Federal Aid in Wildlife Restoration Grant W-179-R

2025 Final Report

Elk Habitat Management in Montana

Nicole Bealer, Research Technician, Montana Fish, Wildlife & Parks, nicole.bealer@mt.gov

Dr. Kelly Proffitt, Research Biologist, Montana Fish, Wildlife & Parks, kproffitt@mt.gov

Shane Petch, Wildlife Biologist, Montana Fish, Wildlife & Parks, shane.petch@mt.gov

Dr. Jay Rotella, Professor, Montana State University, rotella@montana.edu

Elisabeth Krieger, Research Technician, Montana Fish, Wildlife & Parks, elisabeth.krieger@mt.gov

Dr. Kaitlin Macdonald, Research Associate, Montana State University, kaitlin.r.macdonald@gmail.com

Emily Mitchell, Wildlife Biologist, Montana Fish, Wildlife & Parks, emily.mitchell@mt.gov

Ryan DeVore, Wildlife Biologist, Montana Fish, Wildlife & Parks, RDeVore@mt.gov

State: Montana
Agencies: Montana Fish, Wildlife & Parks and Montana State University
Grant: Elk Habitat Management in Montana
Grant #: F20AF10828-00
Montana Tracking: W-179-R
Time Period: 01 August 2020 – 30 June 2025

Suggested Citation: Bealer, N., K. Proffitt, S. Petch, J. Rotella, E. Krieger, K. Macdonald, E. Mitchell, R. DeVore. Elk Habitat Management in Montana. 2025. Final Report for Federal Aid in Wildlife Restoration Grant W-179-R. Montana Fish, Wildlife & Parks

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Executive Summary

The Elk Habitat Management in Montana project was initiated to gather information on seasonal habitat use and movements of elk and to evaluate the importance of hunter access management in determining elk distributions during the hunting season. The objectives of this project were to 1) delineate seasonal ranges and movement corridors in the Devil's Kitchen, Custer Forest, and Missouri Breaks study areas, 2) conduct state-wide analysis of factors associated with overabundant elk populations, and 3) conduct habitat selection analyses in the Devil's Kitchen, Custer Forest, and Missouri Breaks study areas.

We captured 65 female elk in the Devil's Kitchen study area and collected 1,167,870 GPS locations. We captured 49 female elk and 29 male elk in the Custer Forest study area and collected 913,440 GPS locations. Finally, we captured 56 females and 37 males in the Missouri Breaks study area and collected 911,367 GPS locations. Movement information collected in all areas was shared on a monthly basis with state and federal agency partners. We compiled estimates of seasonal ranges and movement corridors for each area based on GPS data from collared individuals. All three populations displayed high overlap between their summer and winter ranges, demonstrating a lack of significant seasonal range shift. Approximately 56% of the Devil's Kitchen population, 29% of the Custer Forest population, and 17% of the Missouri Breaks population exhibited migratory movements. Multiple notable individual elk movements were observed during the monitoring period, including the movement of a male elk in the Missouri Breaks area that crossed the Missouri River to the north and a male elk in the Custer Forest area that dispersed to South Dakota.

To meet our second objective, we carried out a broad-scale analysis to understand the characteristics of hunting districts that are related to problematic elk populations, i.e., populations that are above the prescribed population objective, and to identify management tools that may be effective in managing these populations to levels that correspond with population objectives. We focused on evaluating the relationship between harvest metrics, hunter access, and landscape characteristics and two response variables: the estimated population growth rate and the difference between population abundance and objective. We used population survey data and harvest data to estimate population growth rates for individual hunting districts with an integrated population model. We then evaluated how harvest metrics, hunter access, and landscape characteristics related to population growth and the degree to which populations are over objective using multiple linear regression models.

We found that the proportion of hunter accessible land in a hunting district was the most important predictor of how far a population was over objective. As the proportion of hunter accessible land in a hunting district decreases the number of elk over the population objective is predicted to increase. We also found that there was some evidence for a relationship between the proportion of security habitat on hunter accessible land and how far a population is over objective. As the proportion of security habitat on hunter accessible land increases the number of elk over the population objective is predicted to decrease. We only found one covariate, female

harvest intensity, to be related to population growth, with the population growth rate predicted to decrease as female harvest intensity increases.

For the Devil's Kitchen habitat selection analysis, we used elk location data collected from the hunting season to address two primary objectives: (1) evaluate the effects of hunting period, harvest regulation, migratory behavior, and snow-water equivalent on elk movements across land with various hunter access management strategies during the hunting season, and (2) evaluate the effects of hunter access management, harvest regulation, and other landscape factors on female elk habitat selection across the four hunting periods. To address these objectives, we fit a series of Bayesian multistate models to evaluate the factors influencing the probability that an elk transitioned between hunter access management strategies during the fall hunting season. We also constructed resource selection functions (RSFs) explaining female elk habitat selection in the early shoulder, archery, general, and late shoulder hunting periods.

The top model evaluating factors influencing the probability that an elk transitioned between hunter access management strategies included hunting period as the explanatory variable, suggesting that changes in conditions between the hunting periods were most influential on elk movements between hunter access management strategies. Female elk were generally more likely to remain in the same hunter access management strategy during hunting season, but some movement between hunter access management strategies occurred. Estimates from our model demonstrated moderate probabilities of movement from open access to less accessible private lands during the early shoulder and archery seasons, moderate probabilities of movement between hunter access management strategies in all directions during the general season, and high probability of movement from open access to limited access in the late shoulder season.

The top model explaining female elk resource selection indicated that hunter access management and harvest regulation influence female elk habitat selection in significant and interacting ways. Elk generally avoided hunting pressure by selecting for areas with less hunter access and more restrictive harvest regulations, but their responses varied between hunting periods. Hunter access management more strongly influenced elk habitat selection in the early shoulder and archery seasons, whereas harvest regulation played a stronger role during the general and late shoulder seasons. The strongest elk selection response occurred in the late shoulder season, when the odds of female elk selecting for the BTWMA, which had no harvest or access permitted, were over 30 times higher than the odds of selecting for areas with liberal harvest and open hunter access. The regulation and access restrictions on the BTWMA created a refuge for elk, leading to desirable elk distribution and achieving the goal of providing winter habitat security for elk, but potentially limiting female harvest.

For the Custer Forest and Missouri Breaks habitat selection analysis, we used location data collected from male and female elk during the archery and rifle season to address the following objectives: (1) evaluate relationships between resource selection and landscape and environmental factors that may influence population distributions, (2) assess individual variability in risk-related selection patterns and examine functional responses between individual selection and the gradient of harvest risk, and (3) identify and map security habitat metrics to provide recommendations for security habitat management in prairie landscapes. To address these objectives, we first fit RSFs with individual random effects to evaluate relationships between elk selection and hunter access, canopy cover, distances to motorized routes, herbaceous biomass, and snow water equivalent. Next, we fit univariate models comparing harvest risk and individual habitat selection patterns to assess evidence for risk-related responses. Finally, we calculated security habitat thresholds based on our best-supported RSF models and produced maps identifying areas that provide security for elk during archery and rifle hunting seasons.

Across the archery and rifle seasons, our models indicated that elk typically preferred areas with restricted hunter access over open access as well as greater values of canopy cover, distance to motorized routes, terrain ruggedness, and herbaceous biomass, while they avoided snow water equivalent. However, there were a few notable exceptions to these general patterns. First, we did not detect elk responses to motorizes route distance in the Missouri Breaks (except for males during the archery season), and second, male elk in the Missouri Breaks preferred open access areas over restricted access during the rifle season. Additionally, we found evidence of risk-related responses, though responses varied by season, study area and sex. Risk responses were most evident with canopy cover in the Custer Forest and with terrain ruggedness in the Missouri Breaks, respectively. Lastly, we calculated and mapped thresholds for canopy cover, terrain ruggedness and distances to motorized routes to represent security and preferred security habitat in our prairie study areas.

Project Background

Recently, there has been a focus in the western United States to identify and conserve big game migration corridors and winter ranges, as highlighted in the 2018 Department of Interior Secretarial Order 3362. Seasonal range and movement information is lacking for many elk populations in Montana, particularly in the central and eastern portion of the State. As part of a Montana Fish, Wildlife and Parks (MFWP) initiative to identify elk migration corridors and winter ranges and work cooperatively with partners to conserve these important habitats, there is a need to collect and assess elk movement data. The purpose of this project was to identify seasonal ranges and movement corridors for the Devil's Kitchen, Custer Forest, and Missouri Breaks elk populations in central and eastern Montana (Figure 1), evaluate the effects of hunter access management and other landscape features on habitat selection in these populations, and provide information to enhance elk management in prairie regions.

Our first goal was to delineate migration corridors and seasonal ranges of 3 elk populations in central and eastern Montana including the Devil's Kitchen, Custer Forest, and Missouri Breaks populations. These areas were selected based on the local needs identified by MFWP management biologists, and where considerable community, conservation partner, and agency interest in elk habitat conservation exists. A standardized and comprehensive assessment of movement data ensured seasonal ranges and movement corridors are appropriately quantified, facilitated comparisons among populations, and resulted in a comprehensive communication tool that FWP can use to inform local stakeholders and agency partners as they consider ways to improve elk habitat in land use and planning decisions.

The seasonal range and movement corridor component of the project involved collecting elk location data from GPS-collared elk in the 3 study areas for 3 years (Figure 1). We developed methodologies for delineating seasonal ranges and corridors in collaboration with the USGS corridor mapping team and scientists in other state agencies utilizing Brownian bridge and kernel-based movement models. We estimated seasonal core use areas during winter and summer and summarized the attributes of seasonal ranges. We identified important movement corridors by estimating population-level migration routes (e.g., Horne et al. 2007, Kranstauber et al. 2012, Thurfjell et al. 2014, Avgar et al. 2016). Summaries and maps of location and movement data were presented in documents designed for landowners and managers that are intended for use in local decision making.

Fine-scale location data collected in the Devil's Kitchen study area helped to identify important seasonal habitats and movement corridors and provided information regarding the timing of seasonal movements. This information may now be used to refine harvest management strategies that maximize the effectiveness of elk management in the area. Landowners, MFWP, and community members are presently engaged in a longstanding community working group (Devil's Kitchen Working Group) that regularly meets to discuss elk management in the area. The results of this study will aid these conversations on elk management and facilitate stronger conservation-oriented discussions. Fine-scale location data collected in the Custer Forest and Missouri Breaks also provided new information to inform management aimed at achieving more desirable elk distributions and harvest.

Our second goal was to broadly evaluate factors associated with problematic and non-problematic elk populations. We defined problematic elk populations as elk populations that are over the prescribed population objective. Existing problematic elk populations may be driven by harvest regulations (Conover 2001, Sergeyev et al. 2022), factors that impact elk distributions such as restrictive hunter access management (Burcham et al. 1999, Proffitt et al. 2013, 2016), and other landscape characteristics (Ranglack et al. 2017, Barker et al. 2019, DeVoe et al. 2019) may also play a role in a population being over objective and a formal assessment was necessary to assess whether elk herds that are or are not considered problematic differ among these drivers. This assessment involved analyses of existing data from populations across the state.

To address our second goal, we combined data from aerial population surveys, hunter harvest estimates, and landscape characteristics at a statewide scale to broadly evaluate factors associated with problematic elk populations. Currently, the degree to which elk populations are over objective is hypothesized to relate to the amount of land with restrictive hunter access due to the impacts on elk distributions (Burcham et al. 1999, Proffitt et al. 2013, 2016); however, this hypothesis has not been broadly evaluated, and other attributes such as other landscape characteristics, harvest metrics, or population dynamics may also influence problematic populations. We estimated population growth rates with a previously published integrated population model (Paterson et al. 2019) using aerial population survey data and hunter harvest estimates. We then used linear regression models to assess how different factors relate to the degree elk populations are over objective and to population growth rates.

Our third goal was to evaluate the effects of hunter access management and other landscape factors on elk habitat selection in the Devils Kitchen, Custer Forest, and Missouri Breaks areas during the fall hunting seasons. Lands with restrictive hunter access may serve as refuges, and elk may aggregate in these areas to escape harvest risk during the hunting seasons (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013). If factors such as security habitat, forage, and hunter access management can be identified and related to habitat selection, wildlife managers may use this information to design management plans to manipulate these factors and increase the amount of time elk spend on public land. This could facilitate further opportunity for hunters using public lands and reduce game damage incurred on adjacent private lands. By increasing our understanding of these central Montana and prairie elk populations, FWP will be better able to sustainably provide harvest opportunity, minimize game damage and problematic distributions, and work with private and public land stewards to manage habitat that benefits elk.

MFWP and partners have invested considerable resources in evaluating the effects of factors such as hunter access management and elk security on elk distributions in the mountains and forested landscape of western Montana (Ranglack et al. 2017, DeVoe et al. 2019, Lowrey et al. 2020). However, no such studies have been conducted in central Montana and only one study has evaluated factors affecting elk distributions during the hunting season in prairie environments (Proffitt et al. 2016). This lack of information creates a challenge for wildlife managers in central Montana and the prairie regions. To address our third goal, we built from previous security habitat studies in Montana and provided information and recommendations as to population and habitat management strategies for elk in central Montana and the prairie environments of eastern Montana following a similar approach (Proffitt et al. 2013, 2016, DeVoe et al. 2019, Lowrey et al. 2020). We used location data collected from GPS collared elk in the three study areas to evaluate elk habitat selection.

Information gained from this project will be used for on-the-ground implementation by FWP and partners to manage, protect, and improve important elk habitats and develop strategies to manage elk populations at desired abundances and distributions. Implementation may include working with public and private landowners to improve security and/or habitat quality, remove barriers impeding movement, or may include recommendations for hunter access management.

Our objectives for this project were:

1. Delineate seasonal ranges and movement corridors in the Devil’s Kitchen, Custer Forest, and Missouri Breaks study areas.
2. Conduct state-wide analysis of factors associated with overabundant elk populations.
3. Conduct habitat selection analyses in the Devil’s Kitchen, Custer Forest, and Missouri Breaks study areas.

Study Areas

Devil's Kitchen

The Devil's Kitchen elk population occupies Lewis and Clark and Cascade Counties in central Montana and spans portions of hunting districts (HD) 445, 455, and 446 (Figure 2). This population also exhibits some seasonal use of neighboring HDs 392 to the south and 413 and 416 to the east. The Beartooth Wildlife Management Area (BTWMA), managed by FWP, is located in the western portion of the study area (Figure 2). The BTWMA was purchased in 1970 with primary objectives of providing critical winter range for elk, mule deer, and bighorn sheep, alleviating game damage conflict with local agricultural producers, and providing recreational use including hunting and wildlife viewing. The BTWMA is closed to recreational use from December 1 – May 15. The population objective for HDs 445 and 455 (Devil's Kitchen Elk Management Unit) in the 2023 Montana Statewide Management Plan is 2,500-3,500 elk, but almost all counts from the last decade have all been over 3,500 individuals, with the 2023 count around 6,000 individuals. The population objective for HD 446 (East Big Belt Mountains Elk Management Unit) is 1,500-2,000 elk, but all survey counts from 2019-2023 are over 2,000 individuals. This population was therefore classified as overabundant, spurring efforts to reduce the population size in accordance with state law. Cooperative efforts between state wildlife managers and private landowners produced a unique set of regulations intended to provide landowners and managers with a variety of harvest management tools (see Table 4). Elk distributions and resulting game damage on private lands was a management concern, and information on the local drivers of elk movement and habitat selection during the hunting season was needed to inform further management action. Public hunting access on private lands varied at fine scales both throughout the hunting season and across the study area, though at least some hunting occurred on all properties at some point in the hunting season.

Land ownership in the fall/winter range of this population is predominately private agricultural and cattle range (69%), though a matrix of FWP (11.4%), Forest Service (10.9%), State of Montana (6.7%), and Bureau of Land Management (1.8%) land occurs throughout the study area (Figure 2). Elevation ranges from 1,048 m in valley bottoms to 2,431 m on mountain slopes. The long-term precipitation average in the study area is 470 mm (range = 306 mm – 841 mm) and the average temperature is 16.8 °C in July and -4.8 °C in January. Over the last 6 years, precipitation during the fall hunting season averaged 29.1 mm, and the temperature averaged -2.1 °C. Valley bottoms are primarily grasslands comprised of native and introduced pasture grasses (50% total land cover) abutting irrigated and/or non-irrigated agricultural land in some areas (1% total land cover). Sagebrush-steppe (10% total land cover) and shrublands (5% total land cover) occupy low-mid elevation foothills, giving way to coniferous forests (33% total land cover) at higher elevations. Riparian areas account for a modest portion of total land cover (2%).

Custer Forest

The Custer Forest elk population occupies Powder River, Bighorn, and Rosebud Counties in southeastern Montana and primarily occurs in HD 704, with some use of HD 705 (Figure 3).

The Custer National Forest is situated at the core of the study area, with lands managed by the Forest Service comprising about 30% of the fall elk population range. Aside from the Forest, private lands account for the majority of ownership in the area (55%), in addition to 5% managed by state entities and 10% by the Bureau of Land Management. Elevations range from 907 m to 1,569 m and topography varies from gently rolling hills to rough badlands. Mean annual precipitation was between 334.41 mm and 551.07 mm, with an average of 409.39 mm. Precipitation and temperatures during the rifle period averaged 47.98 mm and 4.54 °C. Mean temperatures for July and January were -4.67 and 22.03 °C. The study area contains a mixture of privately-owned ranchlands; sagebrush steppe and mixed-grass prairies dominated by Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis*), silver sage (*Artemisia cana*), other short-statured shrubs, and a mixture of native cool- and warm-season grasses as well as non-native annual (e.g., cheatgrass (*Bromus tectorum*) and perennial grasses (Kentucky bluegrass (*Poa pratensis*); and xeric forest communities dominated by ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*) with understories comprised of grassland species and shrubs like western snowberry (*Symphoricarpos occidentalis*). Some draws contain deciduous shrubs and trees such as chokecherry (*Prunus virginiana*), American plum (*Prunus americana*), box elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*). The Powder and Tongue River valleys contain plains cottonwood (*Populus deltoides*), Russian olive (*Elaeagnus angustifolia*), and willow species (*Salix* spp.) along with irrigated fields consisting primarily of alfalfa (*Medicago sativa*). Elk were sympatric with white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), and predators included coyote (*Canis latrans*), bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), and American black bear (*Ursus americanus*).

Elk in HD 704 are surveyed within a trend area, rather than a district-wide count. Between 2017 and 2021, elk counts ranged from 810-967 animals. In 2023 and 2025, surveys recorded 1,402 and 1,350 elk, respectively. Most opportunities to hunt elk were allowed through limited drawings and more information on hunting regulations can be found in Table 13. During the three years of study in the Custer Forest, hunters harvested an annual average of 94 elk in the archery season and 285 in the rifle season each year, and female elk comprised 51% of the harvest across the three years. In 2022, hunters spent an estimated 10,458 hunter-days pursuing elk throughout the archery and rifle seasons.

Missouri Breaks

The eastern Missouri Breaks population (hereafter Missouri Breaks) occupies Garfield County and falls primarily within HD 700, with some elk use occurring in small portions of HDs 410 and 701 (Figure 4). Approximately 44% of the study area was privately owned. Land managed by the U.S. Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge adjacent to the Missouri River comprised much of the elk range (27%), in addition to lands managed by the State of Montana (4%) and the Bureau of Land Management (24%). Mean annual precipitation ranged from 338.64 mm to 433.32 mm and averaged 370.12 mm. Mean temperatures for July and January were -6.73 °C and 22.07 °C. During the rifle period, monthly precipitation and temperatures averaged 61.24 mm and 4.18 °C (Oregon State University 2024). Elevations ranged from 681 m to 1,038 m and transitioned from flat to rolling terrain to rugged river breaks and steep slopes closer to the Missouri River. The study area included a mix of privately-owned ranchlands and cultivated cropland; sagebrush steppe and mixed-grass prairies dominated by Wyoming big sagebrush, silver sage, rubber rabbitbrush (*Ericameria nauseosa*), grasses including western wheatgrass (*Pascopyrum smithii*) and blue grama (*Bouteloua gracilis*), dryland sedge species, and forbs such as prickly pear (*Opuntia* spp.), scarlet globemallow (*Sphaeralcea coccinea*) and prairie clover (*Dalea* spp.); and timbered drainages and coulees near the Missouri River, Fort Peck Reservoir and Musselshell River dominated by ponderosa pine and Rocky Mountain juniper. Plains cottonwood (*Populus deltoides*) and willow were common in riparian areas along major drainages. The primary crops in the area are grass and alfalfa hay, spring wheat, and barley. Elk were sympatric with white-tailed deer and mule deer. Predators occupying the area included coyote, bobcat and mountain lion.

Reliable and repeatable biennial surveys for this elk population began in 2008, and counts have remained fairly steady around 1,200 to 1,300 elk since 2012. In the last 3 surveys conducted during the last six years, the population count ranged from 800 to 1,600 elk, the lowest and highest counts on record. However, the low count of 800 was from a survey conducted the winter following the Lodgepole Complex Fire, which burned over 270,000 acres including a significant amount of elk habitat. During the most recent survey conducted in winter 2024, a total of 1,608 elk were counted. This is the highest count on record and is likely due to the survey area being expanded. In HD 700, limited permits and licenses to hunt elk were distributed through drawings only. Hunters successful in drawing an elk permit could harvest either-sex elk during the archery or rifle (quota up to 250) or archery season only (800 quota); hunters successful in drawing a license could harvest antlerless elk during archery or rifle (quota up to 700). Additionally, about 800 licenses were available to harvest antlerless elk in any MFWP Region 7 HD, though these licenses were not valid on National Forest lands or the Charles M. Russell National Wildlife Refuge. Additional information on harvest regulations can be found in Table 12. In the first two years of study in the Missouri Breaks (2022-2023), each year hunters harvested an average of 136 elk in the archery season and 372 in rifle season. Female elk constituted 49% of the harvest over the two years and there were an estimated 11,716 hunter-days spent in the HD in 2022.

