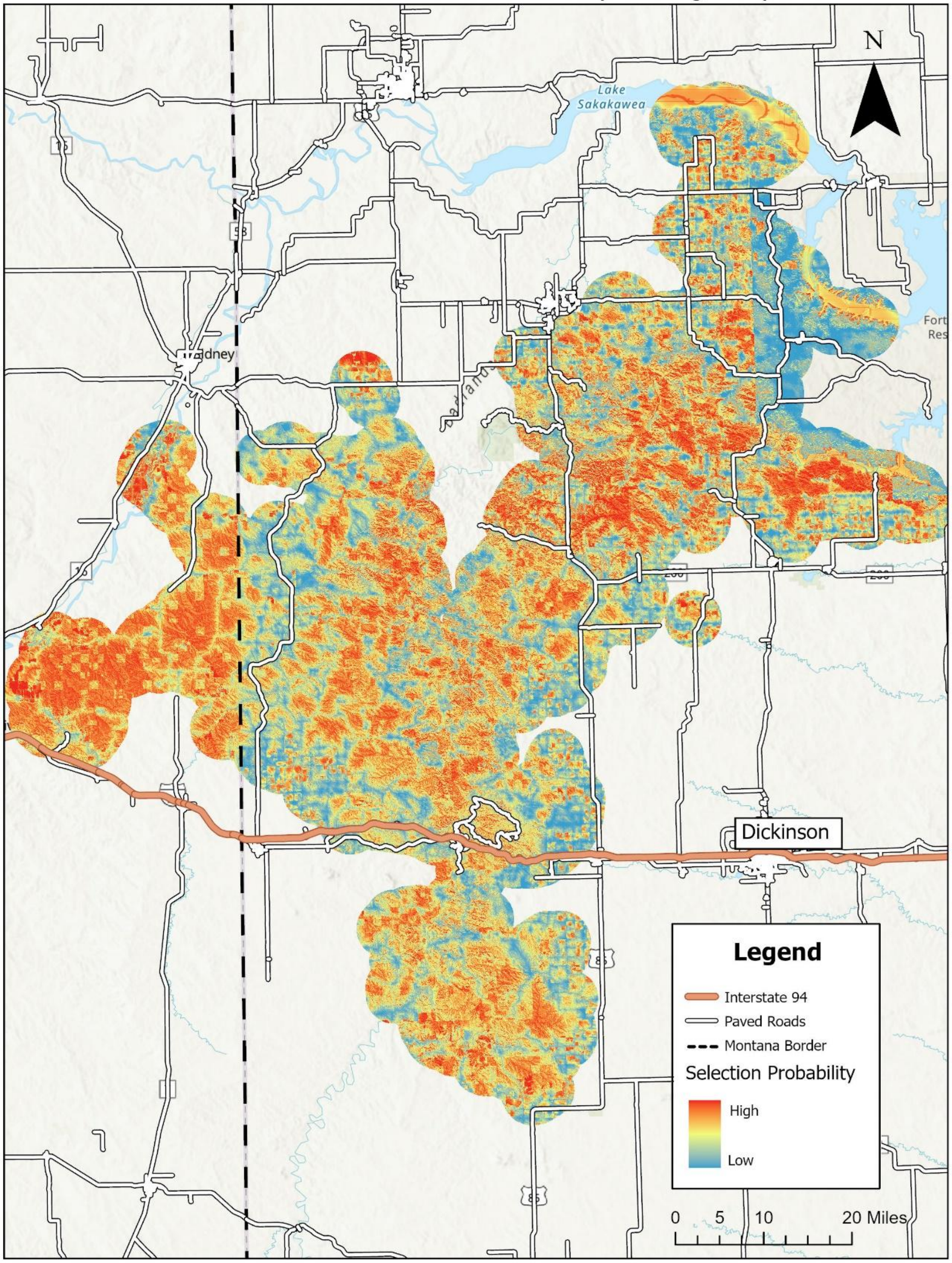


Figure F2. Predicted selection map for male elk in the early fall.

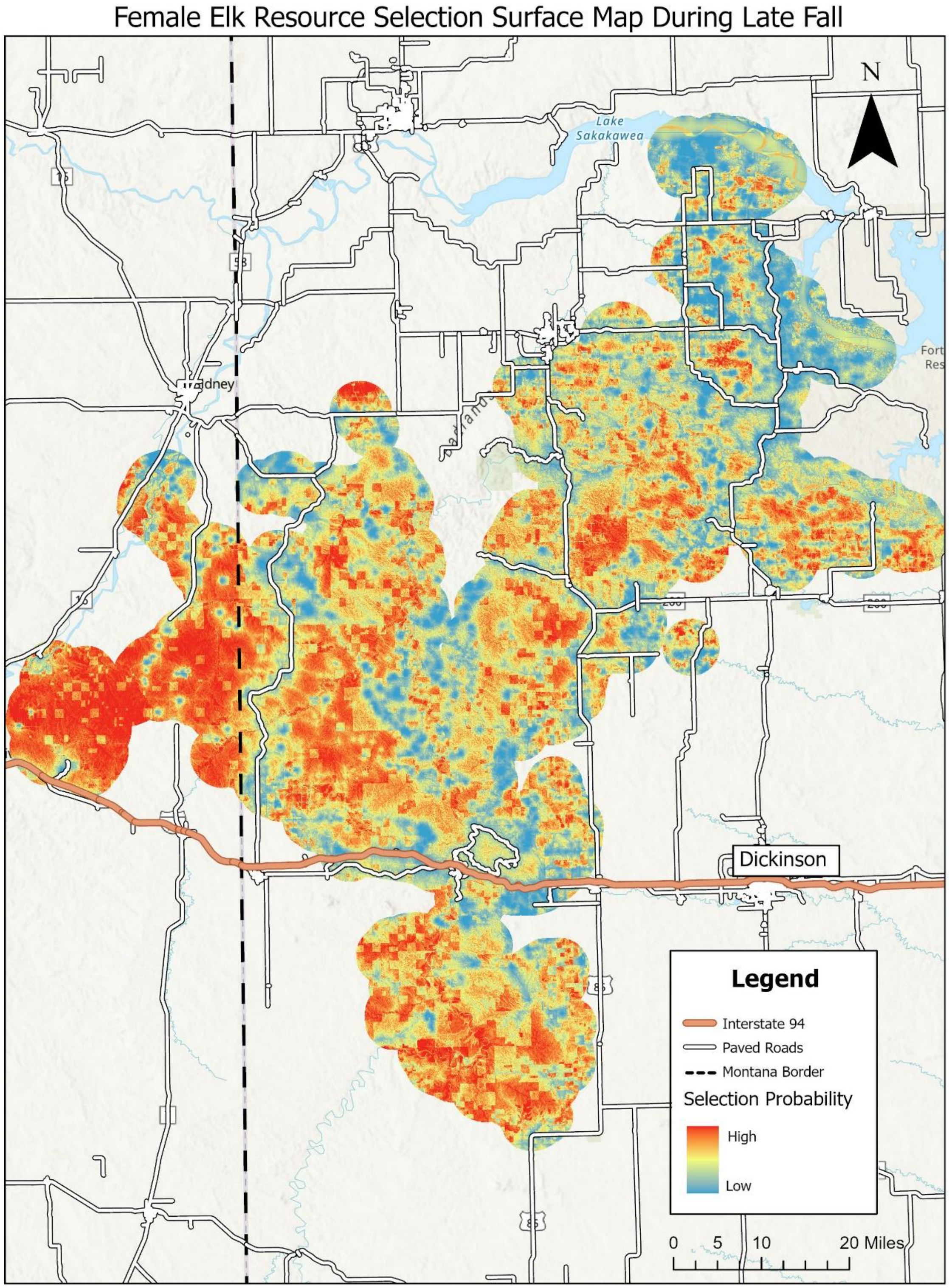


Figure F3. Predicted selection map for female elk in the late fall.

Male Elk Resource Selection Surface Map During Late Fall

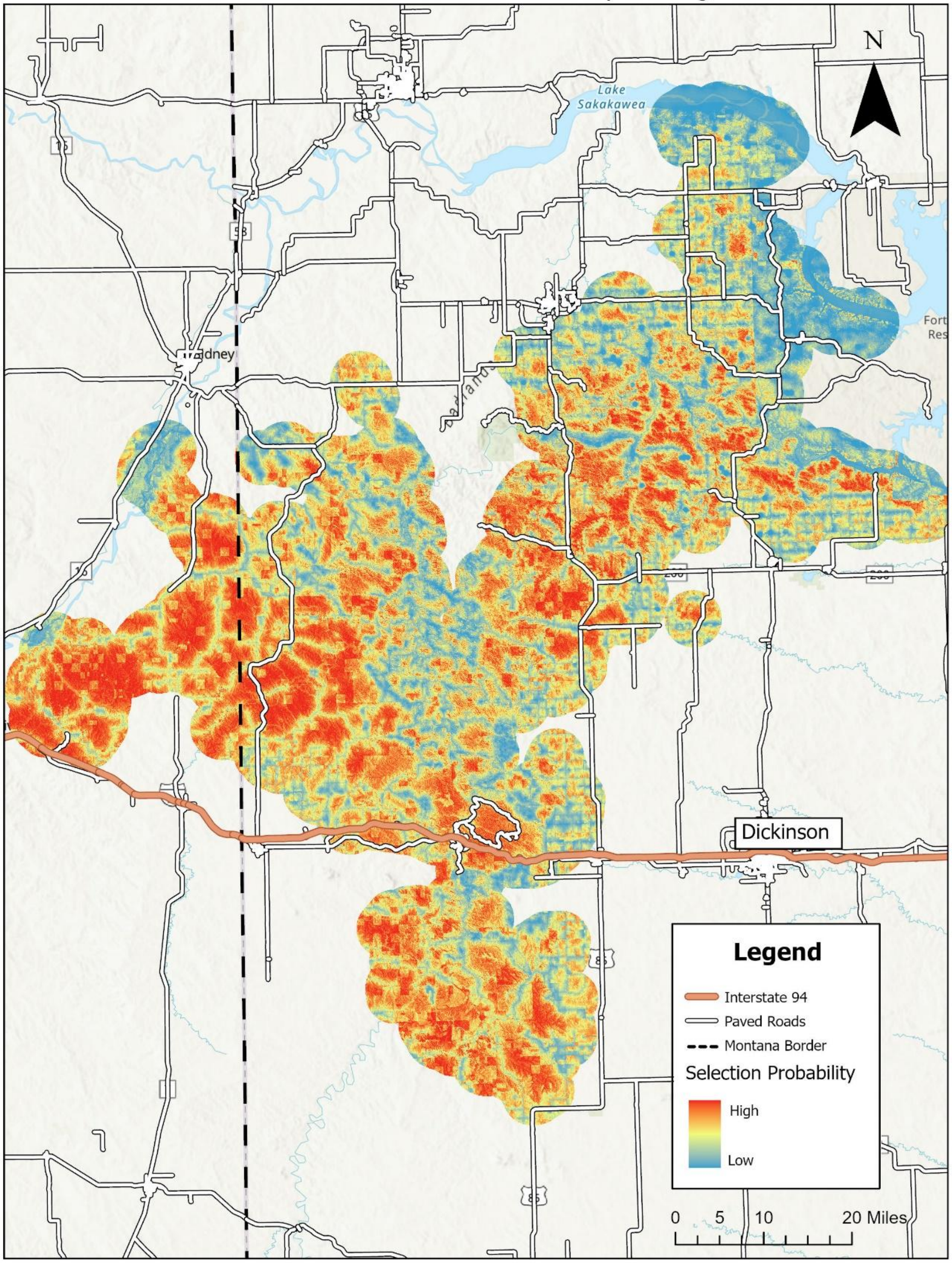


Figure F4. Predicted selection map for male elk in the late fall.

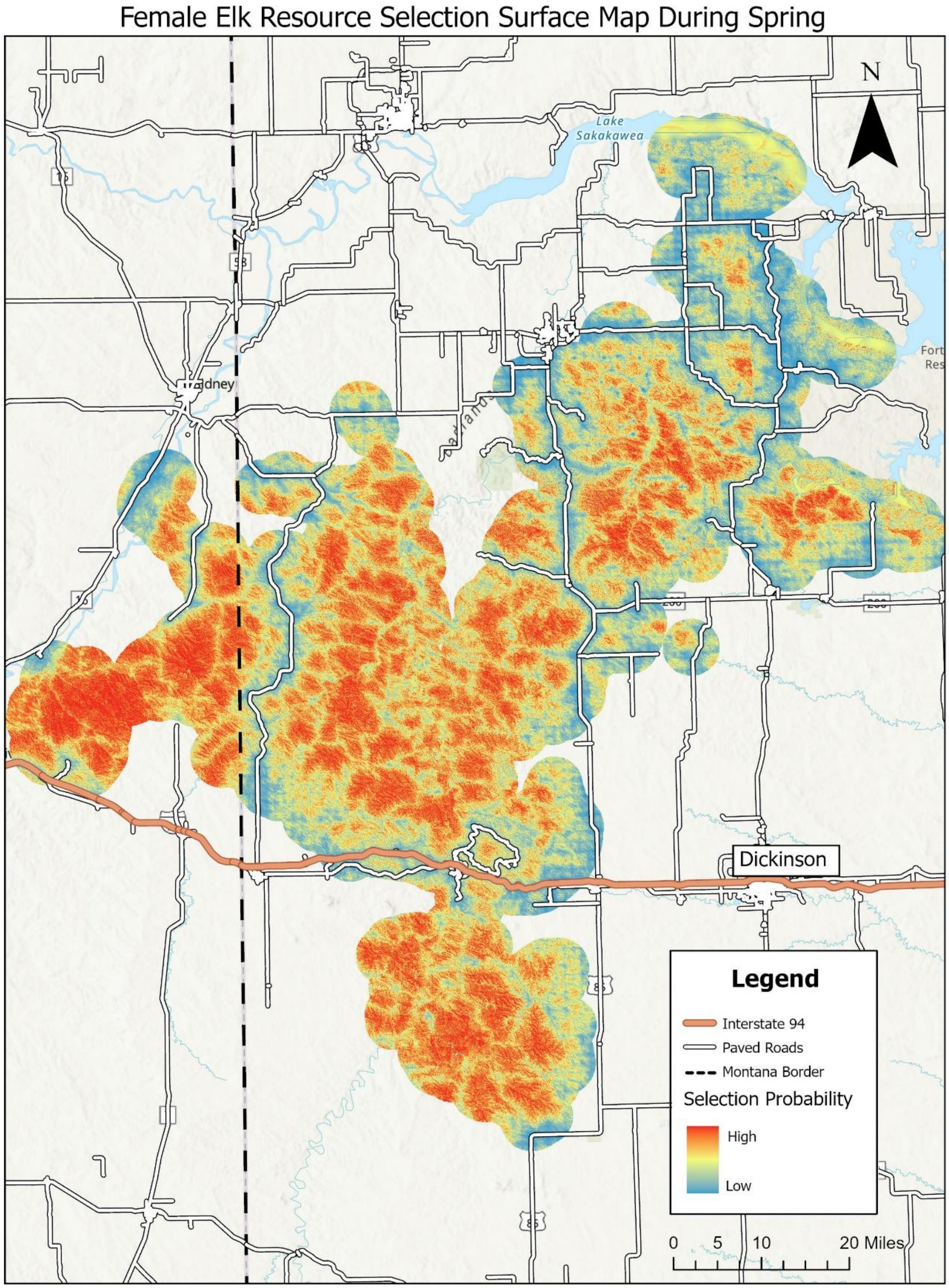


Figure F5. Predicted selection map for female elk in the spring.

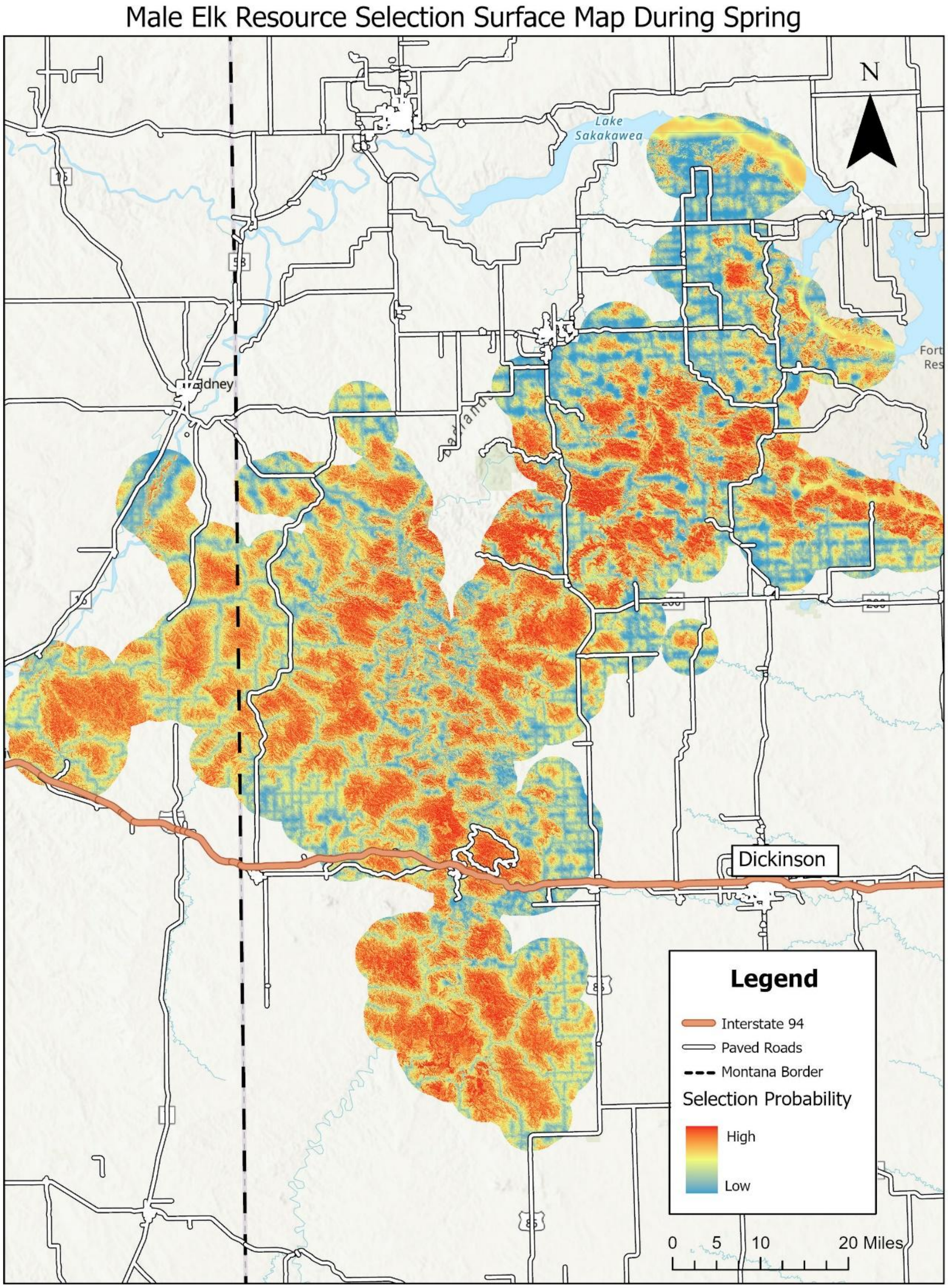


Figure F6. Predicted selection map for male elk in the spring.

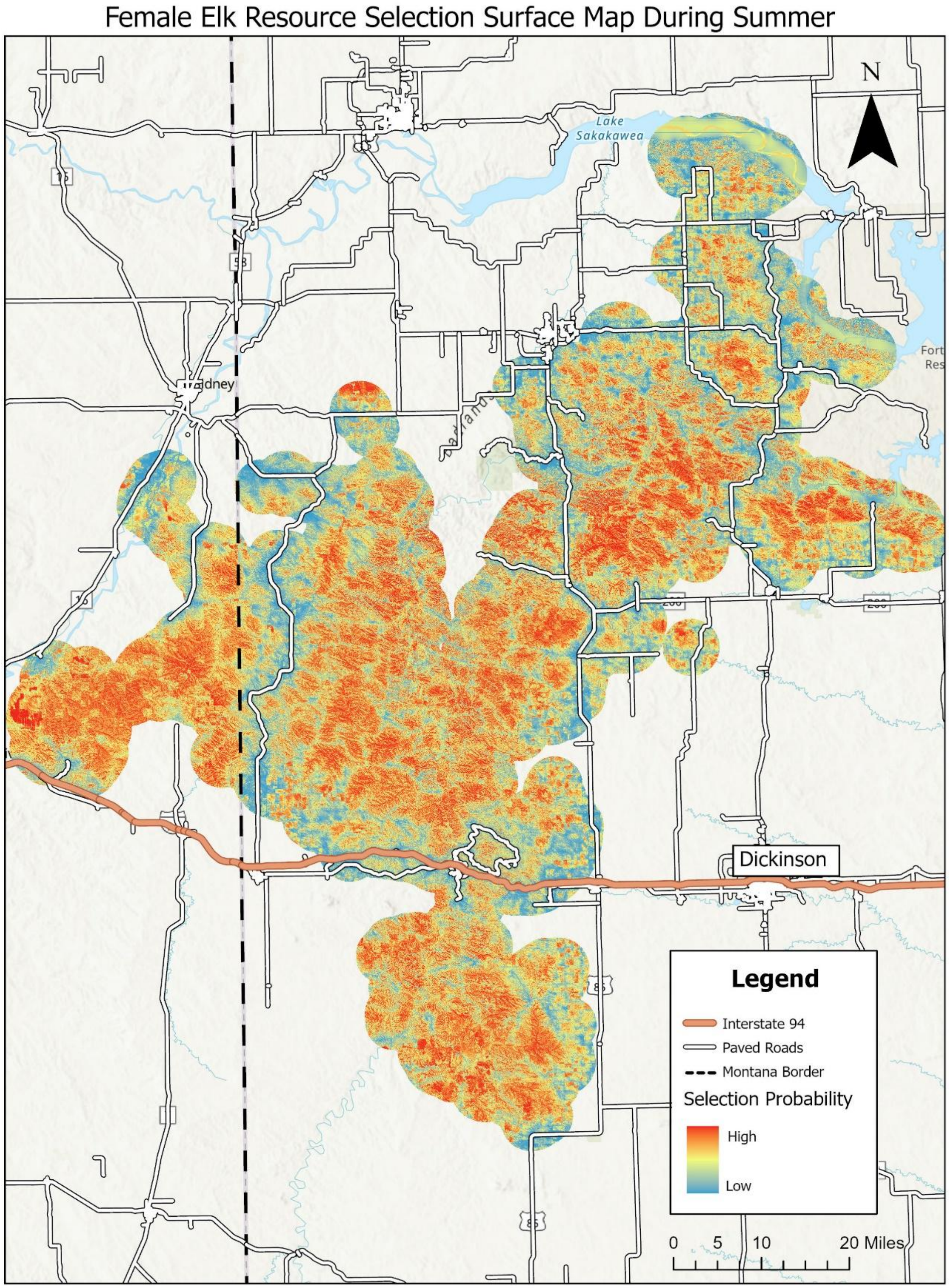


Figure F7. Predicted selection map for female elk in the summer.