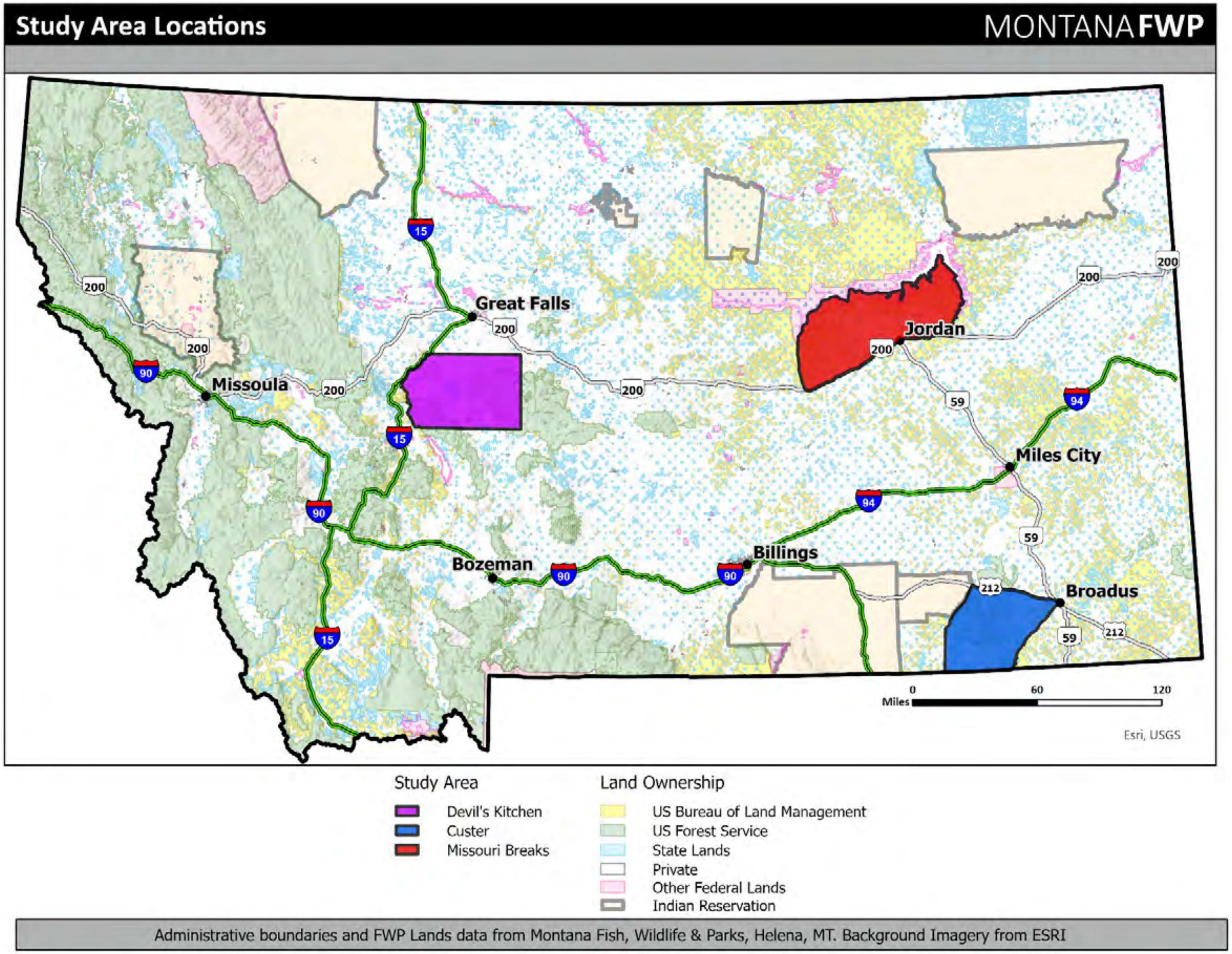

Figure 1. The Devil's Kitchen, Custer Forest, and Missouri Breaks study areas in central and eastern Montana.

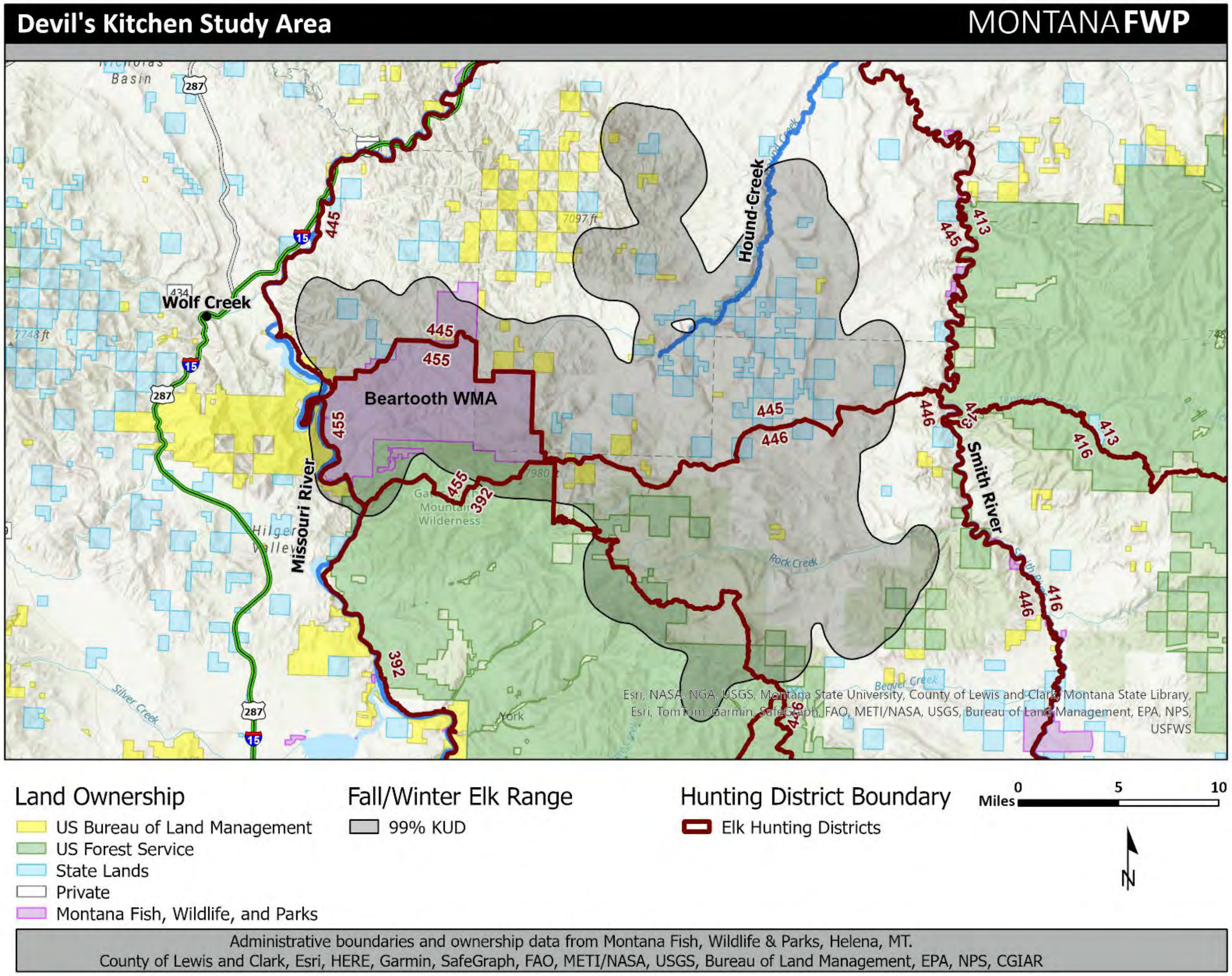

Figure 2. The Devil's Kitchen study area in central Montana. The fall/winter elk range is represented by a 99% kernel utilization distribution (KUD) generated from elk locations occurring during hunting season (Aug 15 – Feb 15) and daylight hours.

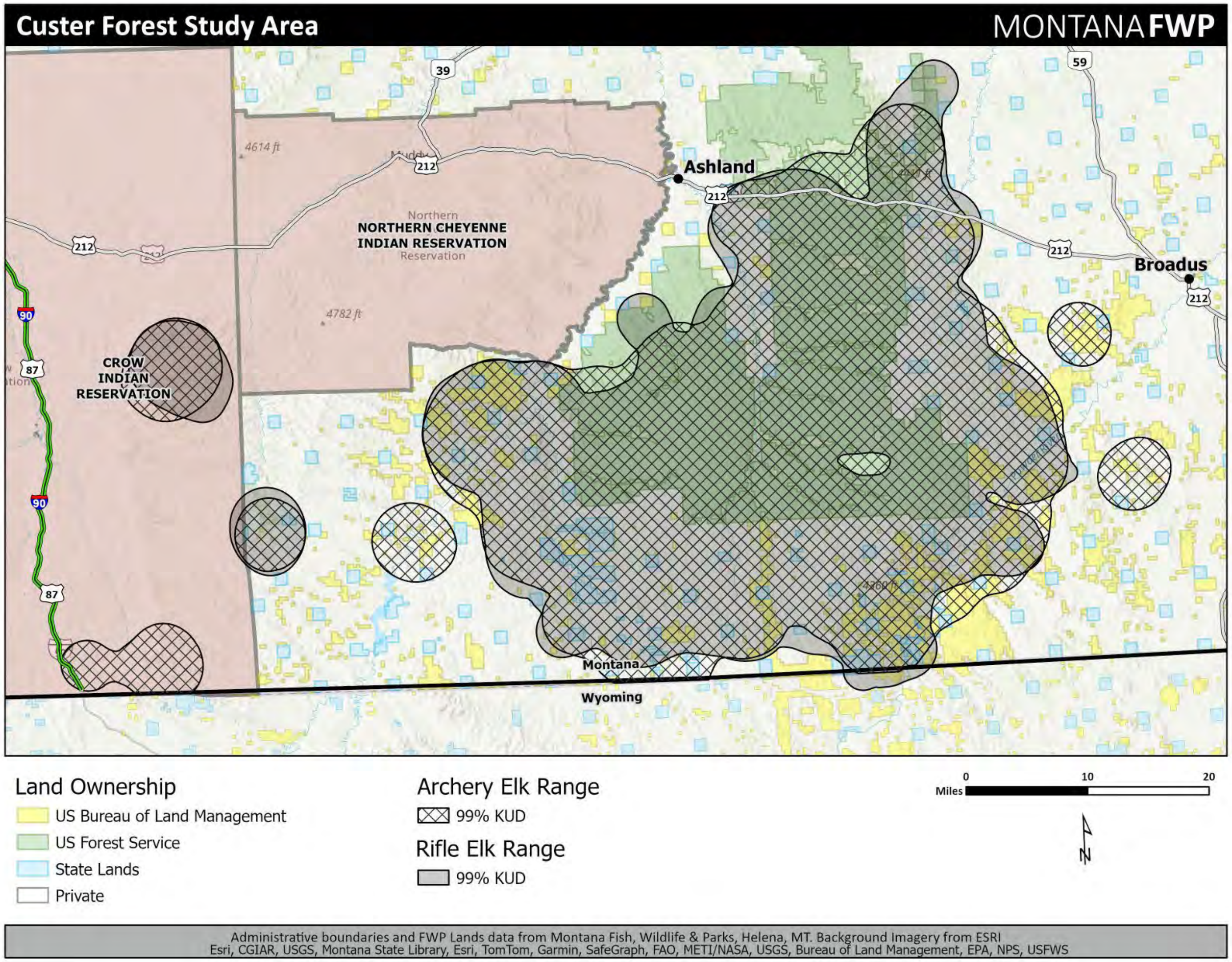

Figure 3. The Custer Forest study area in eastern Montana. The fall elk ranges are represented by a 99% kernel utilization distribution (KUD) generated from elk locations occurring during archery and rifles seasons and daylight hours.

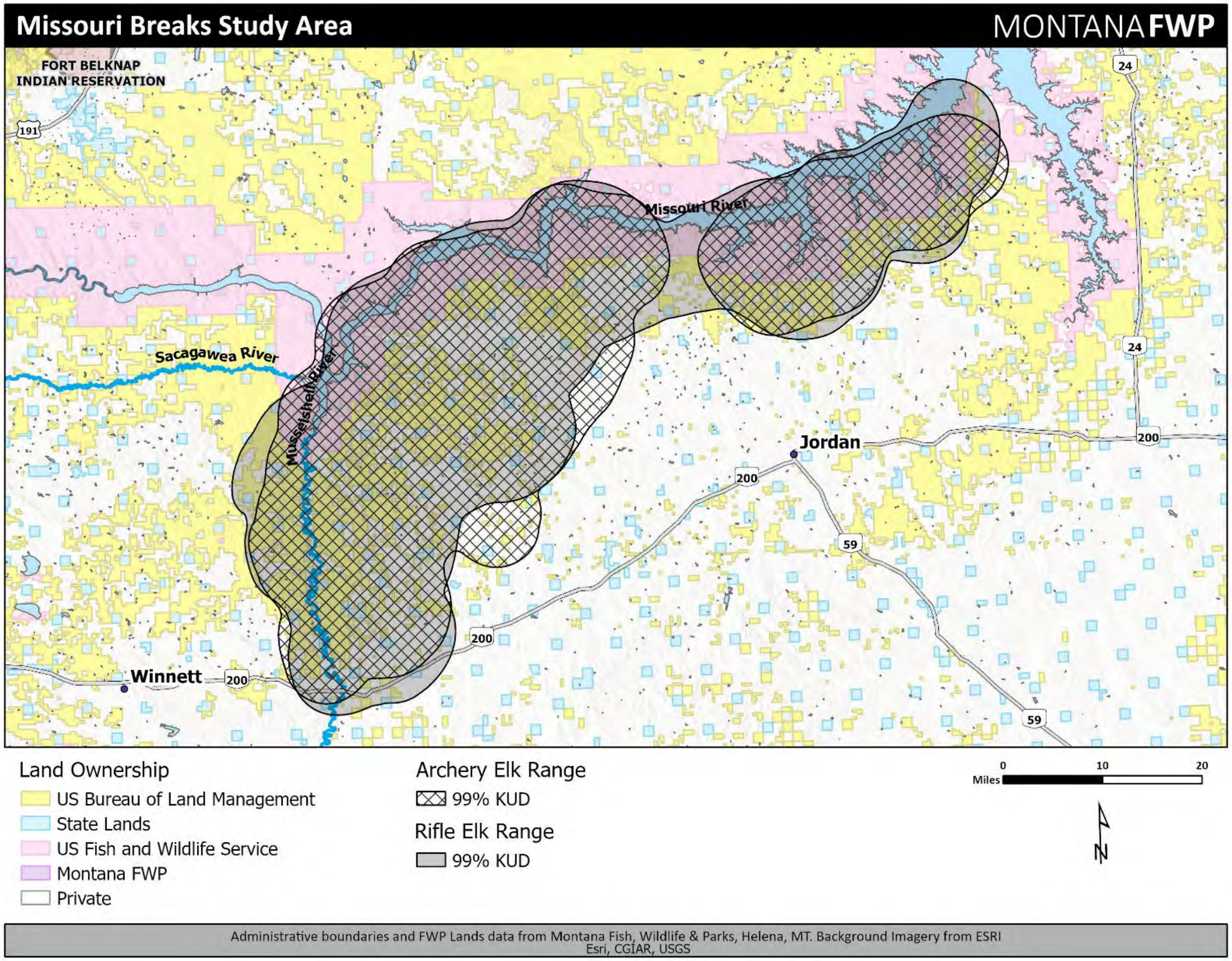

Figure 4. The Missouri Breaks study area in eastern Montana. The fall elk ranges are represented by a 99% kernel utilization distribution (KUD) generated from elk locations occurring during archery and rifles seasons and daylight hours.

Objective 1: Delineate seasonal ranges and movement corridors in the Devil's Kitchen, Custer Forest, and Missouri Breaks study areas.

METHODS

Elk Capture and Monitoring

We used helicopter net-gunning and aerial darting to capture male and female elk in the three study areas. We outfitted captured individuals with Lotek LiteTrack Iridium collars programmed to collect hourly locations for up to 3 years. The collars were programmed to transmit a VHF signal during daylight hours and switch to a mortality signal if stationary for >10 hours. Collars uploaded locations via Iridium satellites to a web platform where data could be viewed and downloaded in near-real-time. For each captured female, we collected a vestigial canine tooth for aging purposes via cementum annuli, a blood serum sample for pregnancy testing and to test for exposure to *Brucella abortus*, a chest girth measurement, and a rump fat thickness measurement via ultrasound. Percent ingesta-free body fat (IFBF) levels were calculated according to methods developed by Cook et al. (2010). Body fat data was only collected during the initial year of capture in each study area. Drop-off devices released collars from animals after their term of deployment.

Seasonal Ranges and Movement Corridors

We used the standardized methods outlined by Lowrey et al. (2021) to estimate seasonal ranges and movement corridors from the sample of collared individuals, an approach that has been applied to elk, mule deer, bighorn sheep, and moose populations across Montana. The Migration Mapper application was used to visually classify migratory behaviors and movement periods using maps of GPS locations and associated net-squared displacement (NSD) curves in spring and fall for each individual. Population-level movement corridors were outlined using two variations of the Brownian bridge movement model (Horne et al. 2007). We used kernel density estimates (KDE) to delineate winter and summer range distributions. We defined winter as the period between the 0.95th quantile of fall migration end dates and the 0.5th quantile of spring migration start dates, and defined summer as the period between the 0.95th quantile of spring migration end dates and the 0.5th quantile of fall migration start dates. We also evaluated elk use of different land ownerships and how individual use varied across the seasons.

RESULTS

Devil's Kitchen Elk Capture and Collaring

We captured 50 female elk in February 2020 and 15 female elk in February 2021 for a total of 65 captured animals in the study area. GPS location data collection started on February 26, 2020 and ended July 13, 2023. After cleaning data and censoring fixes with low precision (i.e., DOP > 10), the elk location data included 1,167,870 locations from 64 individuals (Figure 9). During the monitoring period, we recorded 19 mortalities: 12 were harvested, 2 died of wounding loss, 3 died of natural causes, and 2 were capture-related mortalities. The pooled pregnancy rate for all individuals across both capture years was 86% pregnant (n = 59). The mean IFBF value pooled across years was 7.8% (n = 60, min = 6.2%, max = 13.3%), which closely matches the statewide average of 7.8%. All elk sampled (n = 65) tested negative for exposure to brucellosis. The mean age of females at the end of their monitoring period was 7.8 years old (n = 62, min = 3, max = 19). The mean age of females who died during their monitoring period (excluding 1 individual without age data and 2 individuals who died from capture) was 6.9 years old (n = 16, min = 3, max = 19), while the mean age of females who survived their monitoring period was 8.0 years old (n = 44, min = 3, max = 14). The mean age of females who died from hunter harvest during their monitoring period was 6.7 years old (n = 13, min = 3, max = 19), while the mean age of females who did not die from hunter harvest (excluding 2 individuals who died from capture) during their monitoring period was 8.0 years old (n = 47, min = 3, max = 15).

Custer Forest Elk Capture and Collaring

We captured 40 female and 20 male elk in January 2021, an additional 4 females and 5 males were captured in January 2022, and another 5 females and 4 males were captured in January 2023. GPS location data collection in the Custer Forest study area began 1/28/2021 and ended 2/26/2024. After filtering for accuracy based on dilution of precision, we gathered 913,440 locations from 78 individuals (49 females, 29 males) for an average of 12,019 (range = 893 – 20,941) locations per individual. We recorded 29 collar malfunctions (18 males, 11 females) and 17 mortalities (9 males, 8 females). Eleven elk (6 males, 5 females) have been harvested by hunters, 1 female died from mountain lion predation, 1 male and 1 female died from human-related causes, and 2 males and 1 female died from unknown causes. The pooled pregnancy rate for adult females (excluding yearlings) across all capture years was 60% pregnant (n = 40), well-below the state-wide average of 87%. The mean IFBF value pooled across years was 7.5% (n = 36, min = 6.1%, max = 12.1%), which closely matches the statewide average of 7.8%. Females were on average 3.7 years old (SD = 2.3, range = 1.5 to 10.5 years old) and males were on average 4.2 years old (SD = 1.8, range = 2.5 to 8.5 years old). All elk sampled (n = 39) tested negative for exposure to brucellosis. Monthly reports were generated and distributed to regional

MFWP staff as well as other agency partners, private landowners, and other members of the public.

Missouri Breaks Elk Capture and Collaring

We captured 40 female and 20 male elk in January 2022, an additional 6 females and 10 males in January 2023, and an additional 10 females and 7 males were captured in January 2024. After filtering for accuracy based on dilution of precision, we gathered 911,367 locations from 93 individuals (37 males, 56 females) in the Missouri Breaks study area for an average of 10,015 (range = 103 – 21,121) locations per individual. We have recorded 29 collar malfunctions (21 males, 8 females) and 33 mortalities (13 males, 20 females). Twenty-five elk (9 males, 16 females) have been harvested by hunters, 3 elk (2 males, 1 female) died from wounding loss, and 5 elk (2 males, 3 females) died from unknown causes. The pooled pregnancy rate for all adult females across all capture years was 82% pregnant (n = 56), slightly below the state-wide average of 87%. The mean IFBF value pooled across years was 7.2% (n = 36, min = 6.1%, max = 8.5%), slightly lower than the statewide average of 7.8%. Females were on average 6.0 years old (SD = 2.8, range = 2.5 to 13.5 years old) and males were on average 6.3 years old (SD = 2.1, range = 4.0 to 8.0 years old). All elk sampled (n = 40) tested negative for exposure to brucellosis. Monthly reports have been generated and distributed to regional MFWP staff as well as other agency partners, private landowners, and other members of the public.

Devil's Kitchen Seasonal Ranges and Movement Corridors

Estimates of seasonal ranges and movement corridors based on the sample of collared individuals in the final GPS location dataset are shown in Figures 5-7. The median summer period start and end dates were May 10 and Oct. 28, respectively. The estimated summer range for the Devil's Kitchen elk population covered 1,212 km^2 (Figure 5). The median winter period start and end dates were Jan. 20 – March 7. The estimated winter range primarily occupied the central valley bottoms of the study area, including the BTWMA on the western side of the study area, and covered 1,356 km^2 (Figure 6). Across the entire year, 65% of elk locations occurred on private lands, 21% on FWP lands, 8% on State of Montana lands, 3% on National Forest lands, and 2% on Bureau of Land Management lands. Individual elk land use showed high proportional use of private lands across all seasons with an increase in proportional use of the BTWMA in the fall and winter (Figure 10).

The estimated movement corridors (Figure 7) reinforced local knowledge of a seasonally occurring migratory behavior exhibited by a portion of this population between the BTWMA and private ranchlands in the valley bottom, with movements onto the BTWMA occurring most often in the late fall and early winter months. Seasonal migratory movements occurred in other portions of the study area as well, with a few individuals moving between the higher-elevation National Forest lands to the east and the valley bottom. We also observed movement patterns that appear typical of resident animals throughout the study area. The median start and end dates for migration were March 17 and March 31 for spring and Nov. 1 and Nov. 14 for fall, respectively. Elk spent an average of 14 days migrating in the spring and 18 days migrating in the fall. The mean migratory distance was 12.5 miles. The timing and duration of migratory movements varied slightly between years (Figure 8).

For all animal-years for which sufficient data was available to make migratory classifications in Migration Mapper, 55.8% of the population exhibited a spring migration (n = 154) and 56.0% exhibited a fall migration (n = 134). In 2020, 60.9% of the population migrated in spring (n = 46) and 48.9% migrated in fall (n = 45). In 2021, 38.9% percent of the population migrated in spring (n = 54) and 58% migrated in fall (n = 50). In 2022, 63.6% of the population migrated in spring (n = 44) and 61.5% migrated in fall (n = 39). Out of 134 animal-years where spring and fall were both classified, 30 animal-years (22%) included a switch from migrant to resident or resident to migrant.

Of animals who died (excluding capture-related deaths), 20% migrated during the spring prior to their death (n = 15). Of animals who died from hunter harvest, 21% migrated during the spring prior to their death (n = 14). The low proportion of migratory animals harvested in relation to the overall population proportions suggests that hunters disproportionately harvested animals demonstrating resident behavior.