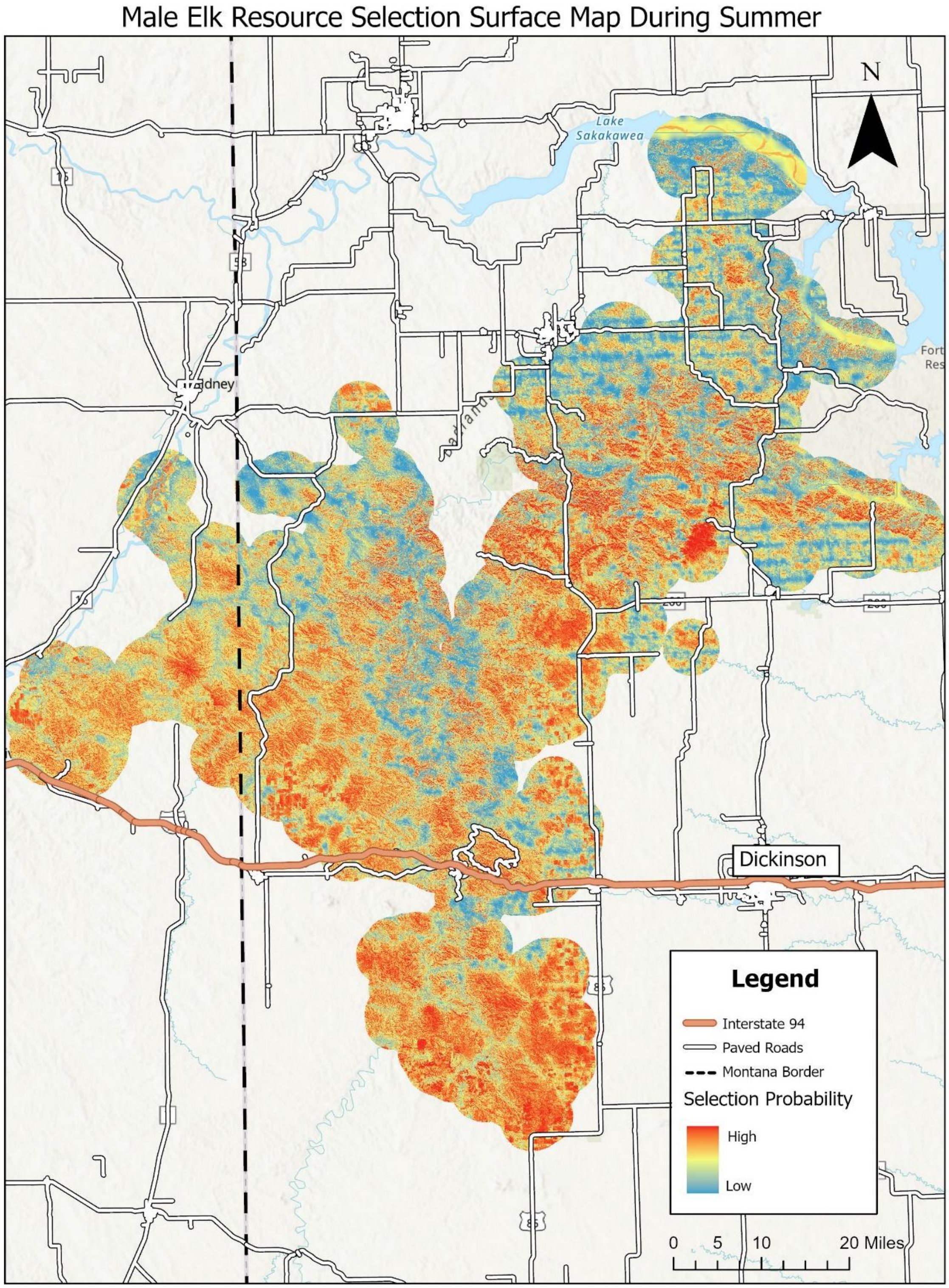


Figure F8. Predicted selection map for male elk in the summer.

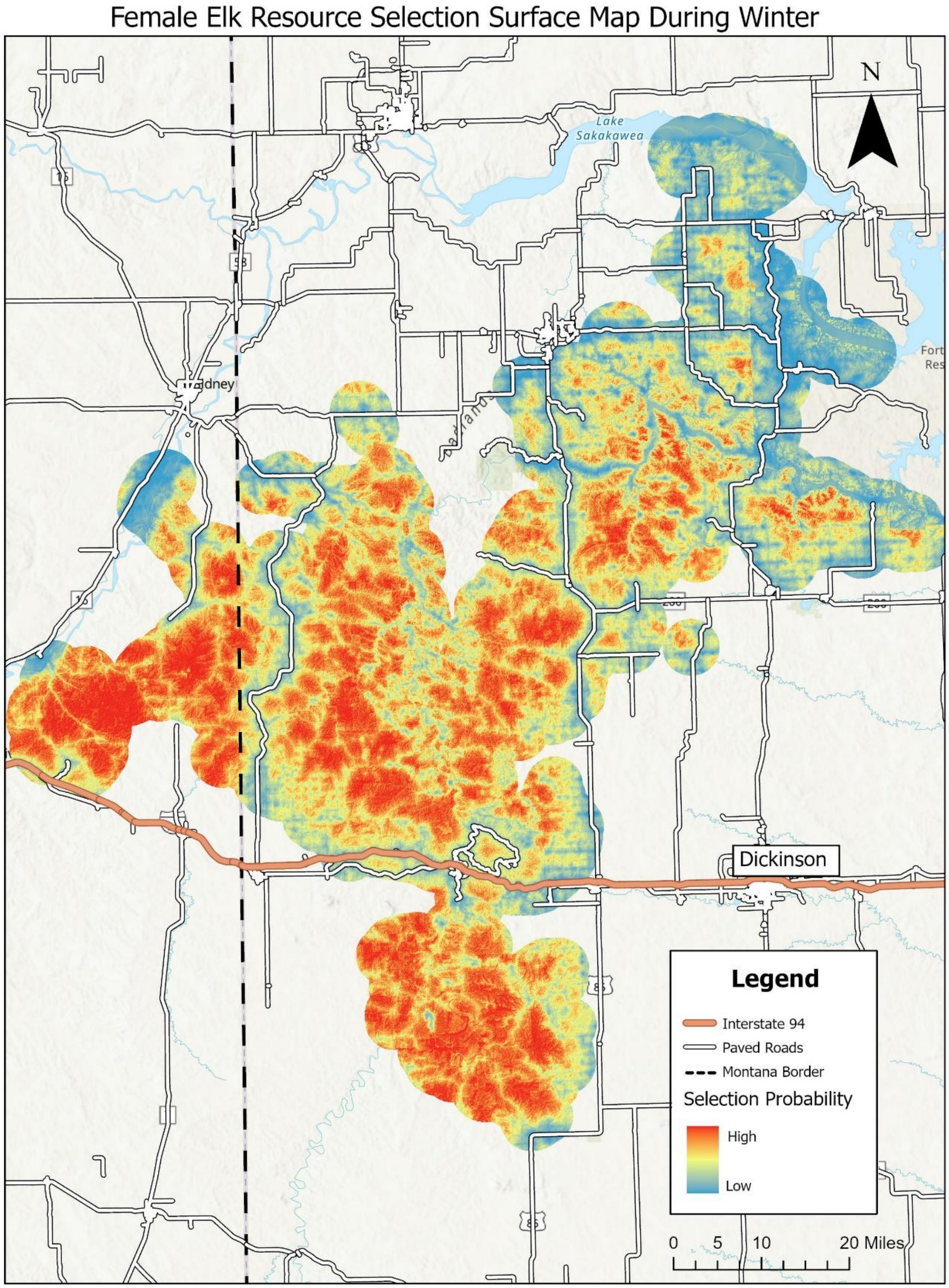


Figure F9. Predicted selection map for female elk in the winter.

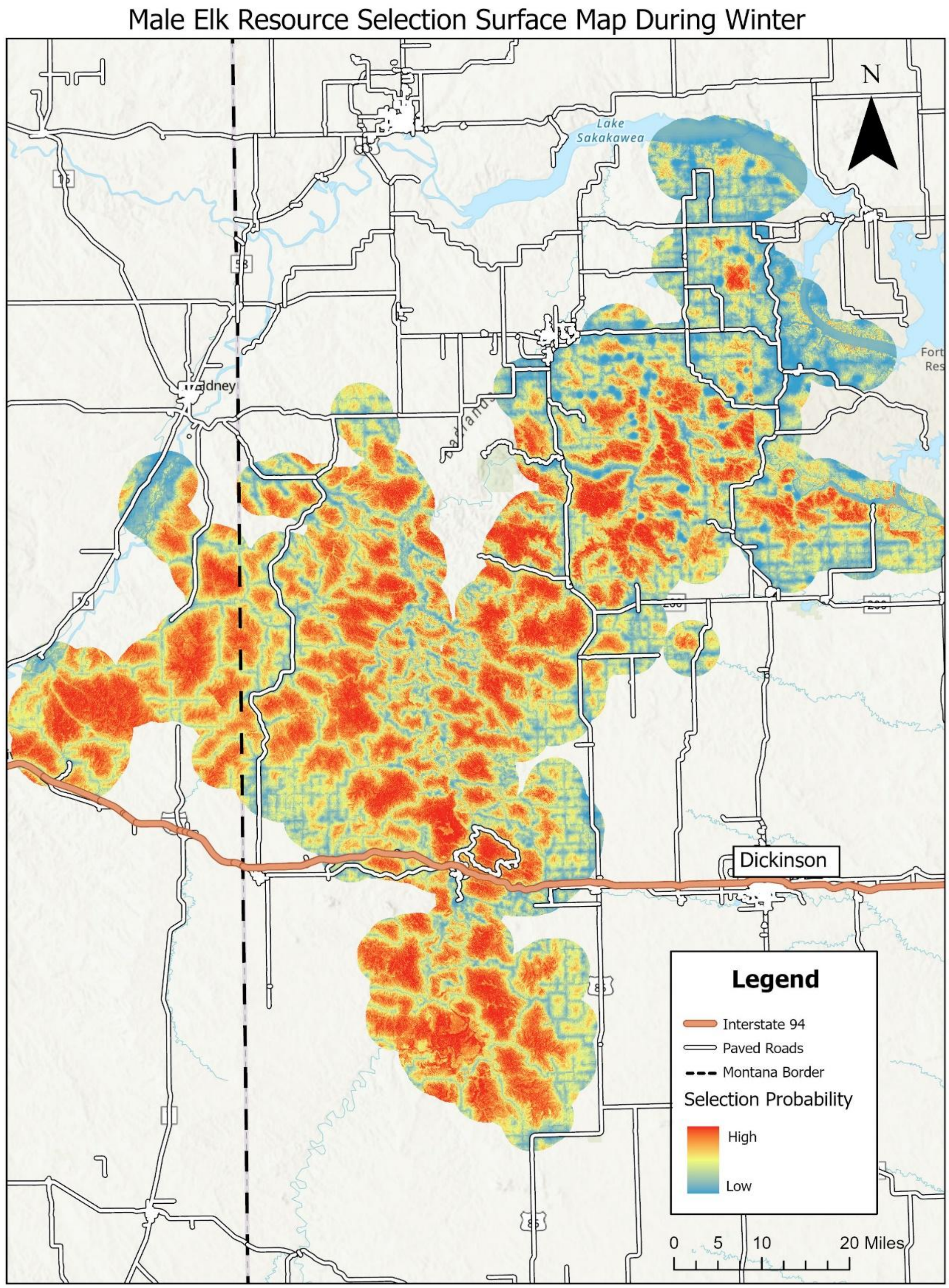
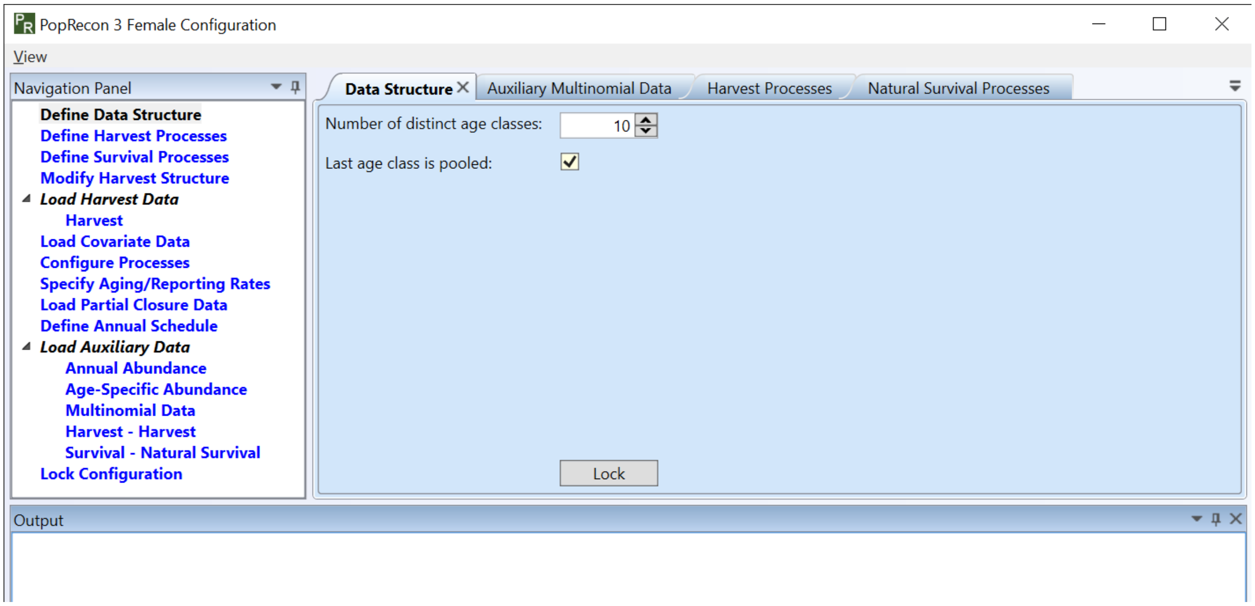


Figure F10. Predicted selection map for male elk in the winter.

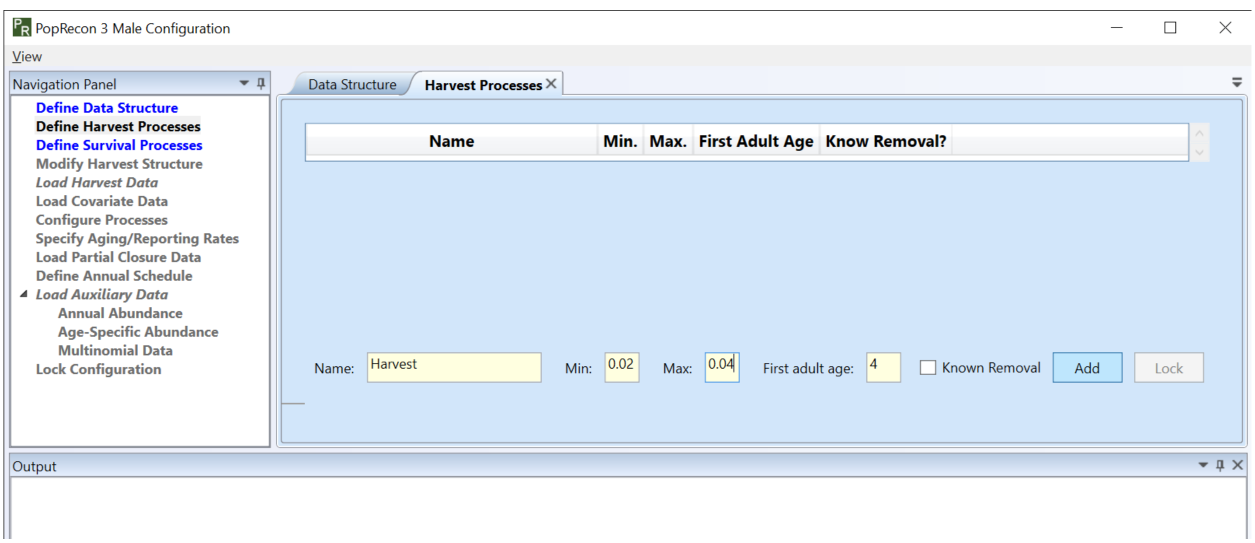
Appendix F – Define Data Age Structure

This is set at 10 age classes with the last age class pooled as 9+.



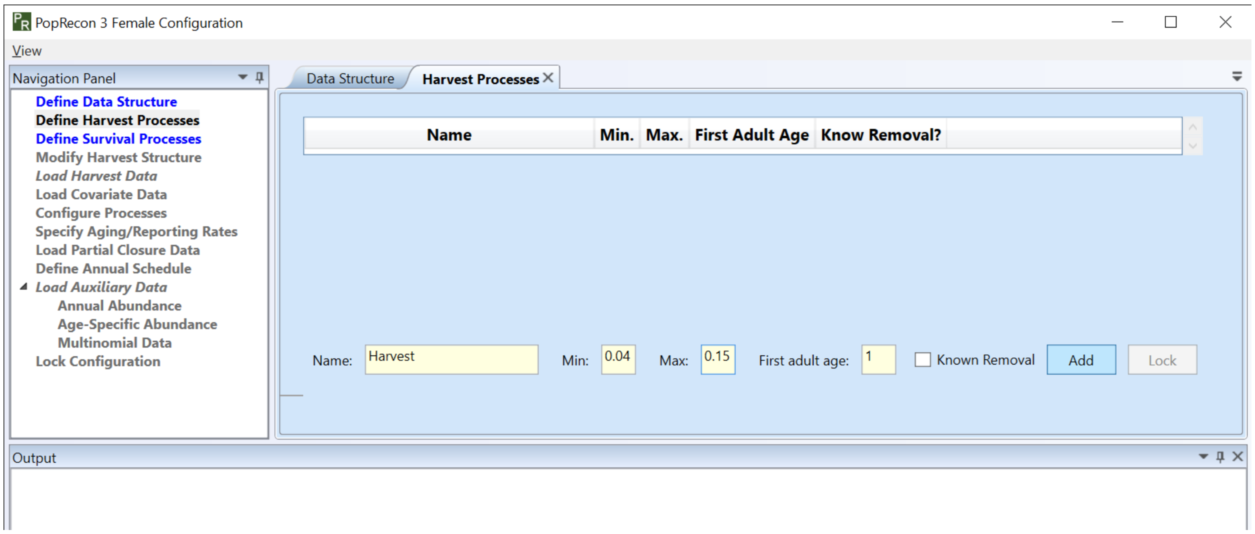
Appendix G – Define Harvest Processes for Males

Enter the name, min, max, and first adult age. Then click Add and Lock.



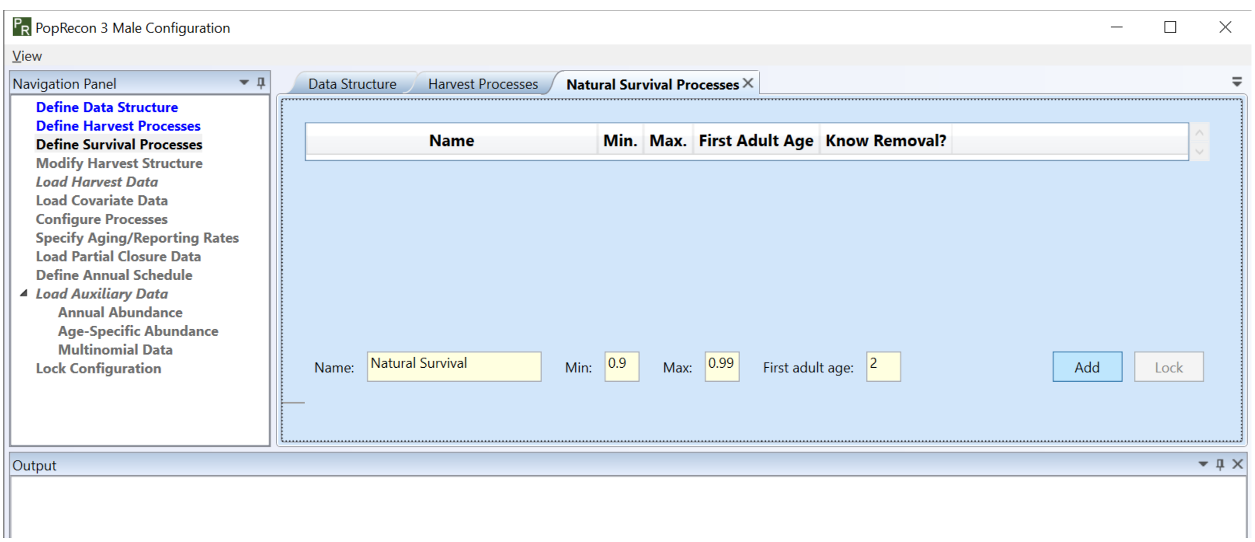
Appendix H – Define Harvest Processes for Females

Enter the name, min, max, and first adult age. Then click Add and Lock.