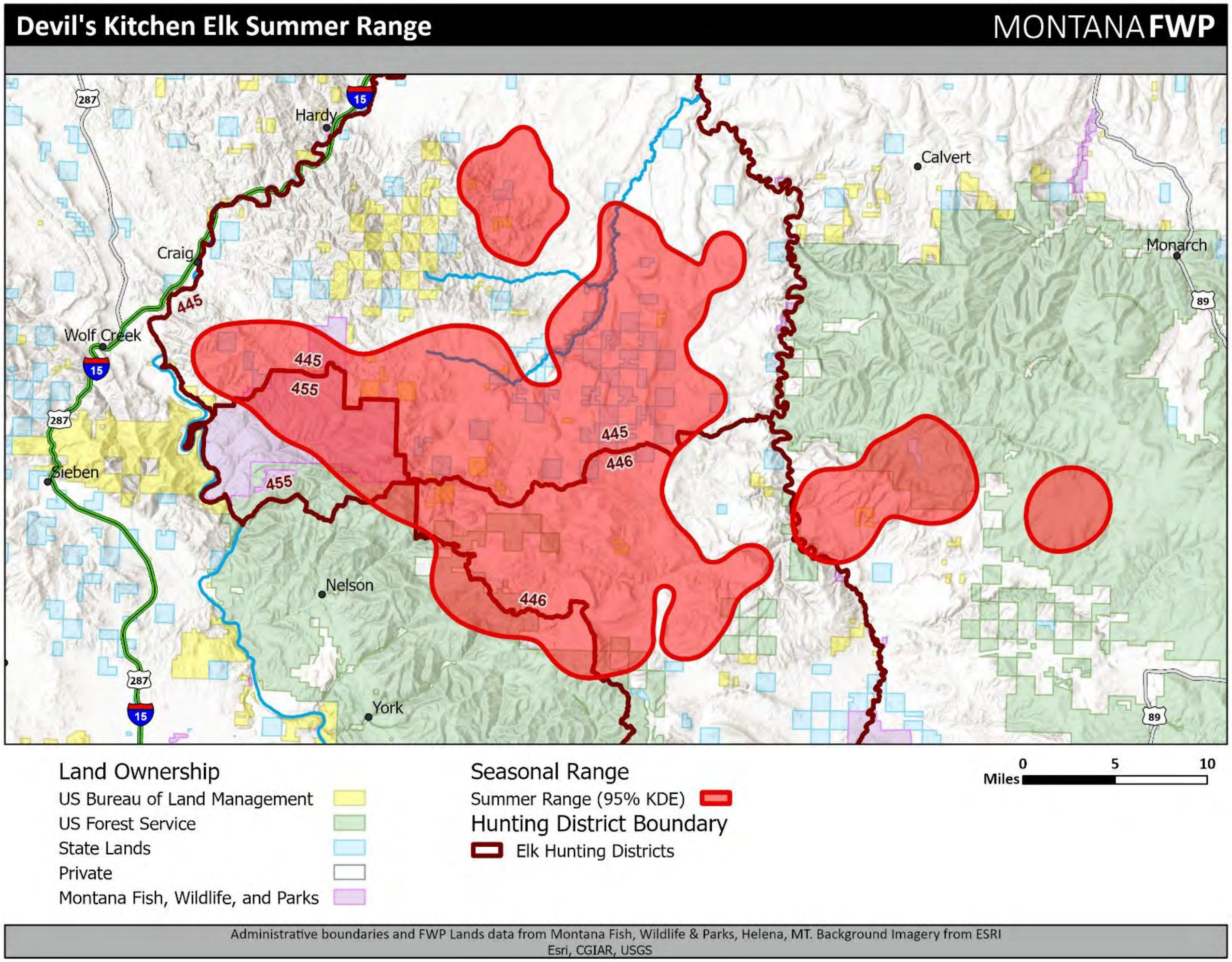

Figure 5. Estimated summer range for elk collared in the Devil's Kitchen area. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

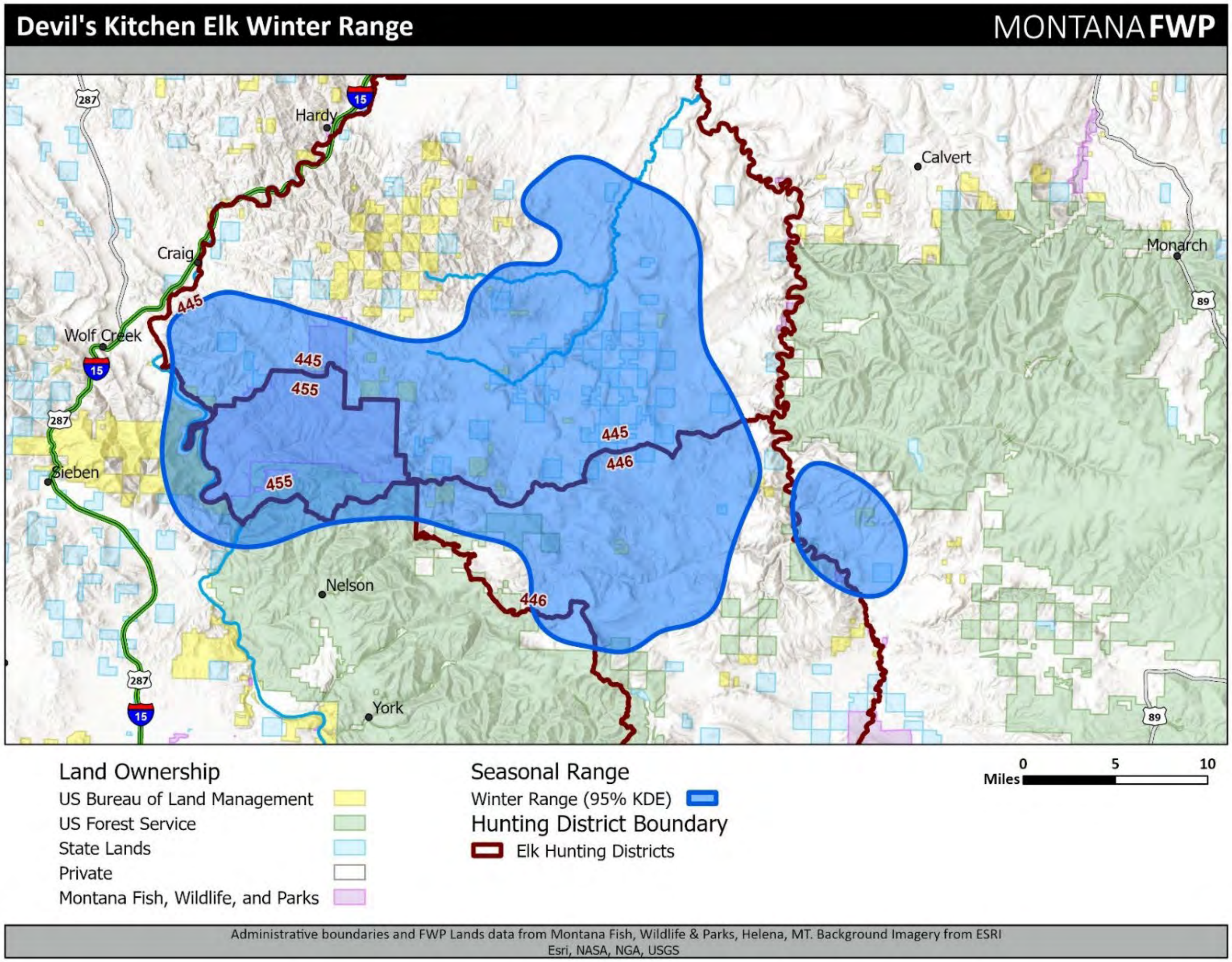

Figure 6. Estimated winter range for elk collared in the Devil's Kitchen area. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

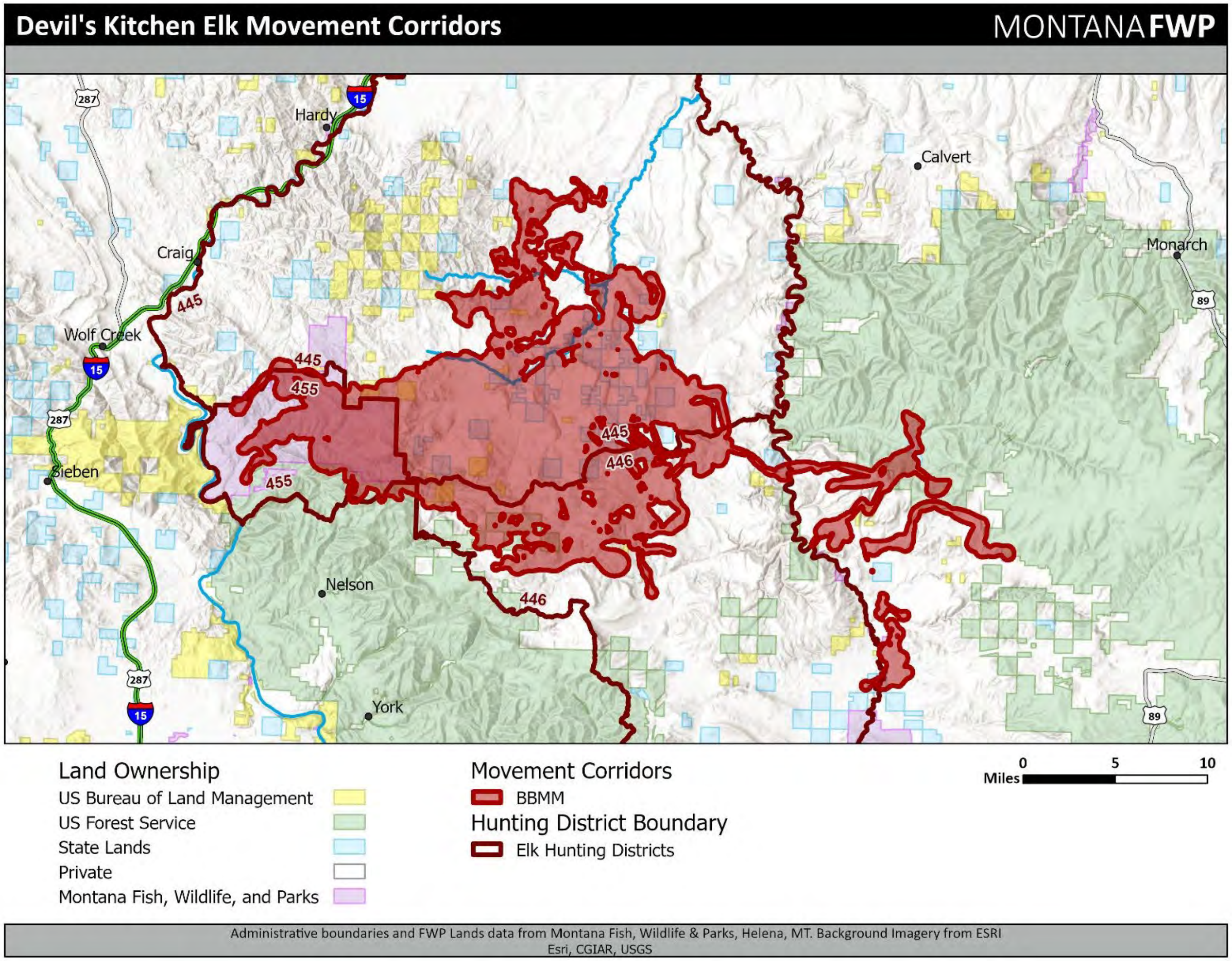

Figure 7. Movement corridors delineated for elk collared in the Devil's Kitchen area. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models.

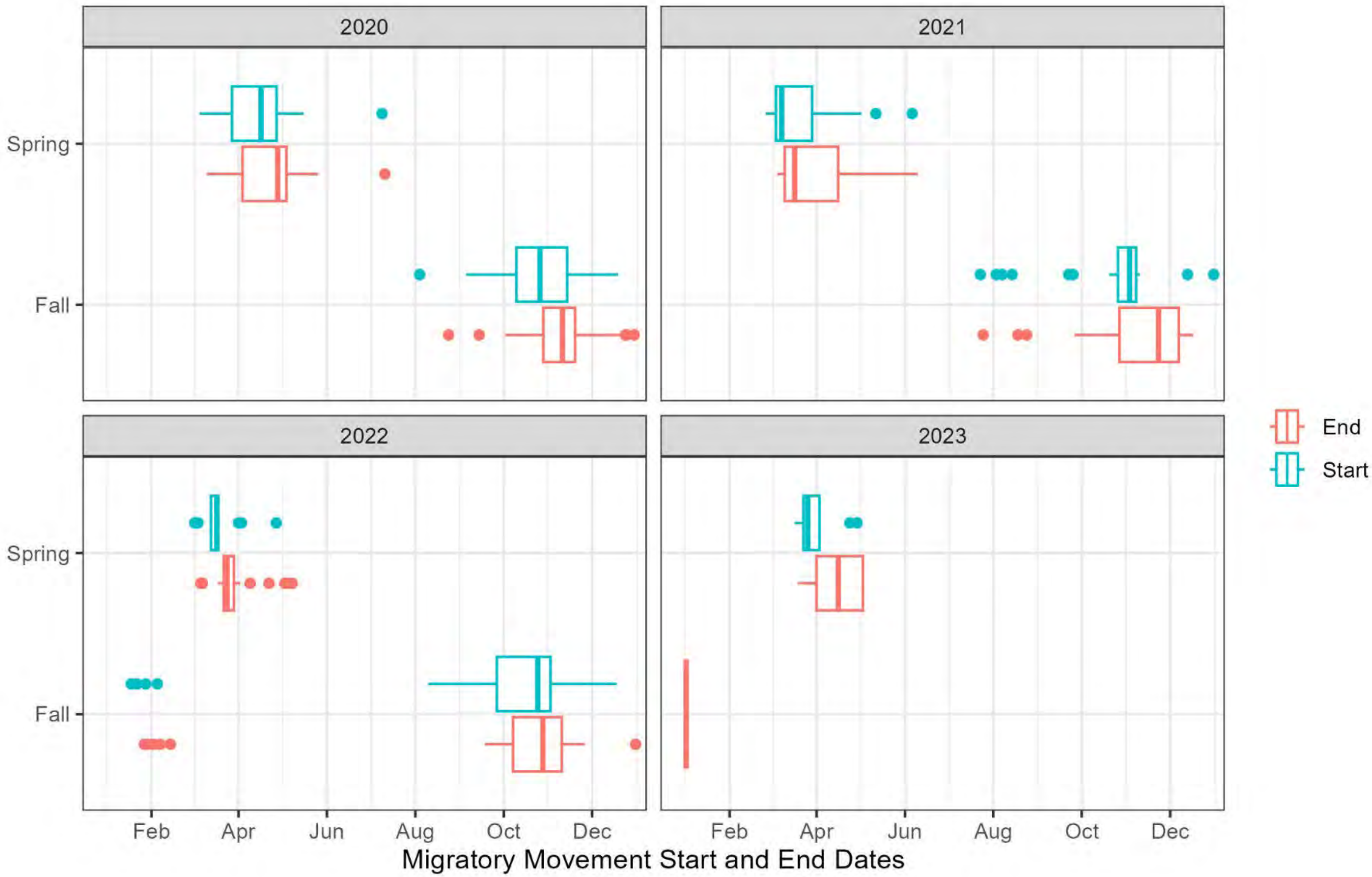

Figure 8. Annual migratory start and end dates from 2020-2023 based on collared elk movements in the Devil's Kitchen study area. Migratory movements were classified using the Migration Mapper application.

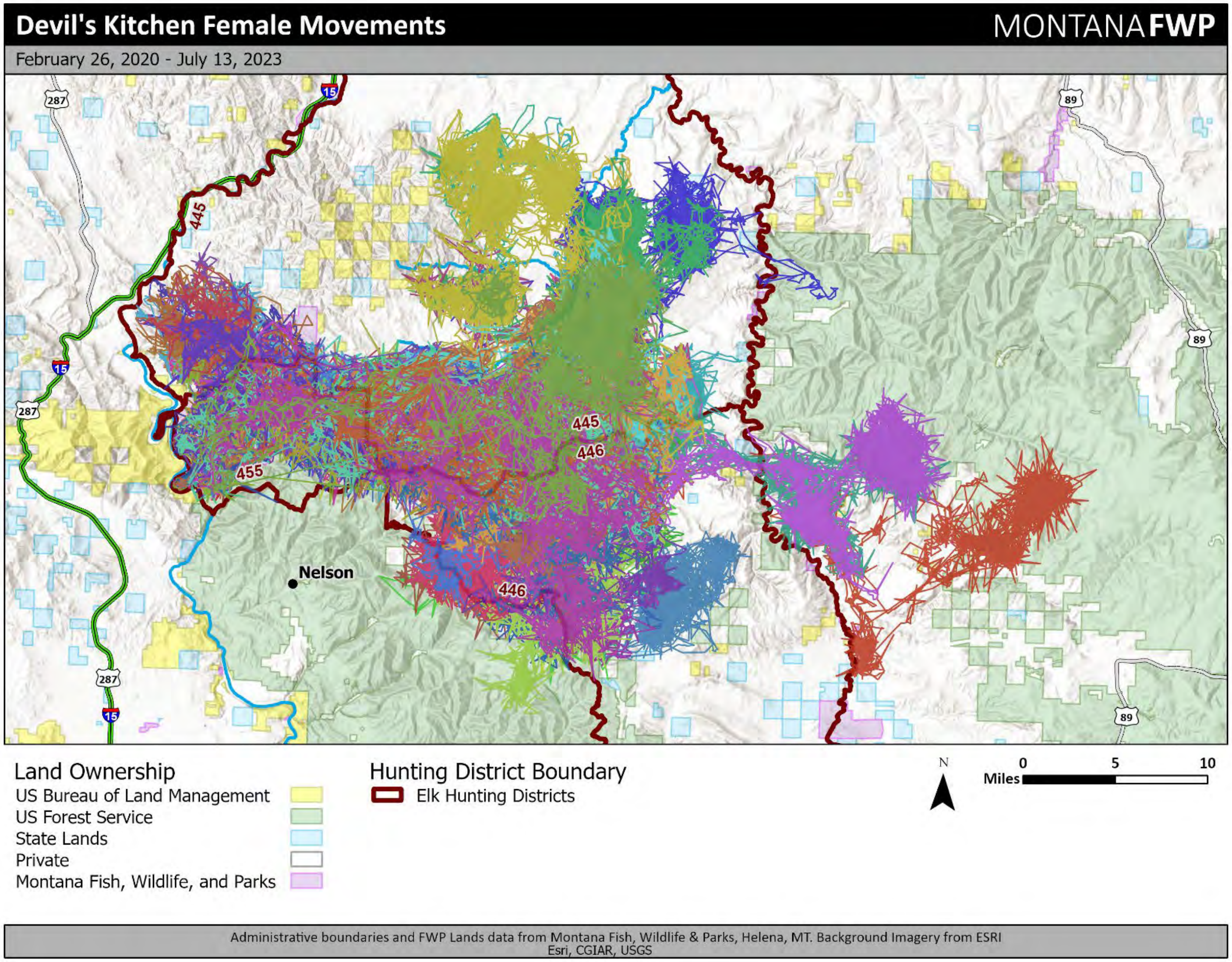

Figure 9. Movements of 64 collared individuals in the Devil's Kitchen study area.

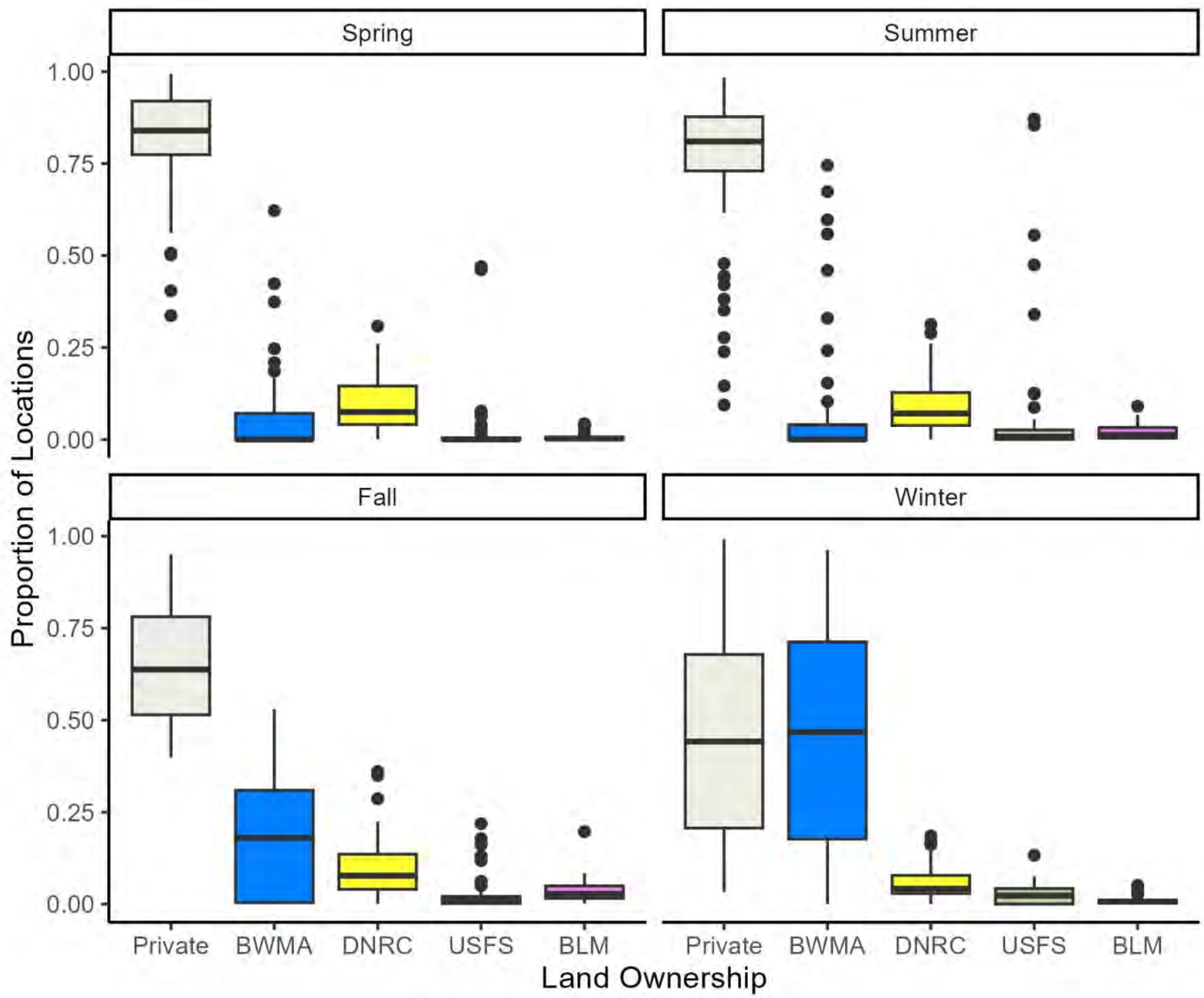

Figure 10. Proportional use of state, federal, and private lands by individual elk and season in the Devil's Kitchen study area. With the exception of some BLM lands that are accessible via helicopter, Montana State Trust and BLM lands in this study area are mostly inaccessible to the public.

Custer Forest Elk Seasonal Ranges and Movement Corridors

Estimates of seasonal ranges (Figures 11 and 12) and movement corridors (Figure 13) were compiled after all location data was collected. The seasonal range estimates (Figures 11 and 12) demonstrate a lack of strong population-level seasonal shift in the Custer Forest study area. The median summer period start and end dates were Aug. 8 and Oct. 25, respectively. The median winter period start and end dates were Dec. 15 and March 21, respectively. A majority of the elk in this population demonstrated resident behavior, although some migratory behavior and dispersal movements were observed. Approximately 29% of the population exhibited migratory behavior. The median start and end dates for migration were May 11 – May 13 for spring and Oct. 20 – Oct. 21 for fall. Elk spent an average of 2 days migrating in the spring and 3 days migrating in the fall. The mean migratory distance was 11.5 miles.

Throughout the duration of monitoring the Custer Forest elk population, we observed a variety of individual movement patterns in both male and female collared elk (Figures 14 and 15). Multiple males and females made temporary movements south into Wyoming. Two females traveled as far west as the I-90 corridor (~100 miles) on the Crow Indian Reservation. Additionally, one female traveled over 100 miles to North Dakota before returning to the study area and one male traveled over 200 miles to northwestern South Dakota where he remained until his collar failed. The large movements undertaken by multiple individuals suggest that elk are able to access and connect patches of habitat across a large portion of southeastern Montana. Lands managed by the BLM are an important component of habitat connectivity in this area of the state.

The location data collected in the Custer Forest area indicates that elk primarily use privately owned lands (48.8% of locations) and the Custer National Forest (39.8% of locations); 6.8% of locations gathered occurred on lands managed by the BLM and 4.7% of locations occurred on lands managed by the state of Montana. Some collared individuals use BLM lands at much higher rates; a maximum of 41% of an individual's locations occurred on BLM managed lands. Land managed by the BLM in the southern portion of the study area between the state line and the edge of the Custer National Forest was frequently used by collared elk. Patterns of the distribution of locations across land ownerships were fairly similar across seasons, with mean decreases in use of Custer National Forest and mean increases of use of private lands during fall (Figure 16).

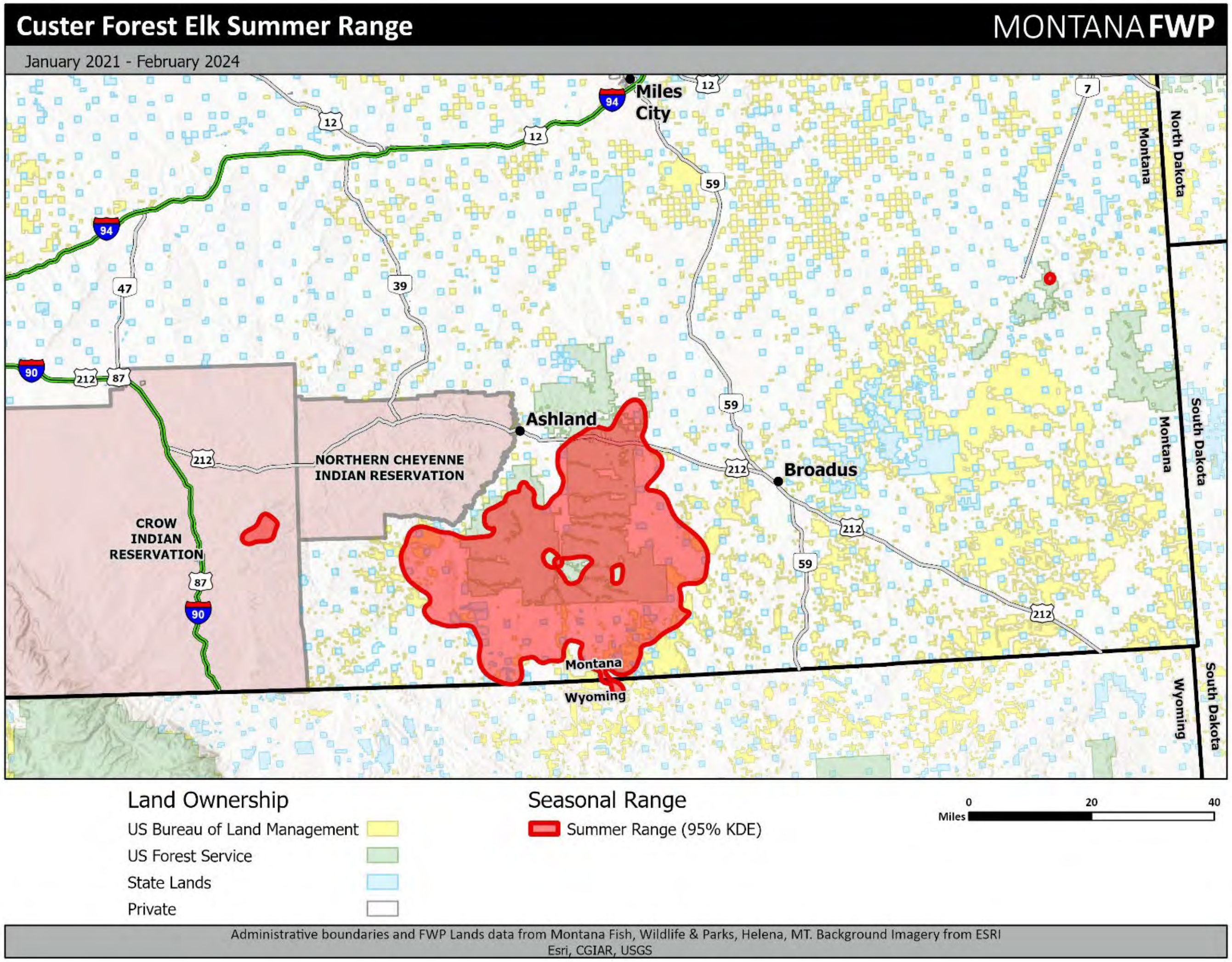

Figure 11. Estimated summer range for elk collared in the Custer Forest area based on locations gathered from January 2021 through February 2024. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

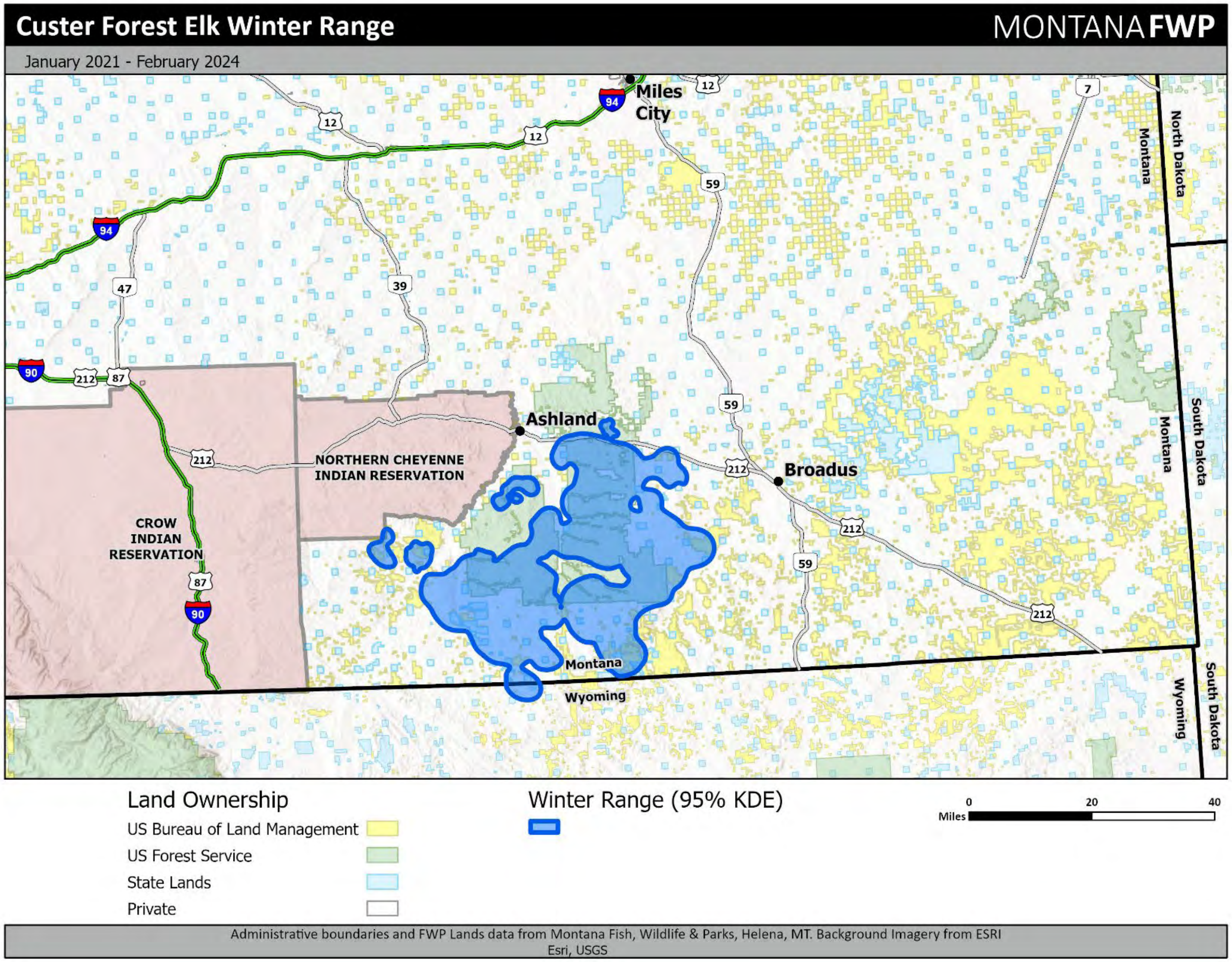

Figure 12. Estimated winter range for elk collared in the Custer Forest area based on locations gathered from January 2021 through February 2024. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

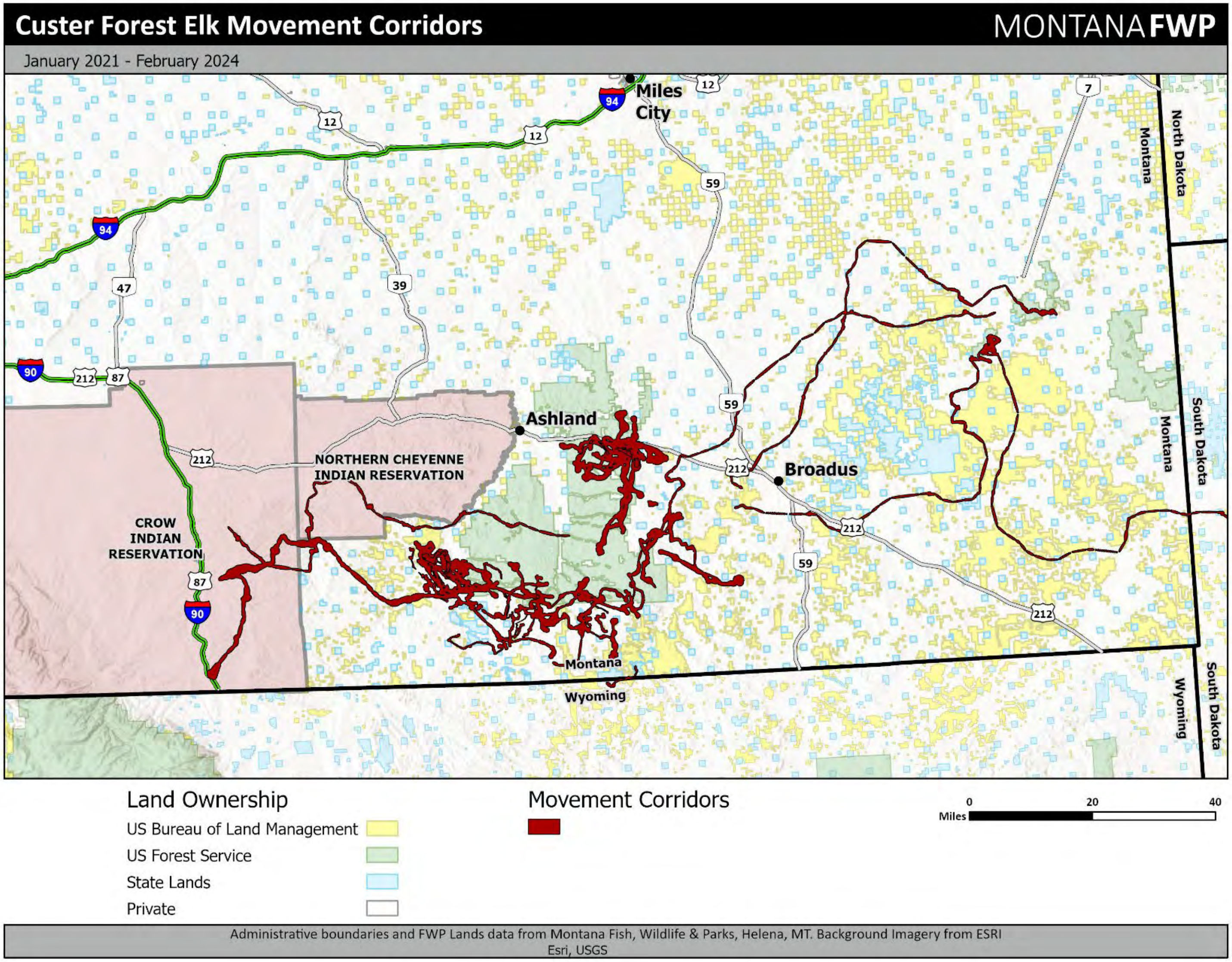

Figure 13. Movement corridors delineated for elk collared in the Custer Forest area based on locations gathered from January 2021 through February 2024. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models.

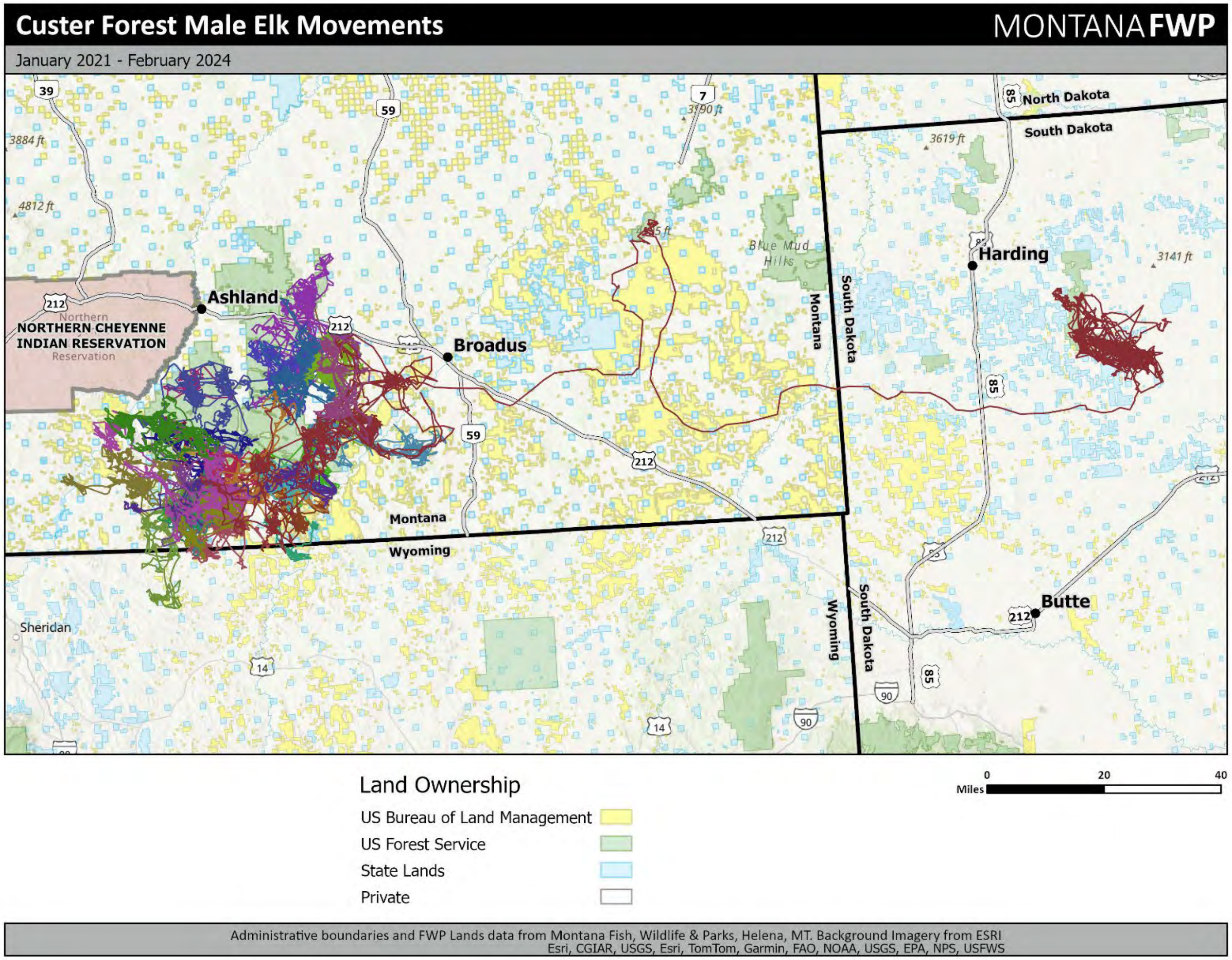

Figure 14. Movements of 29 collared males in the Custer Forest study area through from January 2021 to February 2024. Each color represents the movement track of one individual.

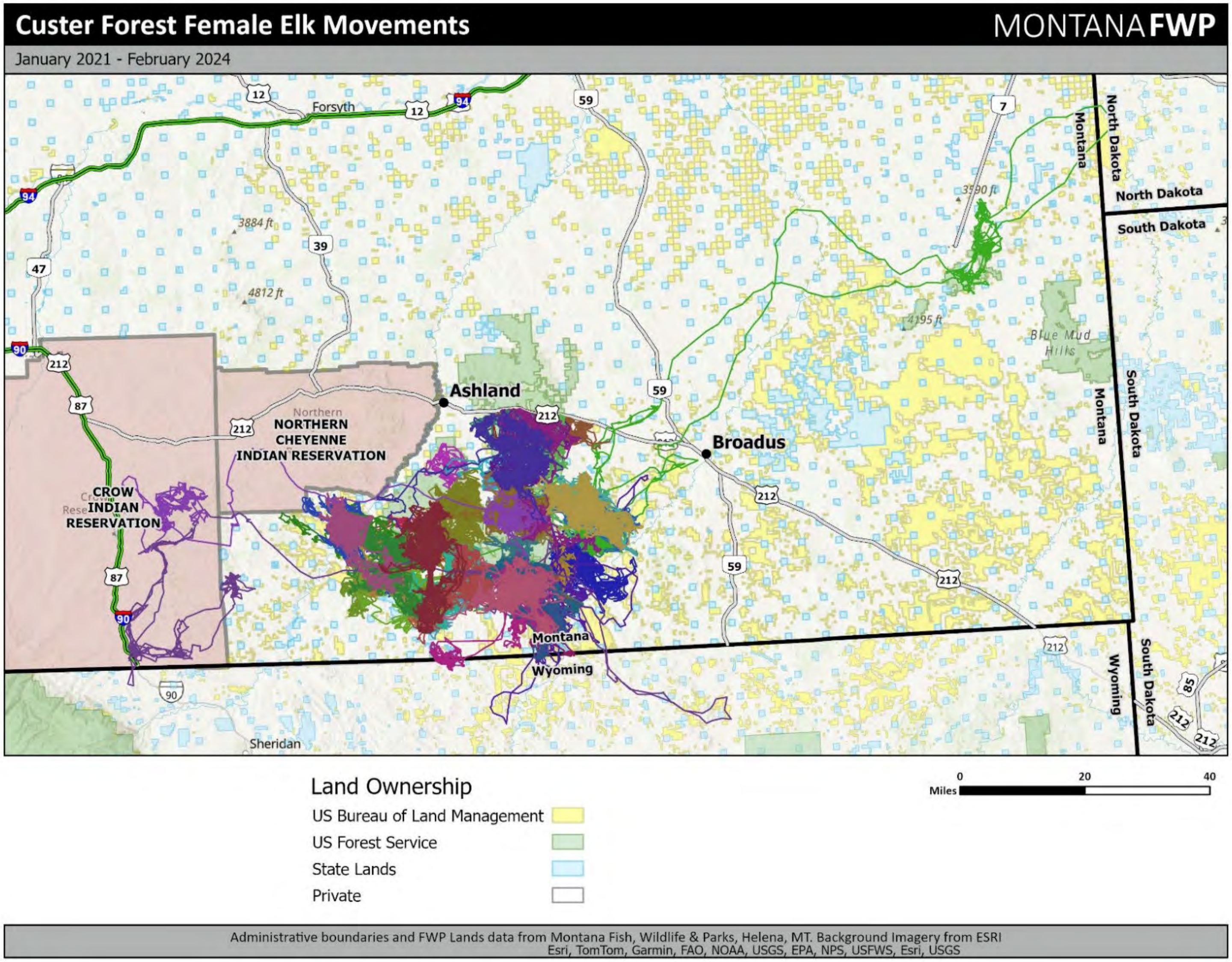

Figure 15. Movements of 47 collared females in the Custer Forest study area from January 2021 through February 2024. Each color represents the movement track of one individual.

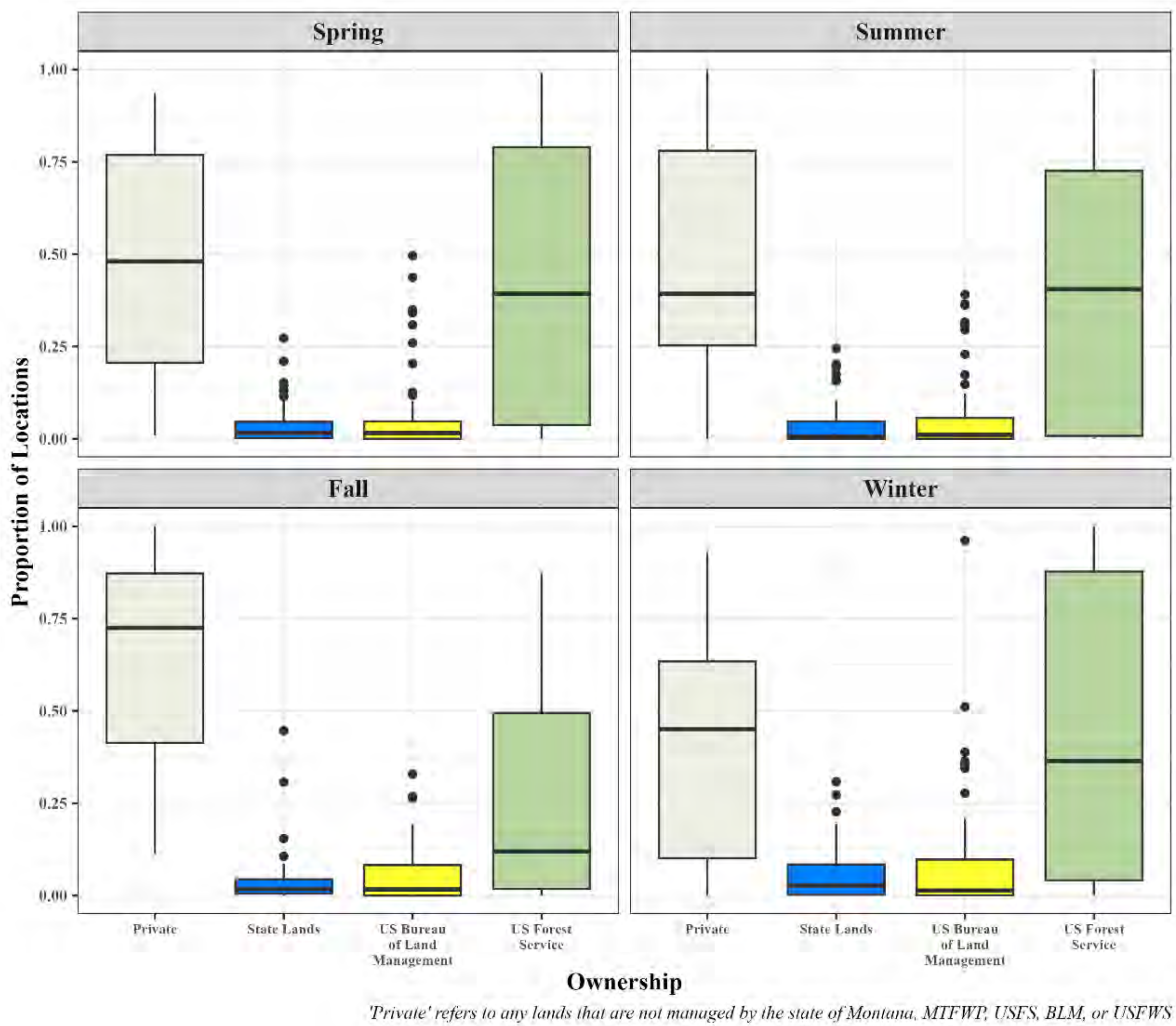

Figure 16. Proportional use of state, federal, and private lands by individual elk in the Custer National Forest study area by season.