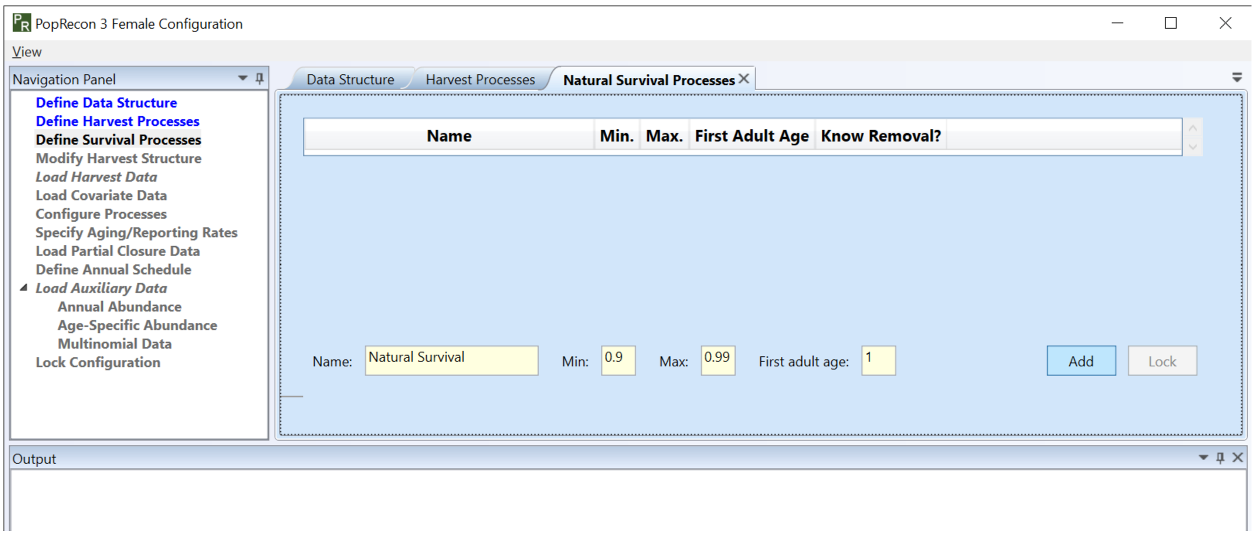
Appendix I – Define Survival Processes for Males

Enter the name, min, max, and first adult age. Then click Add and Lock.



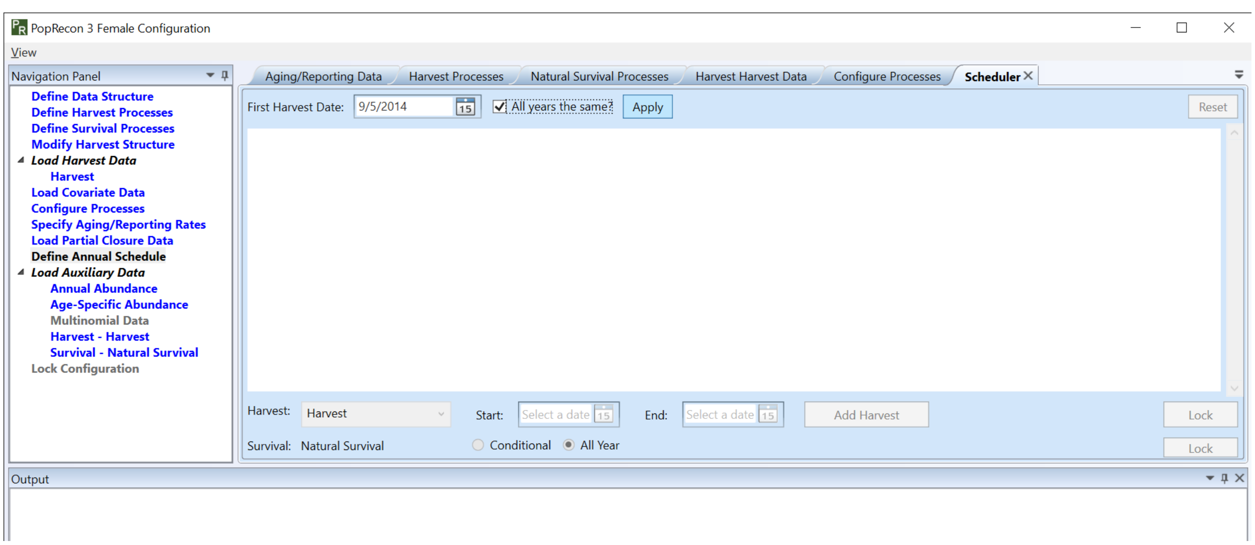
Appendix J – Define Survival Processes for Females

Enter the name, min, max, and first adult age. Then click Add and Lock.

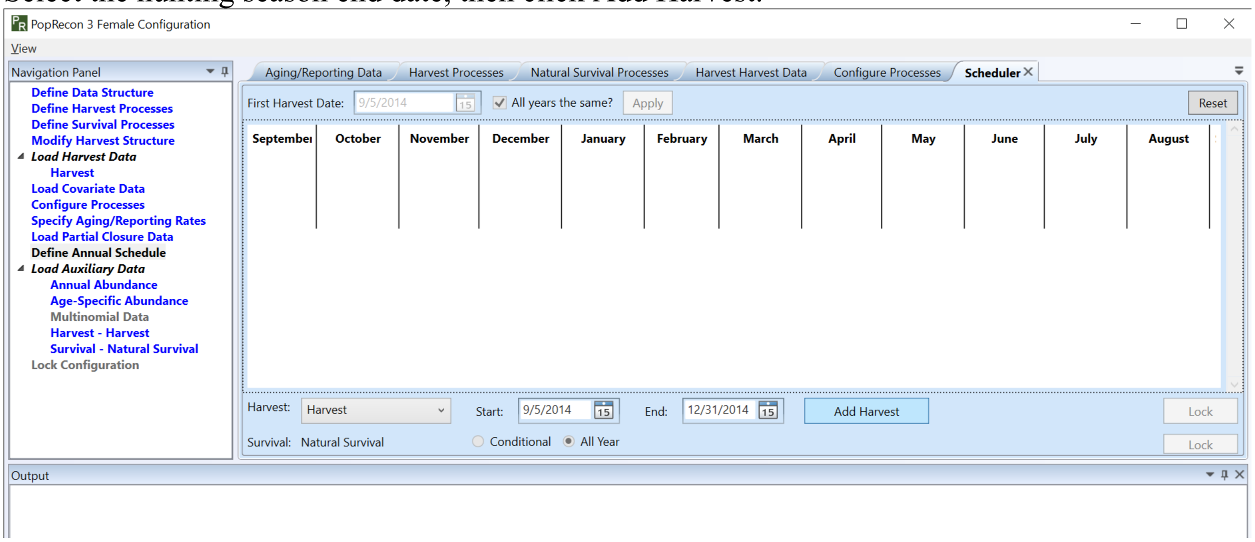


Appendix K – Define Annual Schedule

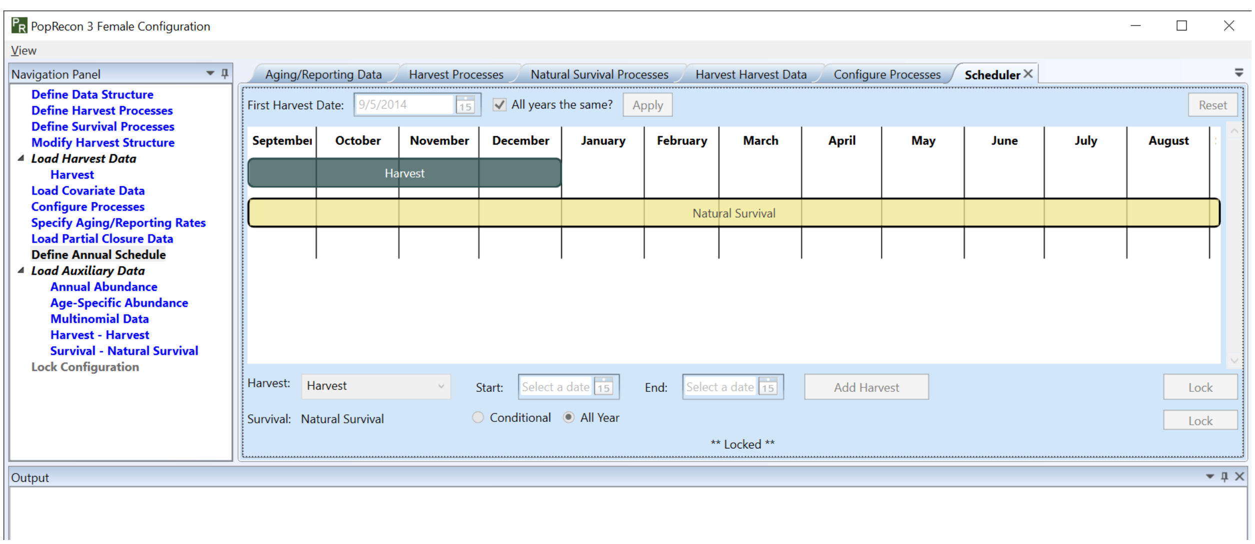
Select the first day of the hunting season. Here you can select all years the same or define different start days for each year. Then click Apply.



Select the hunting season end date, then click Add Harvest.

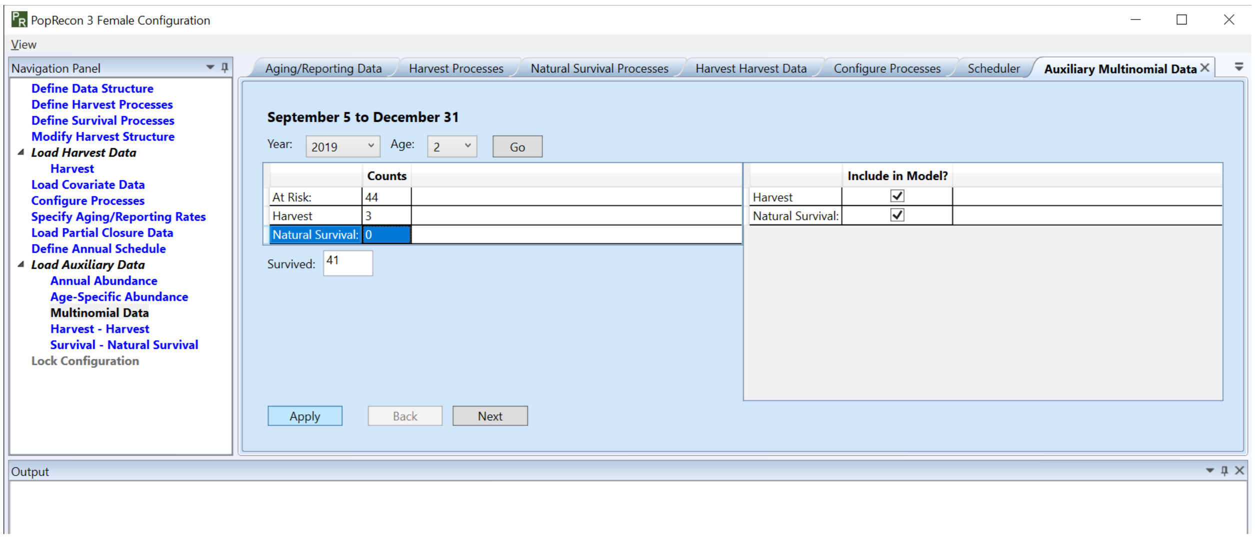


Lock the harvest schedule, then select All Year for Natural Survival and Lock.