Missouri Breaks Elk Seasonal Ranges and Movement Corridors

Estimates of seasonal ranges (Figures 17 and 18) and movement corridors (Figure 19) were compiled after all location data was collected. The seasonal range estimations (Figures 17 and 18) demonstrate a lack of strong population-level seasonal shift in the Missouri Breaks study area. The summer period start and end dates were July 14 and Oct. 17, respectively. The winter period start and end dates were Nov. 17 and May 6, respectively. A majority of the elk in this population demonstrated resident behavior, although some migratory behavior and dispersal movements were observed. Approximately 17% of the population exhibited migratory behavior. The median start and end dates for migration were April 21 – April 22 for spring and Oct. 31 – Nov. 2 for fall. Elk spent an average of 1 day migrating in the spring and 3 days migrating in the fall. The mean migratory distance was 5.2 miles.

We observed a variety of individual movement patterns in both male and female collared elk (Figures 20 and 21). The range of multiple male and female elk has extended across the Musselshell River on the western edge of the study area into elk hunting district 410. One male elk traveled across the majority of the study area (over 50 miles) from east to west over the course of several months, crossed the Missouri River and spent time on the north shore, then returned to the south shore and traveled all the way back to the east end of the study area the following year (Figure 20). Several females have made movements across Highway 200 east of the Musselshell River throughout the monitoring period. This crossing location may offer opportunities for future conservation efforts.

The location data collected in the Missouri Breaks area to indicated that elk primarily use privately owned lands (37.7% of locations), lands managed by the US Fish and Wildlife Service (29.0% of locations), and lands managed by the BLM (28.9% of locations). The data collected indicated that BLM lands are an important component of elk habitat in the Missouri Breaks area. As in the Custer Forest area, there was variation among individuals in patterns of land use, but a consistently large percentage of total locations across all seasons occurred on BLM lands in this study area. Some collared individuals use BLM, USFWS, and private lands at much higher rates; individuals spent up to 71%, 98%, and 94% of their time on BLM, USFWS, and private lands, respectively. Patterns of the distribution of locations across land ownerships are similar across seasons, though on average, use of BLM lands appears to increase during the winter and spring and decrease during summer and fall, whereas use of private land increases during summer and fall and decreases during winter and spring (Figure 22).

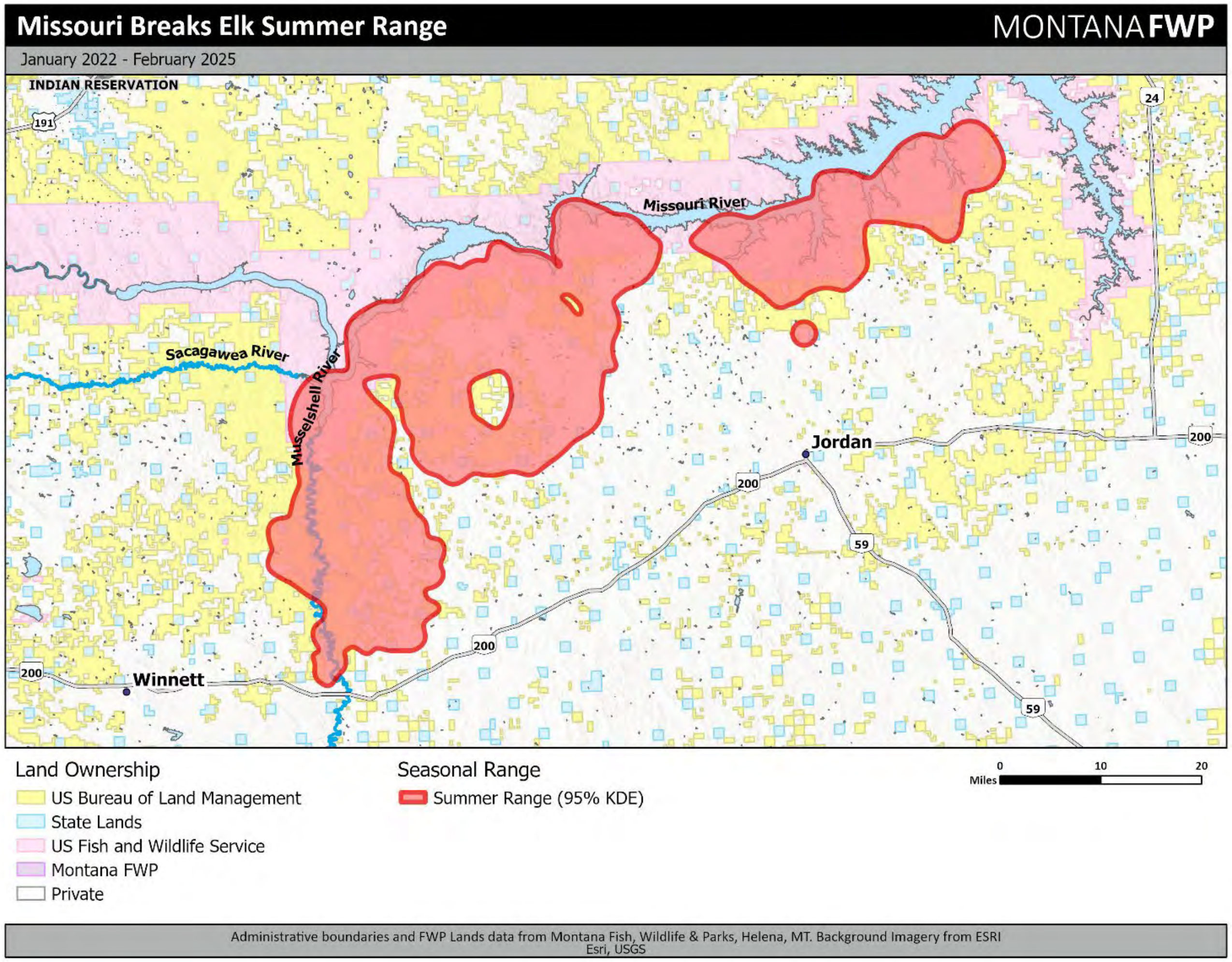

Figure 17. Estimated summer range for elk collared in the Missouri Breaks area based on locations gathered from January 2022 to February 2025. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

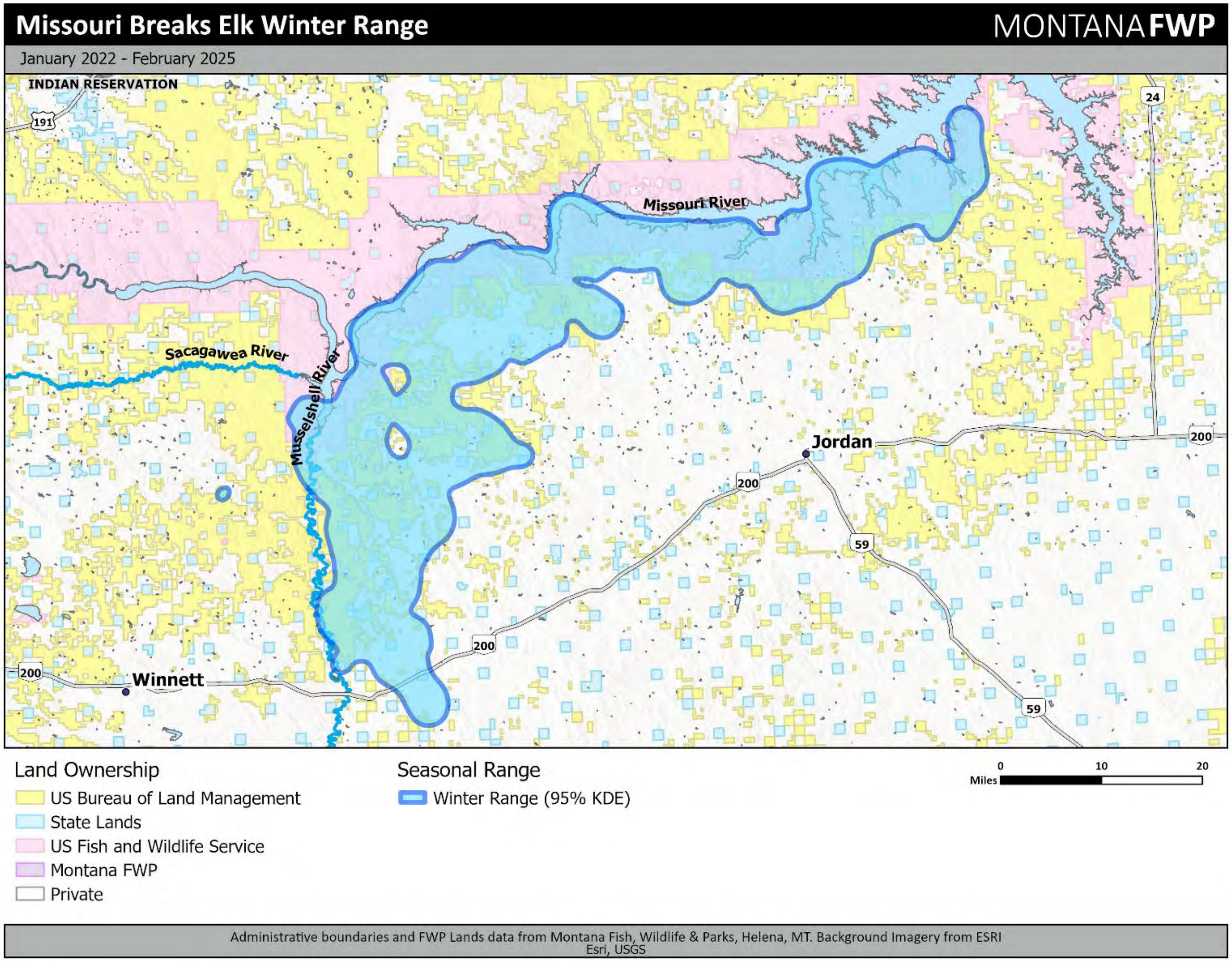

Figure 18. Estimated winter range for elk collared in the Missouri Breaks area based on locations gathered from January 2022 to February 2025. Seasonal ranges were delineated using 95% kernel density estimates (KDE).

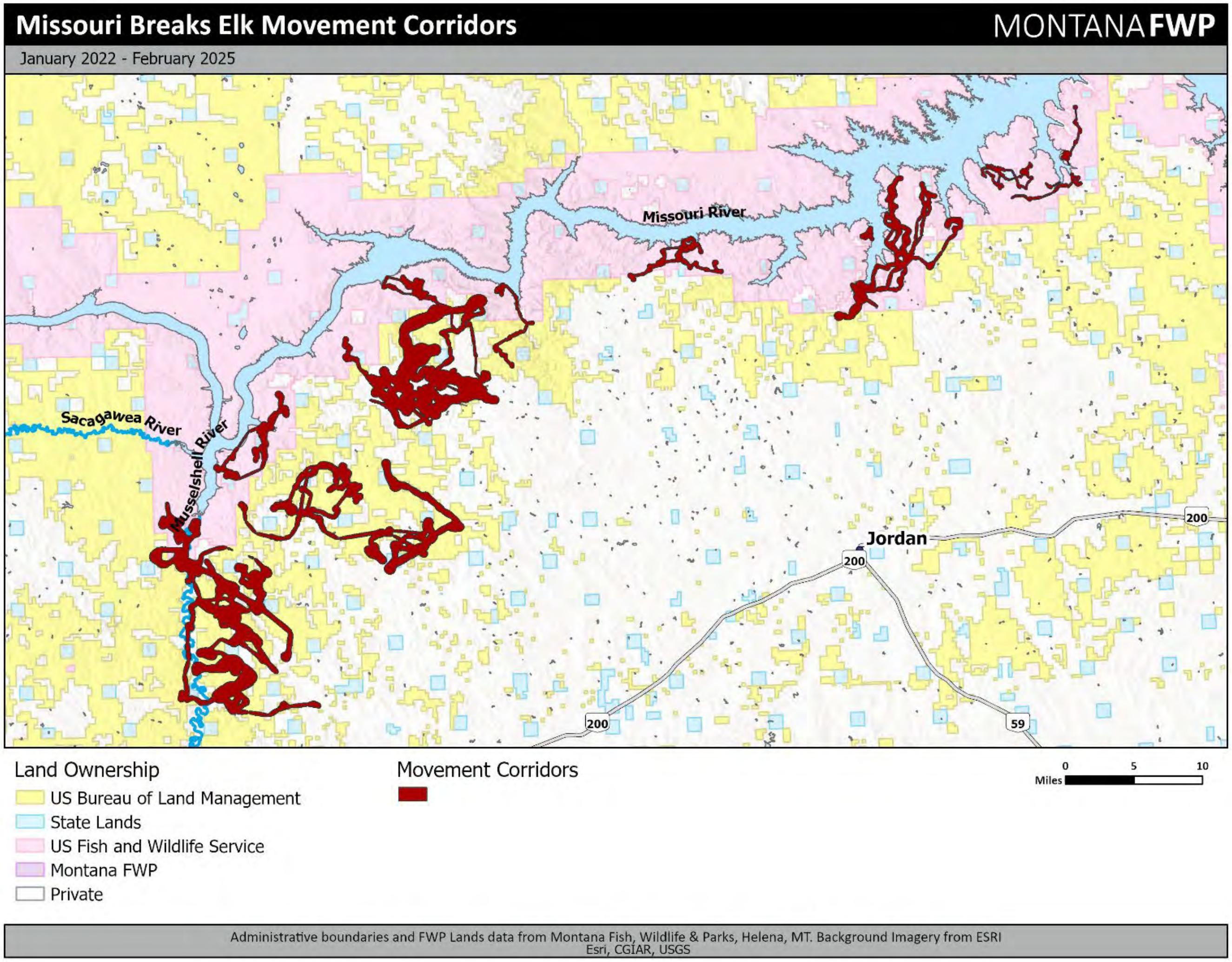

Figure 19. Movement corridors delineated for elk collared in the Missouri Breaks area based on locations gathered from January 2022 to February 2025. Corridors were constructed using the Migration Mapper application and Brownian bridge movement models.

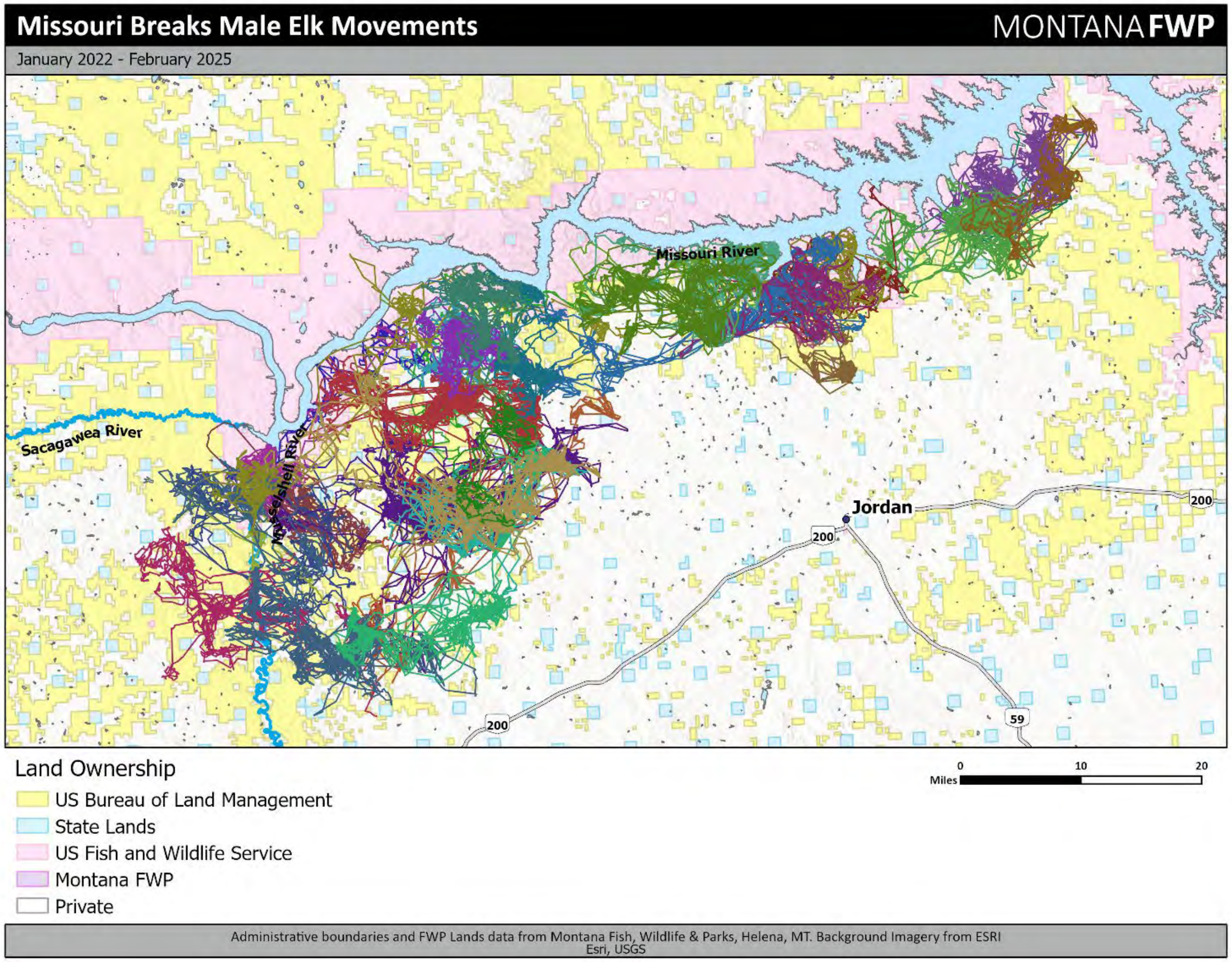

Figure 20. Movements of 36 collared males in the Missouri Breaks study area from January 2022 to February 2025. Each color represents the movement track of one individual.

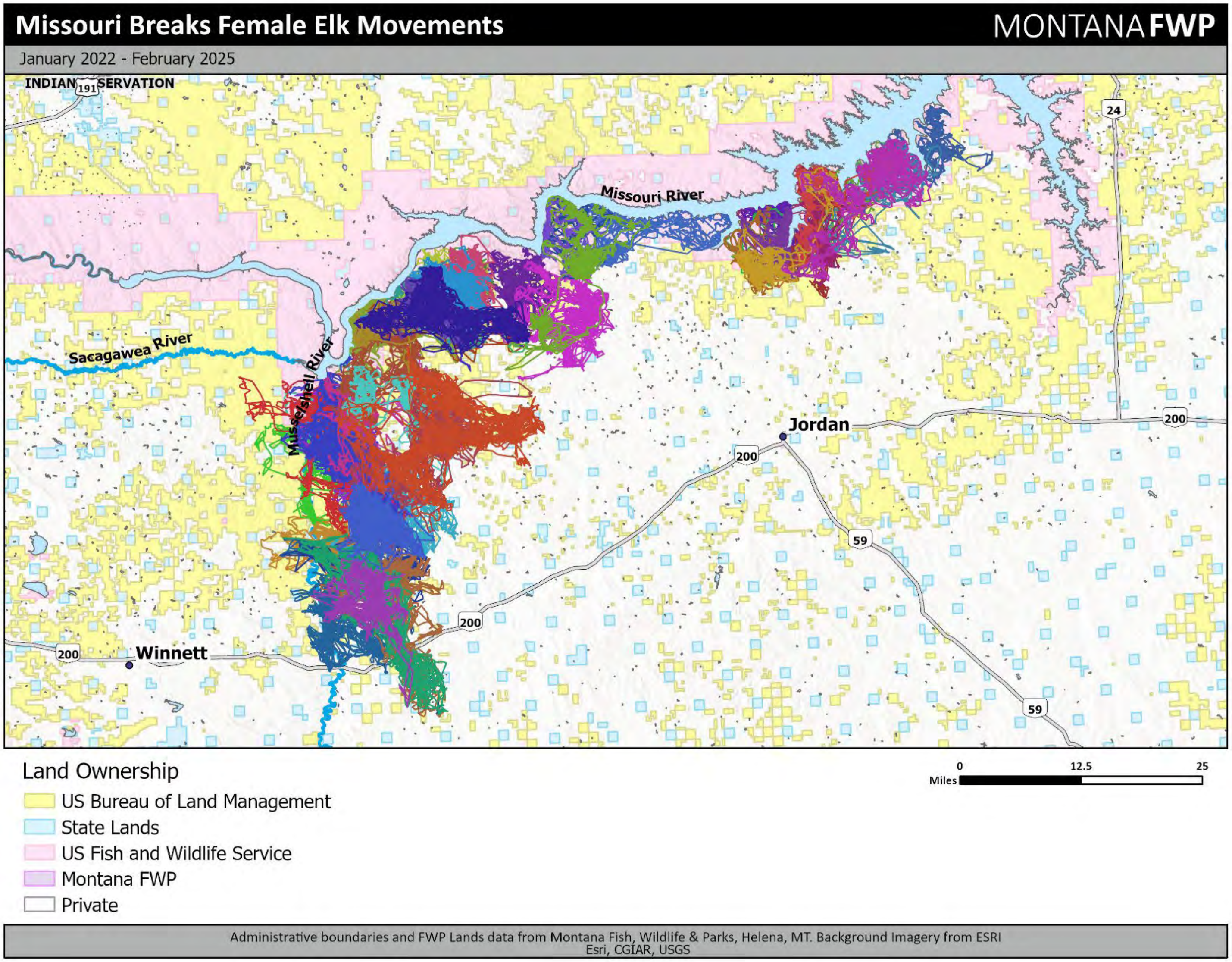

Figure 21. Movements of 55 collared females in the Missouri Breaks study area from January 2022 to February 2025. Each color represents the movement track of one individual.

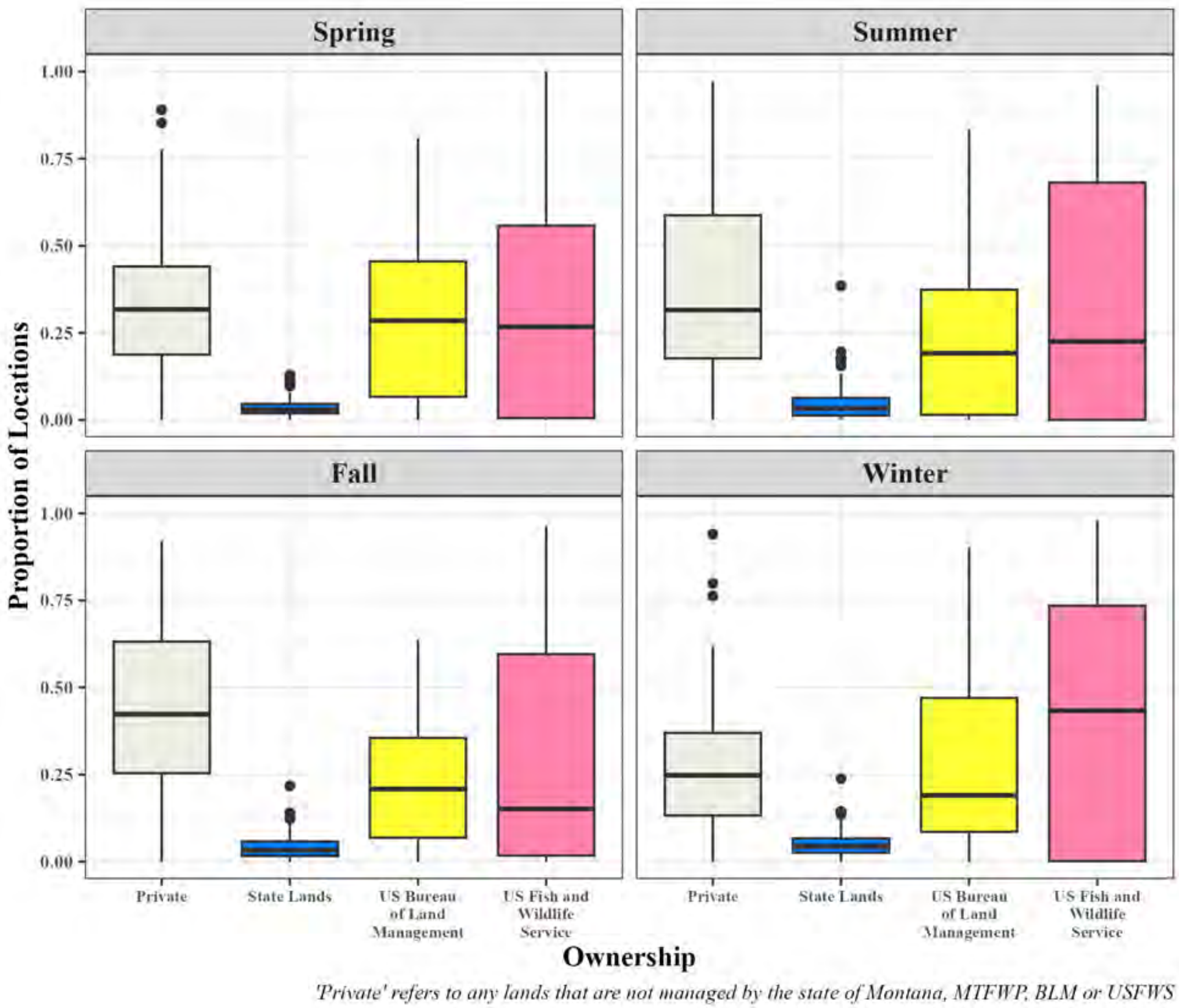

Figure 22. Proportional use of state, federal, and private lands by individual elk in the Missouri Breaks study area by season.