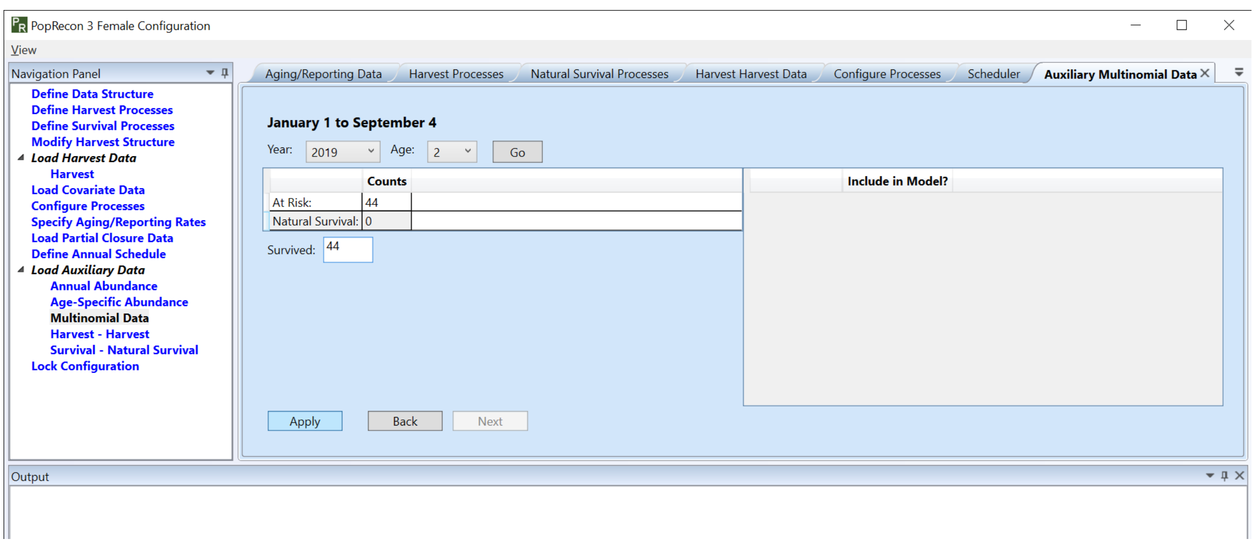


Appendix L – Multinomial Data (Auxiliary GPS Collar Data)

All data is entered separately for each year and each age class. This example shows entering data for 2-year-olds in for 2019. First, data for hunting season is entered. Select 2019 for Year and 2 for Age, then click Go. Enter values for At Risk, Harvested, and Natural Survival. Click Apply, then Next.



Next, data for non-hunting season is entered. Enter values for At Risk and Natural Survival. Repeat this process for all age classes recorded for that year and for each year collar data is available.



Appendix M. Workflow for updating SPR model.

Annual SPR Model Update Workflow

Instructions for adding age-at-harvest data for additional years into PopRecon3

This workflow will walk you through the process of adding additional years of age-at-harvest data to the statistical population reconstruction model developed for the elk population in hunt units E2, E3, and E4. The base model file and formatted data for years 2014 – 2021 have been saved and shared in a folder that can be accessed here: Bruce ND SPR Model Files.

1. Update data formatted for PopRecon3
    a. Open the new age-at-harvest data
    b. Sort data by sex, then by age
    c. Open the file "Bull Age at Harvest Pooled at 9 Ages with Effort Through 2021.csv"
    d. Count all the bull harvests for each age class starting with calves and ending with all bulls 9+ years old and enter them into the SPR data spreadsheet (Column B is yearlings).
    e. Open the new effort data
    f. For males, add up the total number of "Hunt Days" for all "Any" and "Landowner" tags, divide by 10,000, and enter this number for effort in column L of the bull data sheet.

TABLE 1. License information and reported harvest of elk during the 2022 season.

LIC. TYPE	ISSUED	APPLICATIONS	RETURNS	HUNTERS	HUNT DAYS	AVG. HUNT DAYS	CPUE	DAYS PER ELK	TOT. HARVEST	BULL/COW/CALF	HUNTER SUCCESS(%)	SATISFACTION
E1E - Any	14	3,683	14	12	151	12.58	0.079	12.58	12	12/0/0	100.0	4.78
E1E - Landowner	16	123	16	16	210	13.12	0.071	14.00	15	15/0/0	93.8	4.00
E1E - Antlerless	80	180	79	69	782	11.33	0.036	27.93	28	0/27/1	40.6	3.69
E1E - Unit Total	**110**	**3,986**	**109**	**97**	**1,143**	**11.78**	**0.048**	**20.78**	**55**	**27/27/1**	**56.7**	**4.16**
E1W - Any	13	2,389	13	13	161	12.38	0.068	14.64	11	11/0/0	84.6	4.33
E1W - Landowner	12	72	12	12	196	16.33	0.051	19.60	10	10/0/0	83.3	4.60
E1W - Antlerless	55	127	54	50	363	7.26	0.110	9.07	40	0/37/3	80.0	4.68
E1W - Unit Total	**80**	**2,588**	**79**	**75**	**720**	**9.60**	**0.085**	**11.80**	**61**	**21/37/3**	**81.3**	**4.54**
E2 - Any	29	6,455	28	28	376	13.43	0.064	15.67	24	23/1/0	85.7	4.38
E2 - Landowner	21	143	21	21	254	12.10	0.059	16.93	15	13/1/1	71.4	4.46
E2 - Antlerless	90	142	88	72	502	6.97	0.078	12.87	39	0/35/4	54.2	3.94
E2 - Unit Total	**140**	**6,740**	**137**	**121**	**1,132**	**9.36**	**0.069**	**14.51**	**78**	**36/37/5**	**64.5**	**4.26**
E3 - Any	55	8,236	54	52	519	9.98	0.087	11.53	45	43/2/0	86.5	4.42
E3 - Landowner	30	101	30	27	169	6.26	0.101	9.94	17	16/1/0	63.0	4.11
E3 - Antlerless	120	219	118	103	702	6.82	0.083	12.10	58	0/51/7	56.3	3.82
E3 - Unit Total	**205**	**8,556**	**202**	**182**	**1,390**	**7.64**	**0.086**	**11.58**	**120**	**59/54/7**	**65.9**	**4.12**
E4 - Any	10	1,064	9	9	138	15.33	0.043	23.00	6	6/0/0	66.7	4.43
E4 - Landowner	14	14	14	12	184	15.33	0.060	16.73	11	11/0/0	91.7	3.71
E4 - Unit Total	**24**	**1,078**	**23**	**21**	**322**	**15.33**	**0.053**	**18.94**	**17**	**17/0/0**	**81.0**	**4.07**
E6 - Any	2	446	2	2	4	2.00	0.500	2.00	2	2/0/0	100.0	4.00
E6 - Landowner	2	6	2	2	4	2.00	0.500	2.00	2	2/0/0	100.0	
E6 - Antlerless	10	17	10	9	81	9.00	0.049	20.25	4	0/4/0	44.4	2.71
E6 - Unit Total	**14**	**469**	**14**	**13**	**89**	**6.85**	**0.090**	**11.12**	**8**	**4/4/0**	**61.5**	**3.36**
STATEWIDE	**573**	**23,417**	**564**	**509**	**4,796**	**9.42**	**0.071**	**14.15**	**339**	**164/159/16**	**66.6**	**4.08**

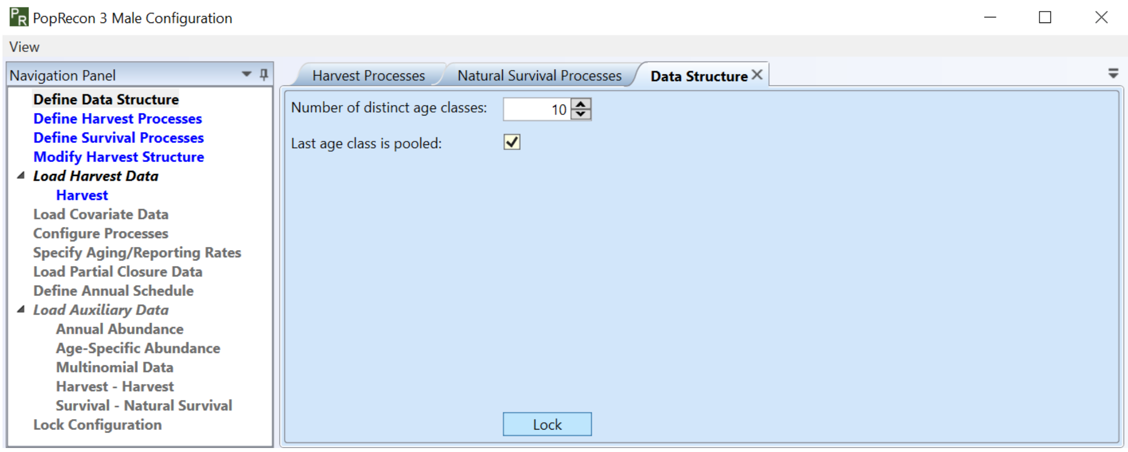
    g. Open the file "Bull Age at Harvest Pooled at 9 Ages with Harvest Totals Through 2021.csv"
    h. Look back at the new effort data and add up the harvested bull totals for units E2, E3, and E4.

TABLE 1. License information and reported harvest of elk during the 2022 season.