Objective 2: State-wide analysis of factors associated with problematic elk populations.

Contemporary wildlife management seeks to balance the conservation of wildlife with the concerns of many stakeholders (Riley et al. 2002, Krausman and Bleich 2013). Wildlife managers are charged with managing wildlife as public trust resources for the benefit of current and future generations (Decker et al. 2014). Many different stakeholders including hunters, landowners, seasonal and long-term residents, recreationalists, ranchers, and farmers have an interest in how wildlife are managed, and their concerns should be considered when wildlife impacts and management interventions are being assessed (Riley et al. 2002, Manfredo et al. 2009). Abundance and distribution of wildlife are of particular importance, and managers seek to balance the biological carrying capacity of the landscape and the acceptance capacity of stakeholders, i.e., the abundance and distribution of wildlife at which the negative and positive impacts of wildlife are balanced (Carpenter et al. 2000, Riley et al. 2002).

Within the state of Montana, elk populations have recovered after overexploitation during the early 20th century to the extent that they are now considered to be overabundant in some areas (Montana Department of Fish, Wildlife & Parks 2023). Elk populations that are overabundant or have undesirable distributions may be problematic due to their impact on stakeholders and the environment. Overabundant elk populations can have negative ecological impacts such as degradation of vegetation communities and disturbance of ecosystem functions (Bradford and Hobbs 2008), or create property damage such as fence destruction, and consumption of feed, crops, and pasture used for livestock production, especially when elk distributions overlap private land (Weisberg et al. 2002, Hegel et al. 2009). The Montana Department of Fish, Wildlife and Parks (FWP) is tasked with ameliorating some of the negative impacts of problematic elk populations by reducing elk abundance to within acceptable limits.

Hunter harvest is a common tool for managing wildlife population abundance (Krausman and Bleich 2013, Miller et al. 2013, Apollonio et al. 2017). Managers working to control population growth of large ungulates through the harvest of adult females can take advantage of the potentially large negative impact that reducing adult female survival can have on population growth (Brodie et al. 2013, Eacker et al. 2017). Harvest of adult female elk can effectively curtail population growth and even have a modest residual effect in subsequent years by altering the age structure of a population if harvest targets are achieved (Paterson et al. 2022). However, the level of hunter harvest of elk in some areas has proven insufficient to effectively meet elk population objectives (Haggerty and Travis 2006). In Montana, elk populations in many hunting districts are over the prescribed population objectives despite regulations in place that target population reduction through female elk harvest (Montana Department of Fish, Wildlife & Parks 2023). As managers work to reduce problematic elk populations (Haggerty and Travis 2006), a better understanding of the attributes associated with overabundant populations may help to identify management actions that can effectively address the distribution and abundance of problematic elk populations.

Several factors may contribute to elk populations being above the population objectives set by Montana FWP. Elk population dynamics will drive populations away or towards population objectives and are important to consider when evaluating factors that contribute to populations being overabundant (Raithel et al. 2007). Other factors such as regulations, hunter effort, and harvest success affect harvest rates (Cooper et al. 2002, Gamo et al. 2017, Rowland et al. 2023). Additionally, when elk exhibit higher selection preferences for certain landscape characteristics, this influences the distribution of elk and may cause elk to become overabundant in areas with certain landscape characteristics. Recent research on elk distributions during the hunting seasons found that in addition to traditional security habitat (Ranglack et al. 2017), elk find security on lands that restrict hunter access (Burcham et al. 1999, Proffitt et al. 2013, 2016, Sergeyev et al. 2022), which can limit harvest on large swaths of land and draw elk away from lands where hunter access and hunting pressure are greater. The status of a population as over the prescribed population objective can be related to the distribution of elk on private land both because elk on private lands may have lower harvest rates if hunter access to private lands are restricted, reducing the efficacy of harvest regulations as a population management tool, and because negative impacts to landowners may lower the acceptance of elk on the landscape therefore lowering the population objective in an area.

Given the current challenges of managing elk populations, there is a need to understand the characteristics of areas with problematic populations. We worked with population survey data and harvest data collected by Montana FWP from administrative regions 2-6 between 2004 and 2020 to estimate population growth rates for individual hunting districts. We then evaluated how landscape variables, harvest, and hunter effort affected two response variables: the estimated population growth rate and the difference between population abundance and objective. We predicted that hunter effort, hunter access, and the amount of security habitat in a given location are negatively related to population growth rates and the degree to which populations are over objective. We also predicted the amount of pasture and crop land in an area is positively related to population growth rates and the degree to which populations are over objective.

METHODS

Elk population units

We included 66 hunting districts from across the state of Montana in our analysis, some of which were combined with one or more adjacent hunting districts. Hunting districts were combined in certain cases to represent population targets, survey reporting, and/or to better represent herds that encompass multiple hunting districts. We use the term elk unit to refer to hunting districts and combinations of hunting districts used in this analysis.

We used data from annual aerial count surveys conducted by Montana FWP to estimate population growth rates and calculate the difference between the most recent survey count and objective for each elk unit. These count data span 17 years between 2004-2020. These data include total counts of all surveyed individuals and classification counts of calves, antlerless, and antlered individuals that could be classified from the air. Total counts and classification counts were not available for every year for every elk unit. For some elk units, classification counts were available for a subset of the years for which total counts were available and often only a subset of the total population was classified. Surveys deemed atypical for a unit by the regional biologist were excluded from this analysis. The causes of atypical surveys include but are not limited to unsuitable weather during survey flights, poor snow coverage impairing detection, and atypical behavior for the herd preventing an accurate count. In addition to count data, we used annual harvest estimates for each unit to estimate annual population growth rates. Harvest estimates were derived from annual phone surveys from a representative sample of licensed hunters with an elk license or permit (Lukacs et al. 2011, myfwp.mt.gov/fwpPub/harvestReports). Harvest estimates included estimates of calf, antlered, and antlerless harvest for all years between 2004 and 2020.

Population model

We used an integrated population model (IPM) to estimate annual population growth rates used in regression modeling. An IPM incorporates two models, a process model describing the biological processes underlying the population dynamics and an observation model that describes how the observation process is linked to the true values arising from the biological process (Schaub and Kéry 2022). Annual population growth rates for each elk unit were estimated using an integrated population model similar to the IPM described in Paterson et al. (2019). Inputs to the IPM included aerial survey counts, classification counts and harvest estimates. Elk units with fewer than six surveys were excluded to ensure that a multi-year geometric growth rate could be estimated. We evaluated a separate IPM for each Montana FWP administrative region included in the analyses (regions 2-6) resulting in five separate integrated population models. We chose to model each region separately because elk units within a region were considered to share similar conditions and allowed for improved estimates of survival and recruitment rates by sharing these vital rates across elk units within a region.

The process model adopts a pre-birth pulse model with the annual population cycle beginning just prior to the birth pulse (May-June) and ending the following spring just after the aerial surveys are complete (March-April). The process model operates as a stage structured model where the number of calves ($N_{t,u}^{c}$), adult females ($N_{t,u}^{af}$), and adult males ($N_{t,u}^{am}$) is a function of multiple vital rates: sex specific adult survival (ϕ_{af}, ϕ_{am}), annual calf recruitment rates (τ_t), calf sex-ratio (0.5), and age and sex specific harvest rates ($h^{c}_{t,u}$, $h^{af}_{t,u}$, $h^{am}_{t,u}$). The process model equations estimating the number of calves, adult females, and adult males are as follows:

$$N^{c}_{t,u} \sim Poisson\left(\tau_t N^{af}_{t-1,u} - h^{c}_{t,u}\right)$$
$$N^{af}_{t,u} \sim Poisson\left(\phi_{af}\left(0.5 * N^{c}_{t-1,ud} + N^{af}_{t-1,u} - h^{af}_{t,u}\right)\right)$$
$$N^{am}_{t,u} \sim Poisson\left(\phi_{am}\left(0.5 * N^{c}_{t-1,u} + N^{am}_{t-1,u} - h^{am}_{t,u}\right)\right)$$

Age and sex class population estimates for each year (*t*) and elk unit (*u*) were modeled to be a realization from a Poisson distribution. The model assumes that annual harvest from each elk unit is additive to natural mortality and therefore survival terms in the model account for mortality excluding hunter harvest. Recruitment is estimated as a single variable accounting for the probability of birth and calf survival to the following spring survey. Estimates of survival and recruitment were shared between all elk units within each region to increase sample size and to improve estimates for units with incomplete survey histories. A random effect of year was added to recruitment to allow for temporal variation in recruitment, which can be substantial compared to adult survival (Gaillard et al. 1998, Raithel et al. 2007). We assumed that elk units within a given administrative region experienced similar conditions to justify sharing these demographic rates.

The observation model linked the total population size to the total count from the survey data and age and sex specific abundance to the number of each age and sex classified during a survey. The observed total count of all elk from a survey in a given year and unit ($Count^{total}_{t,u}$) was modeled to come from a Poisson distribution with the mean equal to the true population size:

$$Count^{total}_{t,u} \sim Poisson\left(N^{total}_{t,u}\right)$$
$$N^{total}_{t,u} = N^{c}_{t,u} + N^{af}_{t,u} + N^{am}_{t,u}$$

The relationship between the classified count data and estimated number of calves, adult females, and adult males $N^{c}_{t,hd}$, $N^{af}_{t,hd}$, $N^{am}_{t,hd}$, is characterized with a binomial distribution for which the number of trials is equal to the total number of calves, adult females, and adult males that were classified and the probability of successes is proportional to the representation of an age and sex class in the true population:

$$Count^{c}_{t,u} \sim Binomial\left(Classified^{total}_{t,u}, \frac{N^{c}_{t,u}}{N^{total}_{t,u}}\right)$$

$$Count_{t,u}^{af} \sim Binomial\left(Classified_{t,u}^{total}, \frac{N_{t,u}^{af}}{N_{t,u}^{total}}\right)$$

$$Count_{t,u}^{am} \sim Binomial\left(Classified_{t,u}^{total}, \frac{N_{t,u}^{am}}{N_{t,u}^{total}}\right)$$

The IPM was evaluated within the Bayesian framework using JAGS (Plummer 2003) with the R package runjags (Denwood 2016) in the R statistical computing environment (R Core Team 2024). Each parameter within the IPM was assigned its own prior. Survival of adult females and adult males was assigned a Beta(1,1) prior. The prior for the intercept on recruitment was Normal(0,1) on the logit scale and the random effect of year was given a normal prior (Normal (0,σ_{τ}^{2})) with σ_{τ}^{2} given a uniform prior (Uniform(0, 10). Population sizes for each elk unit in each year for each age and sex class were assigned a uniform prior that was left-truncated to be greater than the number of animals harvested in the next year:

$$N_{t,u}^{age,sex} \sim Uniform(h_{t+1,u}^{age,sex}, 10{,}000)$$

For each separate administrative region IPM posterior distributions were obtained from three MCMC chains with a total of 200,000 samples thinned to keep every tenth sample for a total of 20,000 samples after a burn-in of 200,000 samples. Model convergence was evaluated visually using trace plots and with the Gelman-Rubin statistic based on a value of 1.1 (Gelman & Rubin, 1992). Two derived parameters were estimated: 1) the highest three year moving average population growth rate and 2) the average growth rate of the final three years and were used as variables in regression modeling. The geometric mean was used in calculating the average growth rate as it accounts for the multiplicative process of population growth.

Population growth and difference between population size and objective covariates

We evaluated six covariates representing factors that may be related to the population growth rate or the relationship between population abundance and population objective (i.e., the degree that each population unit was over objective) including hunter access, security habitat, agriculture cover, population growth, hunter effort, and antlerless hunter success. We defined landscape covariates hunter access, security habitat, and agriculture cover as the proportion of a unit that included a specific landscape type. We limited the area of elk units to only include the area that overlapped the current estimated elk range defined in Montana FWP elk distribution layer and therefore represents the portion of an elk unit that is predicted to regularly contain elk (Montana Fish, Wildlife & Parks 2015). We designated lands that provide hunter access as lands that were freely accessible to hunters (accessible) in contrast to lands with varying degrees of hunter access restrictions (restricted access). To calculate the proportion of an elk unit that provides hunter access, we defined public lands that allow elk hunting and were navigable by public road or waterway and private lands enrolled in Montana’s Block Management Program for the year 2019 that did not require landowner approval as accessible, and all other private lands as restricted access. We defined a location as security habitat if canopy cover was >11% and the average distance to a road was >2.1 km on a buffer area of 20 km^2 surrounding the location (Ranglack et al. 2017). We only designated security habitat for land that provides hunter access (see above). We combined planted pasture and cultivated crop classes from the National Land Cover Database (Homer et al., 2015) to represent agriculture cover and estimate an index of available supplemental forage that could be both an attractant for elk and improve fitness for animals within a unit. We used the number of hunter days from Montana FWP published harvest estimates as the hunter effort metric (days/km^2), which was calculated as the number of hunter days/ area of elk range in an elk unit. We calculated the number of hunter days as the average for the last three years of the dataset. We included a metric of female harvest intensity which was the ratio of female harvest to the elk unit population size (number of cow elk harvested/elk unit population size). We used the average for the last three years for the number of cow elk harvested and the elk unit population size. For the model of the difference between population size and objective, we included as a covariate the highest three-year moving average population growth rate from the entire study period, calculated using the geometric mean, to understand how population dynamics relate to the population difference

Regression models

We used multiple linear regression to evaluate how characteristics of elk units related to 1) the population growth of elk units and 2) the difference between the elk unit abundance and objective. To understand how elk characteristics are related to population dynamics, we used the average population growth rate for the final three years for each elk unit, calculated using the geometric mean, as the response variable. The population growth regression model included all covariates described earlier. To understand how characteristics of elk units are related to the degree populations are over objective, we used the difference between the most recent elk count (final year of survey data is 2020) and the objective for each elk unit as the response variable (positive values occur when populations are over their objective level), and we call this the population difference. . We included elk units that are both over and below the population objective in the analysis. The regression model assessing the population difference included all the covariates described above in addition to two other covariates. First, we included the population objective defined in the 2005 Montana Statewide Elk Management Plan to account for variance in the population objective size. In elk units comprised of multiple hunting districts, we defined the unit's objective as the sum of the objective for each hunting district. Second, we included the highest three-year moving average population growth rate from the entire study period. Covariates that depend on a parameter estimated from the IPM were included in the models as latent parameters arising from a normal distribution centered on the true parameter value with the variance equal to the squared standard deviation of the posterior distribution from the IPM. This allowed for error propagation from one model to the next. All covariates were assumed to have linear relationships with response variables. We used reversible jump Markov chain Monte Carlo (RJMCMC) to determine which covariates held the most support for inclusion in the model. RJMCMC executes model selection by attaching an indicator variable to coefficients in the model and jumping between different sets of indicator variables in each iteration of sampling, essentially jumping between different models (Green 1995). Covariates that explain more of the variance in the response variable will be chosen more often. The proportion of times a covariate is included in a model provides a measure of support for the covariate. We provide conditional model coefficients, which means the estimate is conditional on a covariate being included in the model, i.e., the indicator variable takes on a value of one rather than zero. We also provide model-averaged estimates that include the entire posterior regardless of whether the indicator was zero or one. Therefore, covariates with high inclusion probabilities will be weighted more heavily in the model average, while those with low inclusion probabilities will have estimates pulled towards zero.

Model fitting

The normal linear regression models were fit in the Bayesian framework using the NIMBLE (de Valpine et al. 2017, 2023) package in the R statistical computing environment (R Core Team 2024). Model convergence was evaluated using visual inspection of trace plots and with the Gelman-Rubin statistic based on a value of 1.1 (Gelman & Rubin, 1992). We evaluated all covariates for collinearity using Pearson's correlation coefficient with a threshold of 0.7. All covariates were centered and scaled by one standard deviation. For each analysis, the posterior distribution was obtained from three chains run for 250,000 iterations with an initial burn-in of 150,000 samples, resulting in 100,000 samples for inference. The regression coefficients and the intercept in the population difference analysis were given a prior of Uniform(-10,000, 10,000). For the population difference analysis, the true maximum population growth rate was normally distributed with a prior on the mean of Uniform(0, 10) and a prior for the standard deviation of Uniform(0, 10). For the population growth analysis, the intercept and coefficients were each given a prior of Uniform(-30, 30).

RESULTS

IPM estimates

We used data from 66 elk units from across the state of Montana, omitting data from administrative region one in the northwest corner of the state and region seven in the southeast corner of the state due to insufficient data. An IPM was evaluated for each region with region two including 14 elk units, region three including 24 elk units, region four including 20 elk units, region five including 5 elk units and region six including 3 elk units. We were interested in estimates of two parameters derived from the IPMs that were carried forward into regression modeling: 1) the average population growth rate for the final three years and 2) the maximum three-year moving average population growth rate for the entire study period. The average population growth rate for the final three years estimated from the IPMs was 1.01 (SD = 0.07; Range: 0.85, 1.17). We found that 61% of the elk unit populations were growing ($\lambda > 1$) based on estimated average population growth rates for the final three years. Of the elk units that exhibited population growth in the final three years, 75% of those elk units were also over the population objective. The estimated mean maximum three-year average population growth rate across the entire study period estimated from the IPMs was 1.11 (SD= 0.06, Range: 0.94, 1.32). We found that all but one elk unit had a maximum three-year average population growth rate greater than 1.

Regression modeling

We used data from 66 elk units located in administrative regions 2-6 to evaluate regression models of population growth and population difference. There was large variation in the difference between population abundance and objective, and the average difference was 566 elk above the objective (SD: 1,208; Range: -594, 8,535). Of the 66 elk units evaluated, 77% were above the population objective, with the remaining elk units at or below objective. The included covariates exhibited a range of values (Appendix A). The mean proportion of hunter accessible land in an elk unit was 0.58 (SD: 0.27, Range: 0.01, 0.99). The mean proportion of hunter accessible land within an elk unit that was considered security habitat was 0.15 (SD=0.14, Range: 0.00, 0.52). The mean percentage of land within an elk unit that was considered pasture or crop land was 0.03 (SD=0.04, Range: 0.00, 0.21). The mean number of hunter days per km^2 was 8.0 (SD = 4.1, Range: 0.94, 19.1). The mean female harvest intensity was 0.11 (SD=0.05, Range: 0.01, 0.27). The mean population objective was 915 elk (SD:739, Range: 75, 4000).

Population growth regression model

Results for modeling efforts aimed at explaining variation in population growth rates indicated that an elk unit with average values for all covariates is predicted to have a three-year geometric mean population growth rate of 1.02 (90% Highest Density Interval (HDI): 1.00, 1.03). Variable-selection results indicated support for a relationship between elk unit population growth rate and only one covariate, female harvest intensity (female harvest/elk unit population size), which had a model inclusion probability greater than zero (Table 1). Higher model inclusion probabilities provide a measure of support for the covariate being in the model with an inclusion probability of zero indicating no support for the covariate being in the model. Female harvest intensity had a slightly negative relationship with the population growth rate, with the conditional coefficient estimate of -0.04 (90% HDI: -0.05, 0-0.02) exhibiting a slightly stronger relationship than the model-averaged coefficient of -0.01 (90% HDI: 0.05, 0) (Figure 23). The population growth model predicts that when 5% and 15% of the total population is taken as female harvest and all other covariates are held at their average values, the population growth rate is predicted to be 1.03 (90% HDI: 1.0, 1.07) and 1.01 (90% HDI: 0.96, 1.03), respectively, based on model-averaged estimates. Using model-averaged estimates, a female harvest intensity of 0.19 or higher is predicted to result in a population shrinking, although the 90% HDI does include values over 1 at all harvest intensities. The model averaged predictions account for model-selection uncertainty regarding how best to model the relationship between female harvest intensity and elk unit population growth. Predictions that are based only on the best-supported model ignore model-selection uncertainty and are termed conditional estimates (i.e., they are conditional on a given model structure) and provide estimates that are more precise than model-averaged predictions. Conditional estimates from the best-supported model that includes only female harvest intensity indicate that an elk unit population is predicted to shrink at a harvest intensity of 0.16, with a 90% highest density interval that includes values lower than one. The model inclusion probabilities were zero for all other covariates therefore there was no support from the results for a relationship between the elk unit population growth rate and the level of hunter effort, the proportion of hunter accessible land, the proportion of security habitat, or the proportion of pasture and crop land (Table 1).

Table 1. Results of model selection results based on reversible jump Markov Chain Monte Carlo methods that evaluated models with all possible combinations of the covariates for explaining variation in geometric mean population growth rate. Results indicate the proportion of models selected that include each covariate and the mean coefficient estimates from the posterior for the population growth model. The provided means, standard error, and 90% highest density intervals are for model-averaged estimates.