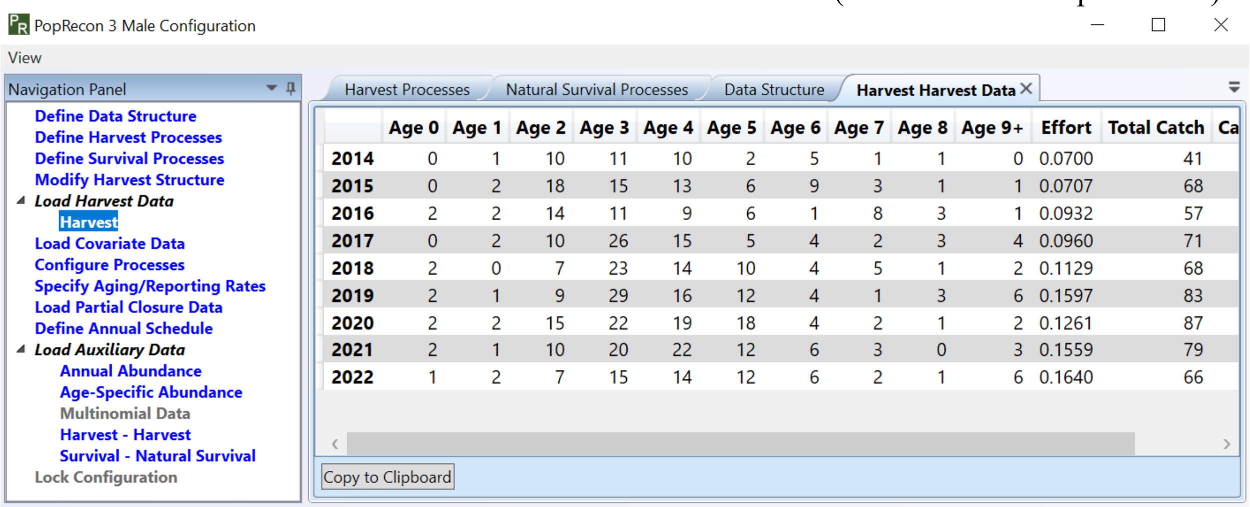
LIC. TYPE	ISSUED	APPLICATIONS	RETURNS	HUNTERS	HUNT DAYS	AVG. HUNT DAYS	CPUE	DAYS PER ELK	TOT. HARVEST	BULL/COW/CALF	HUNTER SUCCESS(%)	SATISFACTION
E1E - Any	14	3,683	14	12	151	12.58	0.079	12.58	12	12/0/0	100.0	4.78
E1E - Landowner	16	123	16	16	210	13.12	0.071	14.00	15	15/0/0	93.8	4.00
E1E - Antlerless	80	180	79	69	782	11.33	0.036	27.93	28	0/27/1	40.6	3.69
E1E - Unit Total	**110**	**3,986**	**109**	**97**	**1,143**	**11.78**	**0.048**	**20.78**	**55**	**27/27/1**	**56.7**	**4.16**
E1W - Any	13	2,389	13	13	161	12.38	0.068	14.64	11	11/0/0	84.6	4.33
E1W - Landowner	12	72	12	12	196	16.33	0.051	19.60	10	10/0/0	83.3	4.60
E1W - Antlerless	55	127	54	50	363	7.26	0.110	9.07	40	0/37/3	80.0	4.68
E1W - Unit Total	**80**	**2,588**	**79**	**75**	**720**	**9.60**	**0.085**	**11.80**	**61**	**21/37/3**	**81.3**	**4.54**
E2 - Any	29	6,455	28	28	376	13.43	0.064	15.67	24	23/1/0	85.7	4.38
E2 - Landowner	21	143	21	21	254	12.10	0.059	16.93	15	13/1/1	71.4	4.46
E2 - Antlerless	90	142	88	72	502	6.97	0.078	12.87	39	0/35/4	54.2	3.94
E2 - Unit Total	**140**	**6,740**	**137**	**121**	**1,132**	**9.36**	**0.069**	**14.51**	**78**	**36/37/5**	**64.5**	**4.26**
E3 - Any	55	8,236	54	52	519	9.98	0.087	11.53	45	43/2/0	86.5	4.42
E3 - Landowner	30	101	30	27	169	6.26	0.101	9.94	17	16/1/0	63.0	4.11
E3 - Antlerless	120	219	118	103	702	6.82	0.083	12.10	58	0/51/7	56.3	3.82
E3 - Unit Total	**205**	**8,556**	**202**	**182**	**1,390**	**7.64**	**0.086**	**11.58**	**120**	**59/54/7**	**65.9**	**4.12**
E4 - Any	10	1,064	9	9	138	15.33	0.043	23.00	6	6/0/0	66.7	4.43
E4 - Landowner	14	14	14	12	184	15.33	0.060	16.73	11	11/0/0	91.7	3.71
E4 - Unit Total	**24**	**1,078**	**23**	**21**	**322**	**15.33**	**0.053**	**18.94**	**17**	**17/0/0**	**81.0**	**4.07**
E6 - Any	2	446	2	2	4	2.00	0.500	2.00	2	2/0/0	100.0	4.00
E6 - Landowner	2	6	2	2	4	2.00	0.500	2.00	2	2/0/0	100.0	
E6 - Antlerless	10	17	10	9	81	9.00	0.049	20.25	4	0/4/0	44.4	2.71
E6 - Unit Total	**14**	**469**	**14**	**13**	**89**	**6.85**	**0.090**	**11.12**	**8**	**4/4/0**	**61.5**	**3.36**
STATEWIDE	**573**	**23,417**	**564**	**509**	**4,796**	**9.42**	**0.071**	**14.15**	**339**	**164/159/16**	**66.6**	**4.08**

i. Enter this total in line N of the file with harvest totals
j. Save both bull files under a new name indicating it has been updated for the current year.
k. Repeat same process for cow files (for cow effort, you will add up "Hunt Days" for all "Antlerless" tags; for cow harvest totals, add up all cows and calves harvested in the three relevant hunt units)

2. Confirm Base Model Parameters
    a. Launch PopRecon3 software
    b. Go to File/Open and select the file named "Base Model 2021.xml"
    c. Confirm that the following parameters are set as follows:
        i. Males
            1. Data Structure (tab) = 10 Pooled (You will need to enter and lock this in each time you run the model)
            2. Harvest Process (tab) = Min 0.2, Max 0.4, First Adult 4
            3. Survival (tab) = Min 0.9, Max 0.99, First Adult 2
        ii. Females
            1. Data Structure (tab) = 10 Pooled (You will need to enter and lock this in each time you run the model)
            2. Harvest Process (tab) = Min 0.04, Max 0.15, First Adult 1
            3. Survival (tab) = Min 0.9, Max 0.99, First Adult 1

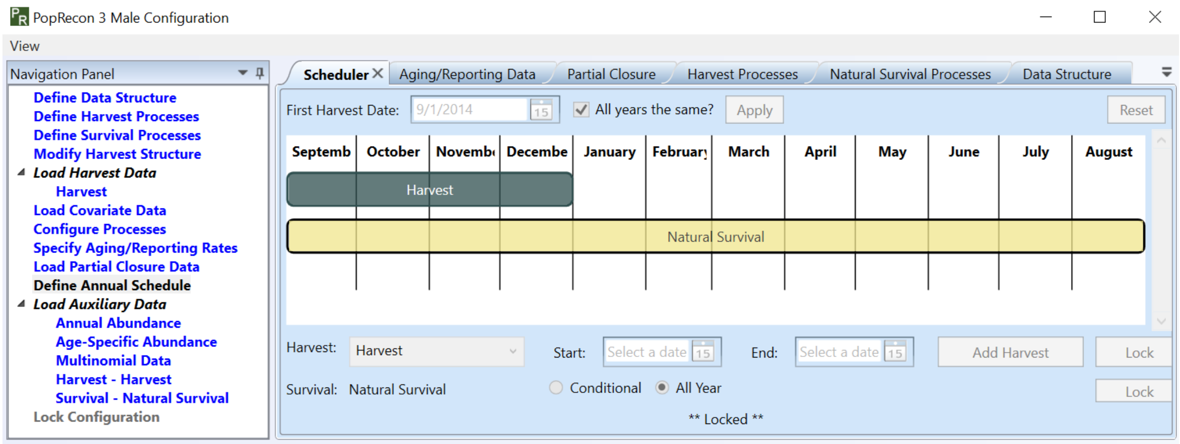


3. Male Configuration
   a. Harvest – load new bull data formatted for model (what we did in step *1i* above)



	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9+	Effort	Total Catch	Ca
2014	0	1	10	11	10	2	5	1	1	0	0.0700	41	
2015	0	2	18	15	13	6	9	3	1	1	0.0707	68	
2016	2	2	14	11	9	6	1	8	3	1	0.0932	57	
2017	0	2	10	26	15	5	4	2	3	4	0.0960	71	
2018	2	0	7	23	14	10	4	5	1	2	0.1129	68	
2019	2	1	9	29	16	12	4	1	3	6	0.1597	83	
2020	2	2	15	22	19	18	4	2	1	2	0.1261	87	
2021	2	1	10	20	22	12	6	3	0	3	0.1559	79	
2022	1	2	7	15	14	12	6	2	1	6	0.1640	66	

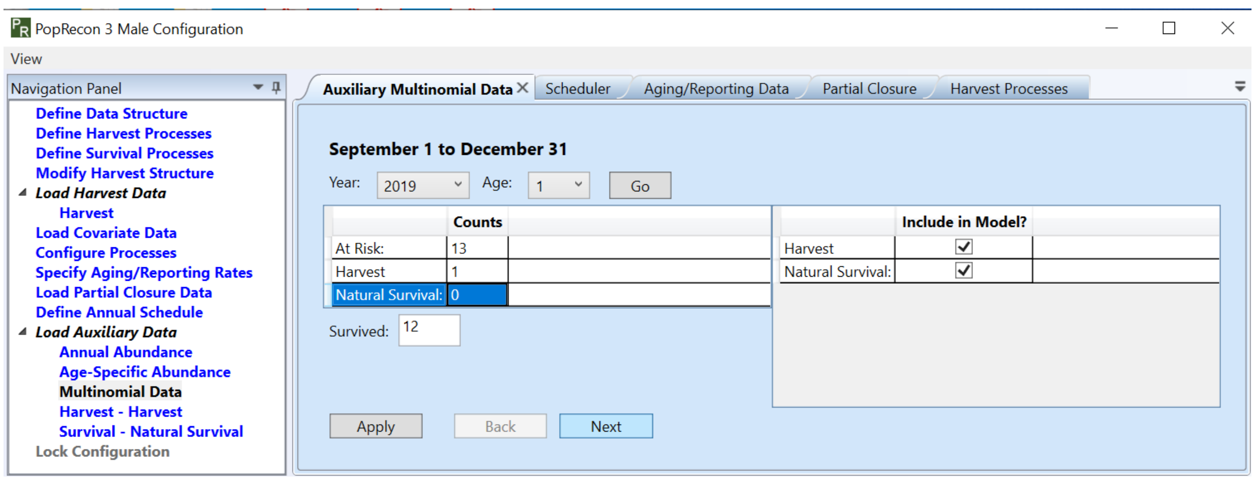
   b. Configure Processes – select Random Effects and Apply (Done Each Model Run)
   c. Specify Aging/Reporting Rates:
      i. Select "Year-Specific" and Apply
      ii. Open bull data with harvest totals file **(Outside of PopRecon)**
      iii. Copy the harvest totals column **(Column N)**
      iv. Go back to PopRecon3, select "Copy from Clipboard" and Apply
      v. Select Lock
   d. Define Annual Schedule:
      i. First Harvest Date = 9/1/14
         1. Check "All Years the Same" box and Apply
      ii. End = 12/31/14
         1. Select "Add Harvest" and Lock
      iii. Natural Survival – select "All Year" and Lock