	Conditional Coefficient estimates			Model-averaged coefficients	
	Proportion selected	Mean (SE)	90% HDI	Mean (SE)	90% HDI
Intercept	----------	1.02 (0.01)	1.00, 1.03	1.02 (0.01)	1.00, 1.03
Hunter Effort	0.00	0.00 (0.01)	-0.02, 0.02	0.00 (0.00)	0.00, 0.00
Hunter Access	0.00	0.00 (0.01)	-0.02, 0.02	0.00 (0.00)	0.00,0.00
Security habitat	0.00	0.00 (0.01)	-0.01, 0.02	0.00 (0.00)	0.00, 0.00
Agriculture cover	0.00	0.01 (0.01)	-0.01, 0.02	0.00 (0.00)	0.00, 0.00
Female harvest	**0.31**	**-0.04 (0.01)**	**-0.05, -0.02**	**-0.01 (0.02)**	**-0.05, 0.00**

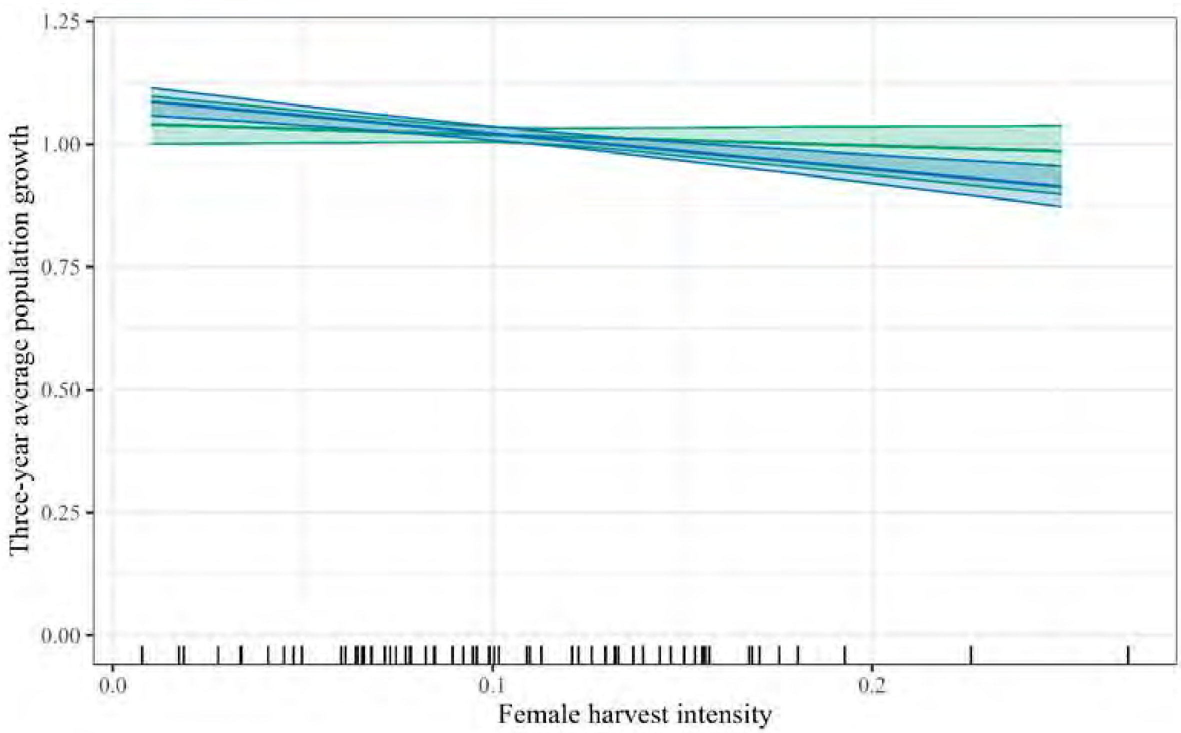

Figure 23. Shown is the predicted relationship between the average population growth rate for the final three years and female harvest intensity. We show model-averaged predictions (green) that include the full uncertainty surrounding the estimate and conditional predictions (blue) that only include instances when female harvest intensity is included in the model and therefore represent more precise estimates. The bands around solid lines represent the 90% highest density interval and vertical black lines on the x axis show where data exists in the dataset.

Difference between elk population size and objective regression model

Evaluation of the difference between population abundance and objective, i.e., population difference, identified three notable outliers, which cause right-skew in the distribution of differences. Therefore, we conducted modeling for this objective using two different versions of the data set. In our first evaluation, we analyzed the full data set, and in the second, we analyzed a reduced dataset that excluded the three outliers. Although there were some differences in the inclusion probabilities of covariates for analyses of the two different datasets, the overall inferences are generally quite similar (Table 2, Table 3). Accordingly, we primarily focus on results from the analysis of the data set without the outliers (Table 3). There was strong support for a relationship between the proportion of hunter accessible land available to elk in an elk unit and the degree that an elk unit was over objective, as evidenced by a high probability of inclusion for that covariate in the model in the model (Table 3). The proportion of hunter accessible land was strongly negatively related to the population difference with a one standard deviation increase in the proportion of hunter accessible land being associated with a decrease in overabundance of elk by 173 individuals (β_{Access}= -173.04, 90% HDI: -331.8, 0.00) (Figure 24). For an elk unit with average values for all other covariates, increasing the proportion of hunter accessible land from 0.45 to 0.85 is predicted to reduce overabundance of elk by 253 individuals (90% HDI: 0, 442). Results suggest that there is moderate support for a relationship between the proportion of security habitat within hunter accessible lands and the population difference (Table 3). We found a moderately strong negative relationship between the proportion of security habitat and the population difference with a one standard deviation increase in the proportion of security habitat predicted to result in a decrease in overabundance by 90 individuals ($\beta_{Security}$= -89.5, 90% HDI: -292.09, 0.05). However, the highest density interval for the model-averaged estimated coefficient is quite wide, which makes apparent that there is notable uncertainty in the relationship (Figure 25). For an elk unit with average values for all other covariates, it is predicted that the number of elk over the population objective declines by 187 individuals (90% HDI: 0, 359) as the proportion of security habitat present in hunter accessible lands increases from 0.05 to 0.25.

Table 2. Model selection results based on reversible jump Markov Chain Monte Carlo methods that evaluated models with all possible combinations of the covariates for explaining variation in the population difference using the full dataset. Results indicate the proportion of selected models that include each covariate and mean coefficient estimates from the posterior. The provided posterior means, standard error, and 90% highest density intervals are provided conditional on the covariate being included in the model and as a model average when the full posterior is included.

	Conditional coefficient estimates			Model-averaged estimates	
	Proportion selected	Mean (SE)	90% HDI	Mean (SE)	90% HDI
Intercept	-----------	519.37 (125.20)	270.78, 762.98	519.37 (125.20)	270.78, 762.98
Objective	-----------	90.70 (133.84)	-174.22, 351.74	90.70 (133.84)	-174.22, 351.74
Hunter Effort	0.11	-49.84 (140.61)	-284.31, 176.37	-5.32 (48.44)	-147.06, 53.59
Hunter Access	**0.89**	**-429.32 (137.80)**	**-659.48, -207.21**	**-383.13 (186.13)**	**-650.07, 0.00**
Security habitat	0.18	-165.72 (167.85)	-450.67, 97.03	-29.08 (94.43)	-340.92, 16.30
Agriculture cover	0.15	-139.75 (160.52)	-391.29, 132.13	-20.79 (79.41)	-295.00, 11.46
Female harvest	0.21	-29.56 (129.16)	-390.00, 35.99	-37.59 (93.94)	-310.38, 0.01
Maximum growth	0.17	150.39 (156.12)	-100.37, 400.05	25.45 (85.46)	-18.75, 303.44

Table 3. Model selection results based on reversible jump Markov Chain Monte Carlo methods that evaluated models with all possible combinations of the covariates for explaining variation in the population difference removing outliers. Results indicate the proportion of selected models that include each covariate and mean coefficient estimates from the posterior. The provided posterior means, standard error, and 90% highest density intervals are provided conditional on the covariate being included in the model and as a model average when the full posterior is included.

	Conditional coefficient estimates			Model-averaged estimates	
	Proportion selected	Mean (SE)	90% HDI	Mean (SE)	90% HDI
Intercept	----------	339.65 (58.18)	221.90, 450.77	339.65 (58.18)	221.90, 450.77
Objective	----------	128.66 (66.81)	-0.59, 261.51	128.66 (66.81)	-0.59, 261.51
Hunter Effort	0.05	-14.03 (65.74)	-119.15, 95.98	-0.64 (14.33)	0.00, 0.00
Hunter Access	**0.78**	**-223.13 (72.32)**	**-342.49, -104.83**	**-173.04 (112.80)**	**-331.80, 0.00**
Security habitat	**0.47**	**-191.62 (78.33)**	**-318.62, -61.25**	**-89.5 (109.57)**	**-292.09, 0.05**
Agriculture cover	0.13	-104.57 (73.73)	-224.83, 18.48	-13.57 (44.05)	-141.13, 0.00
Female harvest	0.06	-26.41 (60.31)	-148.63, 48.48	-2.95 (18.80)	-27.41, 0.07
Maximum growth	0.07	55.76 (72.96)	-59.52, 181.06	3.87 (23.88)	-0.35, 55.07

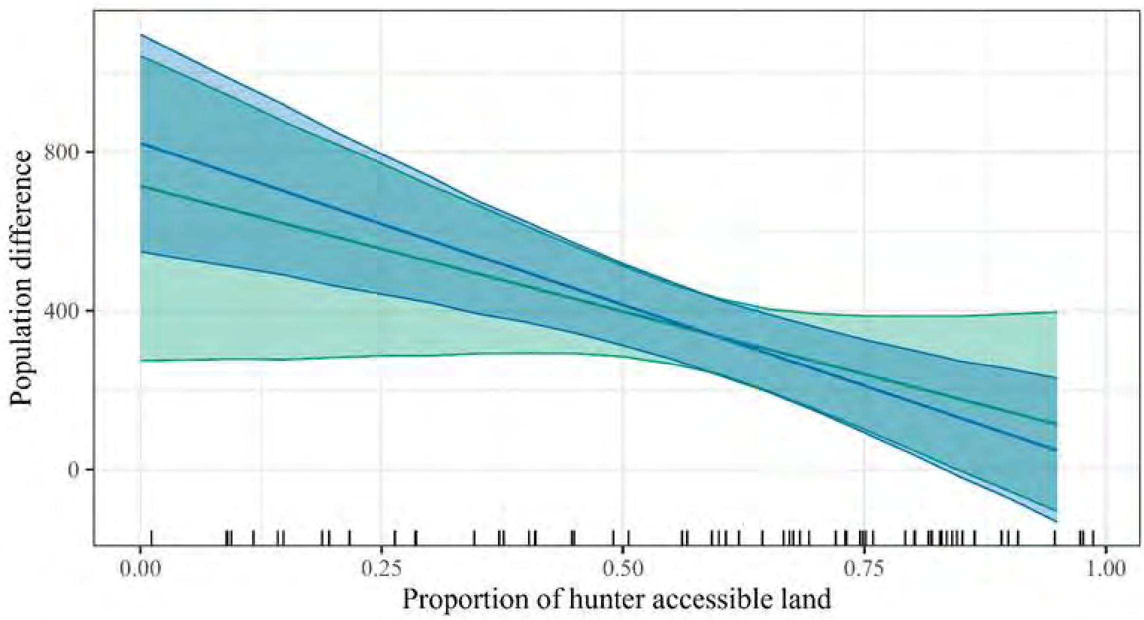

Figure 24. The predicted relationship between the population difference and the proportion of hunter accessible land in an elk unit. We show model-averaged predictions (green) that include the full uncertainty surrounding the estimate and conditional predictions (blue) that only include instances when proportion of hunter accessible land is included in the model and therefore represent more precise predictions. The bands around solid lines represent the 90% highest density interval and vertical black lines on the x axis show where data exists in the dataset.

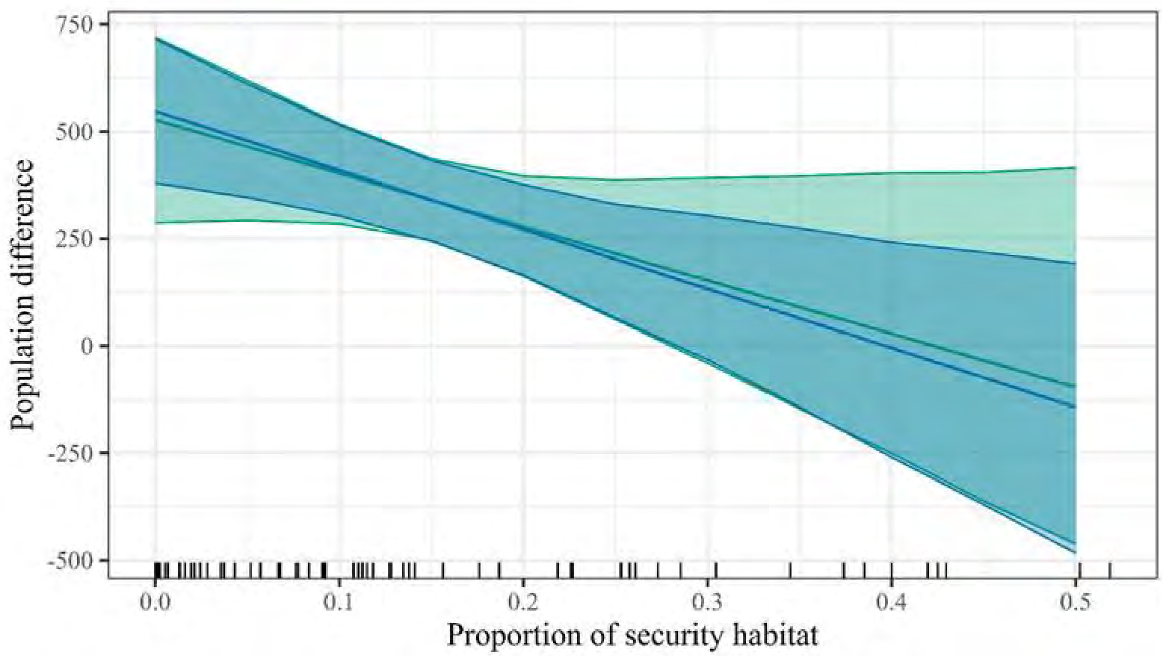

Figure 25. The predicted relationship between the number of elk over or under objective and the proportion of security habitat on hunter accessible land in an elk unit. We show model-averaged predictions (green) that include the full uncertainty surrounding the estimate and conditional predictions (blue) that only include instances when proportion of security habitat is included in the model and therefore represent more precise predictions. The bands around solid lines represent the 90% highest density interval and vertical black lines on the x axis show where data exists in the dataset.

DISCUSSION

Our results suggest that the degree to which an elk unit's population is over objective is strongly related to the proportion of land that is accessible to hunters. There is also evidence to suggest that the proportion of security habitat on hunter accessible lands may also be related to the degree that an elk unit's population is over objective. We found some evidence to indicate that population growth rates tend to decrease as the female harvest intensity increases. However, it is important to note that there was notable uncertainty regarding the strength of the relationship based on model-averaged results. The results presented here reinforce previous findings that hunter access and security habitat play a role in problematic elk distributions (Proffitt et al. 2013, 2016, Ranglack et al. 2017, DeVoe et al. 2019) and suggest these particular landscape characteristics are avenues through which managers might target problematic populations.

Our analysis found that the proportion of hunter accessible land available to elk is the strongest predictor of how much an elk population is over objective and that the relationship is strongly negative. This finding is consistent with evidence from other studies that have found that elk select for lands that restrict hunter access, especially during the hunting season (Proffitt et al. 2013, 2016, Ranglack et al. 2017) and that some elk remain on these private lands for large portions of the year (Burcham et al. 1999). When elk spend more time on private lands that restrict hunter access, the ability of managers to regulate the population through harvest is diminished, and conflicts with landowners may arise (Haggerty and Travis 2006).

We found that as the proportion of security habitat increased in an elk unit the degree to which an elk unit was over objective decreased. One potential explanation for this finding is that in elk units with a greater proportion of security habitat more elk remain on lands accessible to hunters, and in turn are harvested at higher rates bringing the population size closer to the population objective. Although not implausible this explanation contradicts the concept of elk security habitat for which the core management goals are providing increased elk survival while allowing for increased hunter opportunity during the hunting season by encouraging elk to remain on public lands (Hillis et al. 1991). If this first explanation is correct this suggests that security habitat is meeting the goal of redistributing elk to public lands for hunter opportunity, but that security habitat does not provide adequate survival of elk as it is designed to do. An alternative explanation that does not contradict our current understanding of security habitat is that elk units with higher proportions of security habitat also have a greater proportion of hunter accessible lands, which may be associated with an increased tolerance for elk on the landscape and therefore higher population objectives. It is possible that areas with a lower proportion of security habitat include a greater proportion of lands used for livestock production that include stakeholders more sensitive to elk damage and therefore have population objectives well below the biological carry capacity, which may contribute to a greater positive difference between the elk unit population size and objective. Although we did account for the objective population size of an elk unit in our model we did not account for a combined effect of objective and proportion of security habitat in our modeling and future research should consider a possible interaction between the two covariates which may help to explain our results. Additionally, the moderate support for security habitat in the model omitting outliers and the lack of support for security habitat in the model using the full data set suggests that there is more uncertainty regarding the importance of security habitat within hunter accessible lands and that increasing security habitat on hunter accessible lands may not drive populations closer to objective in elk units that are extremely above the population objective.

The negative relationship between the female harvest intensity and population growth aligns with an established understanding that for large ungulate populations, the population growth rate is most responsive to variation in adult female survival (Gaillard et al. 1998). It is interesting that a stronger relationship between population growth and female harvest intensity was not estimated given the strong reductions in population growth through female harvest shown in a simulation study of elk (Paterson et al. 2022). The more modest relationship exhibited in our study may be due to several factors. We used estimates of population growth from an IPM and accounted for this estimation error in our regression model, which likely increased uncertainty surrounding the relationship. In our calculation of female harvest relative to the total population, we used harvest numbers estimated from surveys (Lukacs et al. 2011) and population counts, which are considered to be an index of population size. Therefore, this covariate is likely an index of the female harvest intensity unlike in a simulation where all parameters are known to be truth. Finally, the population growth rate is largely influenced by both adult female survival and calf recruitment (Gaillard et al. 1998, Raithel et al. 2007, Brodie et al. 2013). Therefore, variable calf recruitment among elk units may account for some of the variation in population growth rates from this study, which diminishes the strength of the relationship with female harvest when compared to what was found in a previous simulation study (Paterson et al. 2022). Our findings suggest that in areas where harvest regulations translate to rates of successful harvest, increasing the proportion of females targeted by hunting is reasonably likely to reduce elk population sizes.

It is notable that there was little to no support for a relationship between some covariates and the degree that an elk unit's population is over objective. First, the lack of association between the highest three-year geometric mean growth rate and the population difference indicates that being over objective is less related to whether a population is increasing in abundance and more a function of landscape characteristics that limit hunting opportunities. We did not find evidence for a relationship between hunter effort and elk unit population growth rates or the degree to which an elk unit is over objective. The fact that we found no relationship between hunter effort and either of the response variables suggests that hunter effort may be decoupled from harvest rates that would impact population growth rates and the difference between elk population size and objective. Although, our study measures hunter effort across a large spatial and temporal scale, which potentially limits the ability of our analysis to find a relationship between hunter effort and the elk unit population difference or population growth rate. Lastly, the lack of relationship between the proportion of pasture and crop land in an elk unit and the population difference suggests that an increased proportion of these lands is not associated with problematic populations per se, but that hunter access restrictions on these lands may drive the degree to which an elk unit is over objective. Additionally, the potential nutritional benefits to elk provided by increased prevalence of pasture and crop lands in an elk unit (Barker et al. 2019) do not appear to translate either to increases in the degree to which a population is over objective or to increases in the population growth rate.

Management Implications

We found that two landscape characteristics, proportion of hunter accessible land and proportion of security habitat on hunter accessible lands, impact how far a population is over objective and provide avenues through which mangers may be able to target over objective populations. The relative amount of hunter accessible land in an elk unit was the most important predictor of how far an elk unit is over objective, therefore when it is possible to do so, making more lands available for hunting will likely have the greatest impact on bringing populations closer to objective. We also found that increasing security habitat on hunter accessible lands was related to decreases in the degree to which an elk unit was over objective. This finding contradicts the concept of security habitat and could simply be the result of a positive association between security habitat and hunter accessible lands that leads to greater tolerance and population objectives in elk units that have greater proportions of security habitat. Therefore, we suggest increasing the proportion of hunter accessible lands in an elk unit may be the single most useful action for decreasing the degree to which elk unit populations are over objective.

Objective 3: Elk habitat selection analysis in the Devil's Kitchen, Custer Forest, and Missouri Breaks study areas

3.1 Devil's Kitchen Analysis

Wildlife management agencies across the western United States are increasingly being tasked with managing elk herds that exceed numeric population goals and strain public tolerance through conflict with landowners (Krausman and Bleich 2013). The population dynamics of elk and other large ungulate species are largely driven by adult female survival rates (Gaillard et al. 2000, Eacker et al. 2017), and the primary tool available to reduce survival rates and decrease overabundant populations is the liberalization of adult female harvest regulations (Sinclair et al. 2006, Loe et al. 2016, Gruntorad and Chizinski 2020). Wildlife managers may also utilize hunter harvest and other management actions to create desirable elk distributions that reduce conflict with private landowners (Jones et al. 2021). While the wildlife on private lands is a public resource managed in the public trust by state wildlife managers (Mahoney and Geist 2019), public access to private lands for hunting is provided at the discretion of individual landowners. Therefore, when elk distributions overlap private lands, manipulating elk distributions or reducing elk abundance through hunter harvest can be challenging due to varying hunter access management decisions made by landowners (Haggerty and Travis 2006, Proffitt et al. 2016).

Managers seeking to alleviate conflict with landowners by reducing overabundant elk populations may adjust harvest regulations to increase the number of female elk hunting licenses available or extend the period of legal harvest. However, changes in harvest regulation structure alone may or may not result in female harvest rates sufficient to reduce the population growth rate. Where overabundant elk populations and private lands overlap, the success of hunter harvest as a tool for elk population management depends not only on the harvest regulations applied, but also on the varying levels of hunting access on private lands. It has been well-documented that human hunting pressure can alter the way elk move across the landscape and use resources during the hunting season (Vieira et al. 2003, Proffitt et al. 2009, Cromsigt et al. 2013, DeVoe et al. 2019, Mikle et al. 2019). Lands with limited hunter access may serve as refuges, and elk may aggregate in these areas to escape harvest risk during the hunting seasons (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013). Therefore, an increase in license availability or season length alone may not result in population reductions if elk can respond to these measures with seasonal movements to areas where hunting access is restricted (Conner et al. 2001, Proffitt et al 2010, Proffitt et al. 2016). Alternatively, wildlife managers may use elk risk responses to their advantage and manipulate harvest risk through harvest regulations or hunter access management to maintain elk on public lands and reduce conflict with private landowners. In such situations, managers may encounter a trade-off between increasing the number of female elk harvested and producing elk distributions that are favorable for agricultural producers. While many studies have shown that elk preferentially select for areas that restrict hunting access where available (Burcham et al. 1999, Conner et al. 2001, Proffitt et al. 2010, Proffitt et al. 2013, Sergeyev et al. 2020), our understanding of the factors that influence elk movement between different strategies of hunter access management and how varying access strategies influence habitat selection remains limited.

A better understanding of elk movements between hunter access management strategies and how hunter access management, harvest regulation, and other landscape attributes influence elk habitat selection may allow managers to more effectively manipulate these factors to meet management objectives for elk distribution and population numbers. By increasing our understanding of this central Montana elk population, FWP will be better able to sustainably provide harvest opportunity, minimize game damage and problematic distributions, and work with private and public land stewards to manage habitat that benefits elk. Our goal was to evaluate the effects of hunter access management strategies, harvest regulations and other landscape features on female elk movement and habitat selection during the hunting season.

METHODS

Elk location data

We used GPS locations from 61 elk collared in the Devil's Kitchen study area that were monitored during hunting season (Aug 15 – Feb 15) and daylight hours. We included only individuals with GPS locations that occurred in HDs 445, 446, and 455, and therefore excluded three individuals with data that occurred in HDs 413 and 416, leaving 58 individuals remaining in the analysis. We associated elk locations with one of 4 hunting periods: early shoulder (August 15 – September 3), archery (September 4 – October 17), general firearm (October 23 – November 28), and late shoulder (November 29 – February 15).

Covariate data

We developed covariates describing factors potentially influencing female elk movements and/or habitat selection during the late fall and early winter, including hunter access management, harvest regulation, migratory status, snow water equivalent (SWE), landcover type, slope, aspect, terrain ruggedness, and a habitat security metric. We defined hunter access management by classifying individual land parcels into discrete hunter access management strategies for each of the 4 hunting periods according to the hunter access management strategy employed during each period (Figures 26 and 27). The hunter access management strategies included open access, moderate access, and limited access, and were based on personal communication with local land and wildlife managers and private landowners. We classified a parcel as open access if it was publicly owned and accessible or privately-owned and enrolled in Montana's Block Management Access system and not requiring a reservation to hunt. A parcel was categorized as moderate access if landowners allowed access to members of the public who enquired, or if it was enrolled in Montana's Block Management Access system but required a reservation which limited the number of hunters. Parcels were classified as limited access if landowners allowed access only for friends and family or outfitted clients, or if no public hunting opportunities were available. Publicly owned but landlocked parcels were classified using the access management strategies of surrounding private lands.