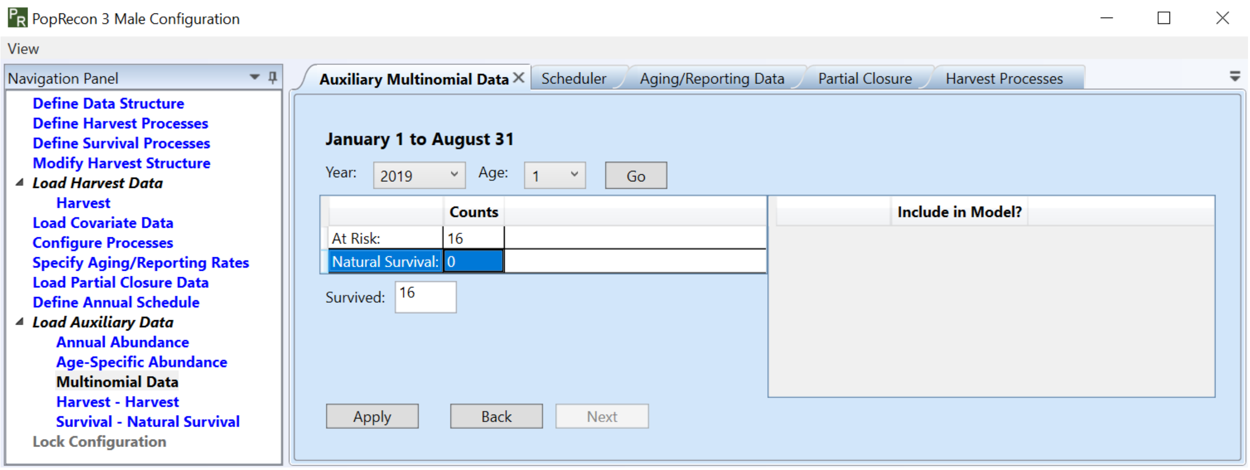
e. Multinomial Data:

i. 2019 – Select **2019** and **Age 1** from drop down boxes and click “Go” (*Very Important to click “Go” each time year or age is changed)

1. At Risk = **13**
2. Harvest = **1**
3. Natural Survival = **0**
4. Click Apply and Next



5. At Risk = **16**
6. Natural Survival = **0**
7. Click Apply



8. Follow same process for Age 3 with totals
9. Select **Age 3** from drop down box and click "Go"
10. At Risk = **4**
11. Harvest = **2**
12. Natural Survival = **0**
13. Click Apply and Next
14. At Risk = **4**
15. Natural Survival = **0**
16. Click Apply

ii. 2020 – Select **2020** and **Age 2** from drop down boxes and click "Go"
1. At Risk = **7**
2. Harvest = **3**
3. Natural Survival = **0**
4. Click Apply and Next
5. At Risk = **7**
6. Natural Survival = **0**
7. Click Apply

8. Select **Age 4** from drop down box and click "Go"
9. At Risk = **1**
10. Harvest = **0**
11. Natural Survival = **0**
12. Click Apply and Next
13. At Risk = **1**
14. Natural Survival = **0**
15. Click Apply

iii. 2021 – Select **2021** and **Age 1** from drop down boxes and click "Go"
1. At Risk = **6**
2. Harvest = **1**
3. Natural Survival = **0**
4. Click Apply and Next

5. At Risk = **13**
6. Natural Survival = **0**
7. Click Apply

8. Select **Age 3** from drop down box and click "Go"
9. At Risk = **2**
10. Harvest = **0**
11. Natural Survival = **0**
12. Click Apply and Next
13. At Risk = **2**
14. Natural Survival = **0**
15. Click Apply

4. Female Configuration
   a. Harvest – load new cow data formatted for model (what we did in step *1i* above)
   b. Configure Processes – select Random Effects and Apply (Done Each Model Run)
   c. Specify Aging/Reporting Rates:
      i. Select "Year-Specific" and Apply
      ii. Open cow data with harvest totals file
      iii. Copy the harvest totals column
      iv. Go back to PopRecon3, select "Copy from Clipboard" and Apply
      v. Select Lock
   d. Define Annual Schedule:
      i. First Harvest Date = 9/1/14
         1. Check "All Years the Same" box and Apply
      ii. End = 12/31/14
         1. Select "Add Harvest" and Lock
      iii. Natural Survival – select "All Year" and Lock
   e. Multinomial Data:
      i. 2019 – Select **2019** and **Age 1** from drop down boxes and click "Go"
         1. At Risk = **5**
         2. Harvest = **1**
         3. Natural Survival = **0**
         4. Click Apply and Next
         5. At Risk = **5**
         6. Natural Survival = **0**
         7. Click Apply

         8. Select **Age 2** from drop down box and click "Go"
         9. At Risk = **44**
         10. Harvest = **3**
         11. Natural Survival = **0**
         12. Click Apply and Next
         13. At Risk = **44**
         14. Natural Survival = **0**
         15. Click Apply

16. Select **Age 3** from drop down box and click “Go”
17. At Risk = **18**
18. Harvest = **0**
19. Natural Survival = **0**
20. Click Apply and Next
21. At Risk = **18**
22. Natural Survival = **0**
23. Click Apply

ii. 2020 – Select **2020** and **Age 2** from drop down boxes and click “Go”

1. At Risk = **4**
2. Harvest = **1**
3. Natural Survival = **0**
4. Click Apply and Next
5. At Risk = **4**
6. Natural Survival = **0**
7. Click Apply

8. Select **Age 3** from drop down box and click “Go”
9. At Risk = **42**
10. Harvest = **7**
11. Natural Survival = **1**
12. Click Apply and Next
13. At Risk = **48**
14. Natural Survival = **1**
15. Click Apply

iii. 2021 – Select **2021** and **Age 1** from drop down boxes and click “Go”

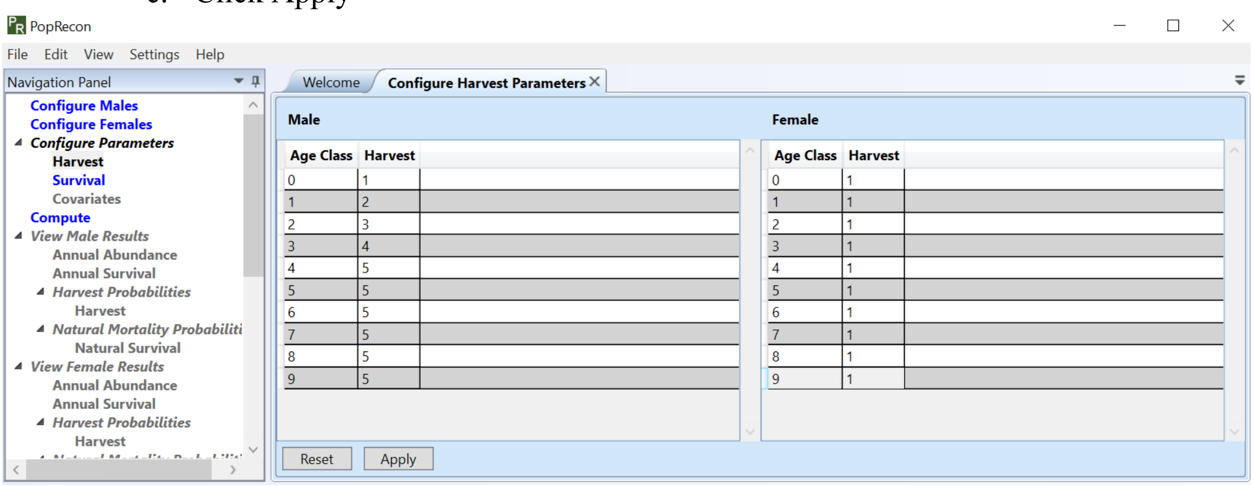
1. At Risk = **3**
2. Harvest = **0**
3. Natural Survival = **0**
4. Click Apply and Next
5. At Risk = **3**
6. Natural Survival = **0**
7. Click Apply

8. Select **Age 2** from drop down box and click “Go”
9. At Risk = **19**
10. Harvest = **0**
11. Natural Survival = **0**
12. Click Apply and Next
13. At Risk = **22**
14. Natural Survival = **0**
15. Click Apply

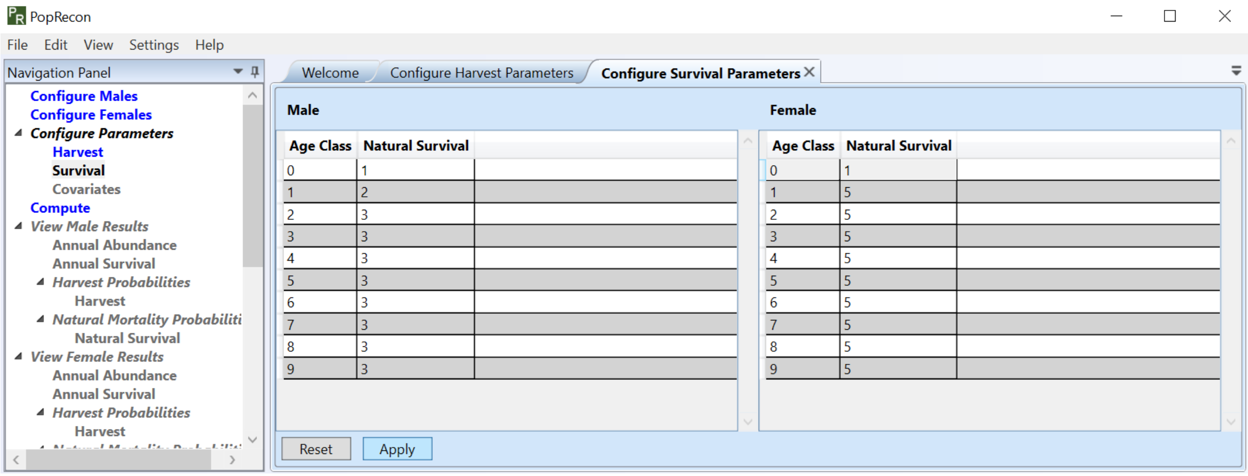
16. Select **Age 3** from drop down box and click "Go"
17. At Risk = **17**
18. Harvest = **1**
19. Natural Survival = **1**
20. Click Apply and Next
21. At Risk = **19**
22. Natural Survival = **0**
23. Click Apply

5. Lock Both Male and Female Configurations
    a. Click "Lock Configuration" on both male and female windows
    b. Go to File/Save to save this model with everything complete to this point. You can open this file if you want to run the model again without having to complete every step (just the highlighted steps above)

6. Configure Main Harvest Parameters
    a. Before computing model results, select "Harvest" under "Configure Parameters" on the main PopRecon window
    b. Enter "1" in the Harvest column for every age class of **Females**
    c. Click Apply



    d. Then select "Survival"
    e. Enter "1" in the Harvest column for the **0 Age Class Females**
    f. Select Apply



7. Run the Model
    a. Select "Compute"
    b. The model will run and produce various tables and graphs of the results for males, females, and combined results