To define harvest regulation, we classified the antlerless harvest regulation scenarios that elk could encounter in the study area as liberal harvest (if general license and antlerless only license valid), restricted harvest (antlerless harvest by permit only), or no harvest (no antlerless harvest allowed; Table 4, Figures 28 and 29). General elk licenses were available to all Montana resident hunters and to some nonresident hunters through a drawing. Elk B licenses were valid for antlerless harvest only and were available to residents through a drawing and/or over the counter, and to nonresidents through a drawing. Elk permits were available through a drawing only, could only be used in combination with the general elk license, and facilitated an enhanced hunting opportunity with fewer hunters on the landscape and the opportunity to harvest mature bull elk.

To define migratory status of each animal-year, we used the same migratory classifications described in Objective 1 and coded as an indicator of whether an individual was a migrant or not. We chose to focus on spring migration because harvest deaths occurring in the fall prevent classification of fall migratory behavior due to limited data.

We used snow water equivalent (SWE) data from the Snow Data Assimilation System (SNODAS; National Hydrological Remote Sensing Center) to calculate the daily SWE value for each 30x30 meter pixel in the study area across all hunting periods. We used landcover data from the Montana Landcover Framework (Montana Spatial Data Infrastructure (MSDI) Land Use/Land Cover Data) and reclassified landcover categories into seven final categories: grassland, conifer woodland, sagebrush steppe, shrubland, riparian, agriculture, and nonhabitat. We derived the slope, aspect, and two terrain ruggedness covariates from the National Elevation Dataset (NED) downloaded with the FedData package in R (R Core Team, 2022). We calculated topographic ruggedness index (TRI, Riley 1999) and vector ruggedness measure (VRM, Sappington 2007) with the spatialEco package in R. Aspect was transformed with a cosine function so that positive values represent northerly aspects and negative values represent southerly aspects.

We defined the security habitat metric covariate as ‘secure’ or ‘not secure’ according to elk security habitat recommendations for archery and rifle hunting periods outlined by Ranglack et al. (2017). These recommendations combine thresholds for distance from motorized routes, canopy cover, and patch size. We sourced canopy cover data from LANDFIRE 2019, and compiled motorized routes data from MSDI, USFS, and DNRC roads layers. Areas defined as secure were required to have 13% or greater canopy cover in archery season and 9% or greater canopy cover in rifle season, be at least 2,760 m away from motorized routes in archery season and at least 1535 m away in rifle season, and be a minimum of 20.23 km^2 during rifle season (no minimum patch size during archery season).

Elk movements between hunter access management strategies

We fit a series of Bayesian multistate models to evaluate the factors influencing the probability that an elk transitioned between hunter access management strategies during the fall hunting season. We used animal-years as the sampling unit. We randomly sampled one daylight location for each animal-year on each day of the hunting season (August 15 to February 15). The result was a dataset that included one hunter access management strategy selection (and associated covariate values) for each animal-year for each day of the hunting season. We evaluated the influence of hunting period, harvest regulation, migratory status, cumulative SWE, and a constant model representing a null model (no covariates informing the model) on the daily probability of transitioning between hunter access management strategies. We pooled locations from all years and competed a null model and univariate models evaluating the effect of each covariate on the probability of transitioning between hunter access management strategies. Each model tested a different hypothesis about the factors influencing the probability that an elk made a transition from one hunter access management strategy to another.

Overall, we expected transition probabilities across hunter access management strategies to be highest during the general rifle period due to the dynamic nature of this period as elk are navigating the highest levels of harvest risk. We used the harvest regulation model to evaluate the hypothesis that the availability of hunting licenses best described transition probabilities. We predicted that the probability of an elk transitioning into a limited access strategy would increase under liberal regulations. We used the migratory status model to evaluate the hypothesis that the classification of individuals as either migrants or residents would best describe the probability of transitioning across access strategies. We predicted that migratory individuals would transition more frequently than resident individuals overall. We used the cumulative SWE model to test the hypothesis that the cumulative presence of snow on the landscape best described the probability of transitioning across access strategies. We predicted that a threshold might exist where the probability of transitioning would increase as snowpack accumulated and animals moved towards winter ranges, but that at the highest SWE values, transition probabilities would stabilize as elk settled into wintering grounds. Finally, we used the null model to evaluate the null hypothesis that none of the covariates analyzed explained more variation than the regression intercept alone.

To develop these models, we used the nimble (de Valpine et al. 2017) package in R to create a series of Bayesian multi-state models with a multinomial logit link to model the daily probability of transitioning across hunter access management strategies. The probability that an elk made a transition (ψ) from open access on day *t* to open access on day *t+1* is given by the following equation where *l* represents the multinomial logit link:

$$\psi^{Open/Open} = \frac{exp(l\psi^{Open/Open})}{\mathbf{1} + exp(l\psi^{Open/Open}) + exp(l\psi^{Open/Moderate})}$$

$$\text{Where } l\psi^{Open/Open} = \beta_0^{Open/Open} + \beta_1^{Open/Open} * \mathrm{x}$$

The probability that an elk made a transition (ψ) from open access on day *t* to moderate access on day *t+1* is given by:

$$\psi^{Open/Moderate} = \frac{exp(l\psi^{Open/Moderate})}{\mathbf{1} + exp(l\psi^{Open/Open}) + exp(l\psi^{Open/Moderate})}$$

$$\text{Where } l\psi^{Open/Moderate} = \beta_0^{Open/Moderate} + \beta_1^{Open/Moderate} * \mathrm{x}$$

Finally, the probability that an elk made a transition from open access on day *t* to limited access on day *t+1* can be estimated by subtraction:

$$\psi^{Open/Limited} = 1 - \psi^{Open/Open} - \psi^{Open/Limited}$$

This process was repeated for each access strategy transition (e.g., moderate to moderate, moderate to open, moderate to limited, etc.) such that 6 intercept and slope terms were estimated and 3 intercepts and slopes were estimated by subtraction. We ran three parallel chains for each model with 25,000 samples per chain and discarded the first 5,000 samples as burn-in. This resulted in a posterior distribution of 60,000 samples for each model that was available for inference. Posterior convergence was assessed using graphical and numeric outputs. We then ranked models according to Watanabe-Akaike information criterion (WAIC) score to determine which candidate model had the highest support and used this top model as our model of inference.

Elk habitat selection

We evaluated elk habitat selection in response to two human-determined and risk-related factors, hunter access management and harvest regulation, as well as landscape factors, including landcover, SWE, security habitat, terrain ruggedness, slope, and aspect.

First, we compared summaries of used elk locations and the available landscape. For these summaries, we used all elk locations in the daylight hunting season dataset. The available landscape was defined by the 99% kernel utilization distribution (KUD) of daylight hunting season locations representing the fall/winter elk range for this population and additionally constrained to HDs 445, 446, and 455 where it overlapped outside of these districts. Available locations were randomly sampled at a ratio of 2:1 available to used locations. Additionally, we separated the general season into an early general and late general period for the summary of use and availability, as some landowners employed different hunter access management strategies for the first half and second half of the general rifle season.

Second, we constructed resource selection functions (RSFs) in a used-available framework (Manly et al. 2002). For the RSF analysis, we sampled 4 locations per day for each individual to create our sample of used locations. We randomly generated available locations at an approximately 1:10 used to available ratio within the fall/winter elk range. Elk locations and available locations designated as ‘Nonhabitat’ landcover were excluded. We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation to facilitate coefficient comparison. We screened for collinearity and excluded variables with correlation coefficients of $| r | > 0.6$.

We constructed generalized mixed-effects models using the 'lme4' and ‘MuMIn’ packages in R (Hebblewhite and Merrill 2008, Bates et al. 2018). We considered individual elk as the sample unit and incorporated random intercepts to account for variations among individual elk (Gillies et al. 2006). We first carried out model selection on the complete dataset pooled across hunting periods, then fit the top-performing model to each hunting period separately to evaluate similarities and differences in elk habitat selection between periods. We used a three-step process to develop and identify the top-performing models. In step 1, we evaluated univariate models to test linear and pseudothreshold (natural log) functional forms for each continuous covariate (e.g., DeVoe et al. 2019 - excluding aspect due to negative values). In step 2, we evaluated all possible additive combinations of the landscape covariates (landcover, terrain ruggedness, aspect, slope, security habitat, and SWE) to establish the most supported model to generally explain elk habitat selection. In step 3, we combined the most supported landscape covariate combination with the four possible additive and interactive combinations of the hunter access management and harvest regulation covariates (regulation, access, regulation + access, regulation-access). Because not all combinations of hunter access management and harvest regulation existed, the interaction was coded as a new covariate representing the possible combinations of access and regulation. We selected the top model in each step based on the lowest Akaike's Information Criterion (AIC_c) value, or if multiple models were within 2 ΔAIC_c of each other, we chose the model with the fewest variables (Burnham and Anderson 2002). We evaluated resource selection models using five-fold cross-validation based on correlation between RSF bins and area-adjusted frequencies for each withheld sub-sample of the data (Boyce et al. 2002), where a strong positive correlation suggested strong model predictive performance.

Table 4. Harvest regulations effective in the Devil's Kitchen study area, central Montana, USA, 2021-2022. The Regulation Class column indicates how regulations were classified for the harvest regulation covariate. General licenses were valid across the state for the harvest of one elk depending on unit-specific regulations. Individuals could only purchase a single general license each year but there was no quota on the total number available for purchase by resident hunters. Elk B-Licenses were only valid for the harvest of antlerless elk. An annual quota of 6,000 B-license 004-00 and 250 B-License 455-00 were available during the study period. A hunter in possession of a General License could purchase 2 B-Licenses in a given year. Elk permits were only valid with a General License and were allocated through a drawing. A quota of 30-40 Permit 445-20, 50-60 Permit 455-20, and 4,000 Permit 900-20 were available annually during the study period.

District	Hunting Period	License Type	Harvest Regulation	Regulation Class
445	Early Shoulder	General License	Antlerless	Liberal
		B-License 004-00	Antlerless	
	Archery	General License	Either-sex	Liberal
		B-License 004-00	Antlerless	
		Permit 445-20	Either-sex	
	Early General	General License	Either-sex	Liberal
		B-License 004-00	Antlerless	
		Permit 445-20	Either-sex	
	Late General	General License	Antlerless	Liberal
		B-License 004-00	Antlerless	
		Permit 445-20	Either-sex	
	Late Shoulder	General License	Antlerless	Liberal
		B-License 004-00	Antlerless	
446	Early Shoulder	General License	Antlerless	Liberal
		B-License 004-00	Antlerless	
	Archery	General License	Brow-tined Bull or Antlerless	Liberal
		B-License 004-00	Antlerless	
	Early General	General License	Brow-tined Bull or Antlerless	Liberal
		B-License 004-00	Antlerless	
	Late General	General License	Brow-tined Bull or Antlerless	Liberal
		B-License 004-00	Antlerless	
	Late Shoulder	General License	Antlerless	Liberal
		B-License 004-00	Antlerless	
455	Early Shoulder	--	No Harvest	No Harvest
	Archery	Permit 455-20	Either-Sex	Restricted
		Permit 900-20	Either-Sex	
		B-License 455-00	Antlerless	
	Early General	Permit 455-20	Either-Sex	Restricted
		B-License 455-00	Antlerless	
	Late General	Permit 455-20	Either-Sex	Restricted
		B-License 455-00	Antlerless	
	Late Shoulder	--	No Harvest	No Harvest

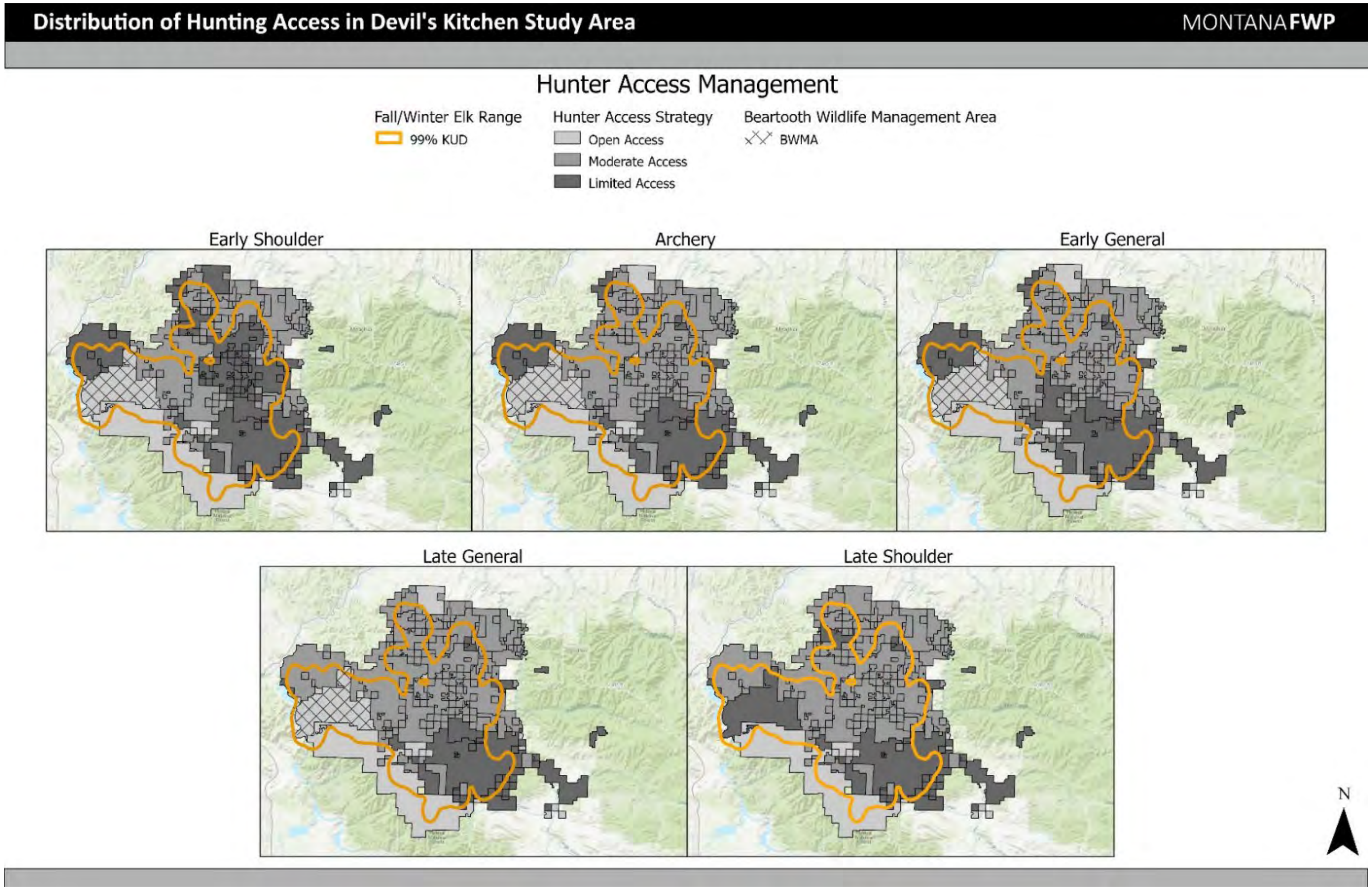

Figure 26. The distribution of hunter access management strategies for each hunting period in relation to a 99% kernel utilization distribution (KUD) of fall/winter elk locations in the Devil's Kitchen study area, central Montana, USA, 2020—2023. We defined open access as publicly accessible public lands or private lands enrolled in Montana's block management access program (BMA) and not requiring a reservation to hunt, moderate access as areas where landowners granted access to members of the public who enquired or were enrolled in the BMA program but required a reservation, and limited access if landowners allowed access only for friends and family or outfitted clients, or if no public hunting opportunities were available. Publicly owned but landlocked parcels were classified using the access management strategies of surrounding private lands.

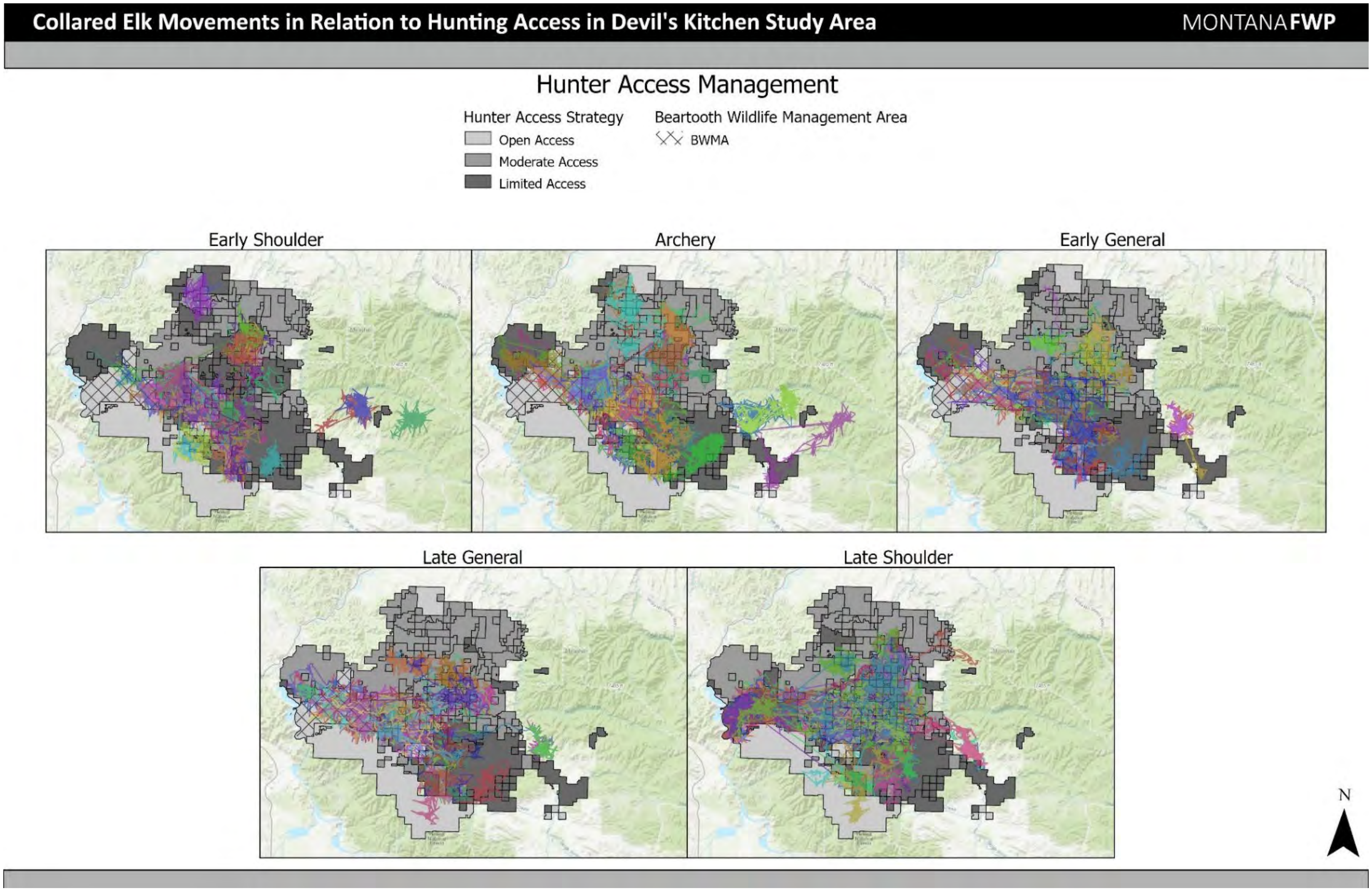

Figure 27. Movements of collared female elk in relation to hunter access management strategies across the five hunting periods in the Devil's Kitchen study area, central Montana, USA, 2020—2023.

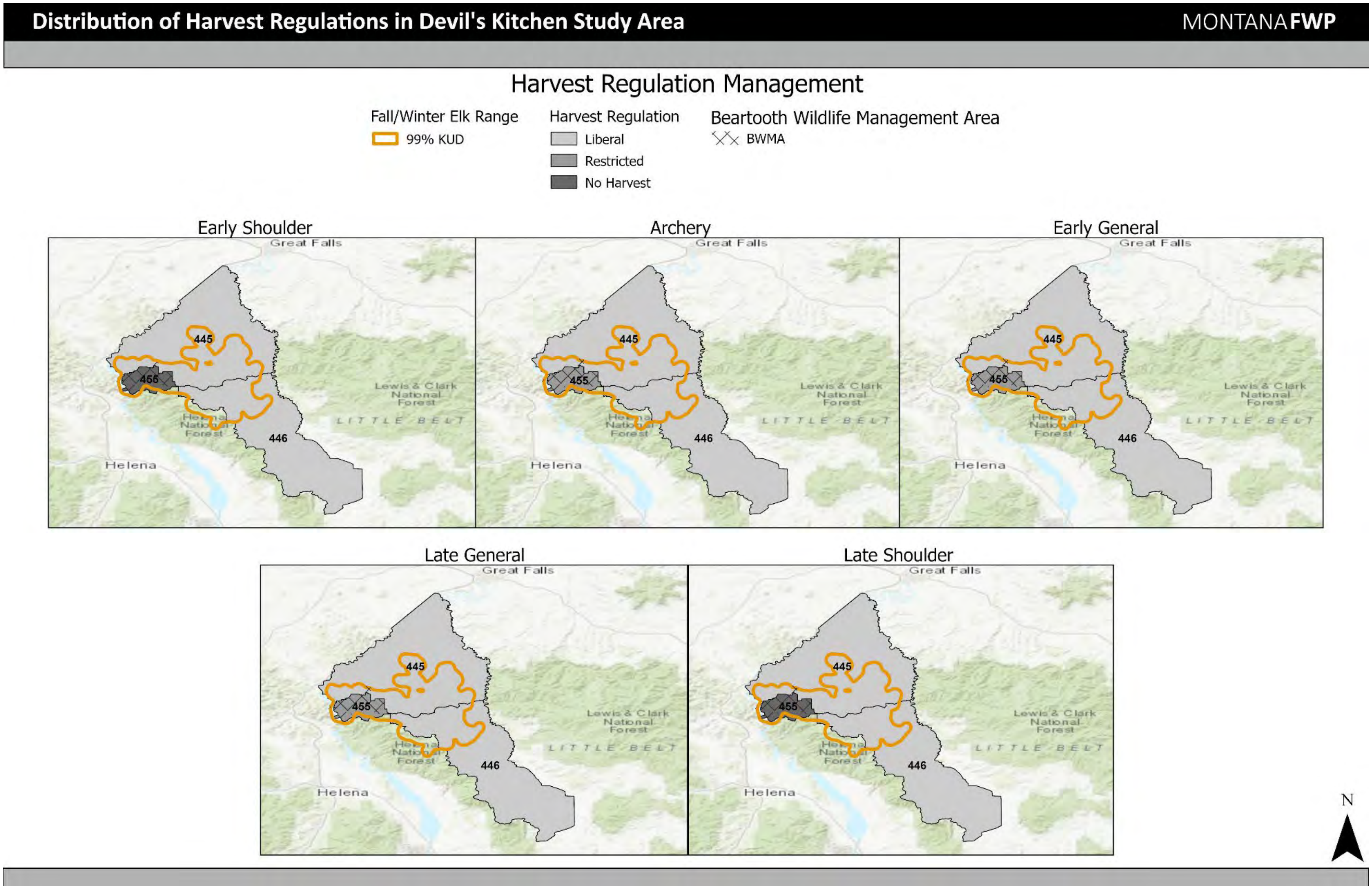

Figure 28. The distribution of harvest regulation classes (see Table 4) for each hunting period in relation to a 99% KUD of fall/winter elk locations in the Devil's Kitchen study area, central Montana, USA, 2020-2023.

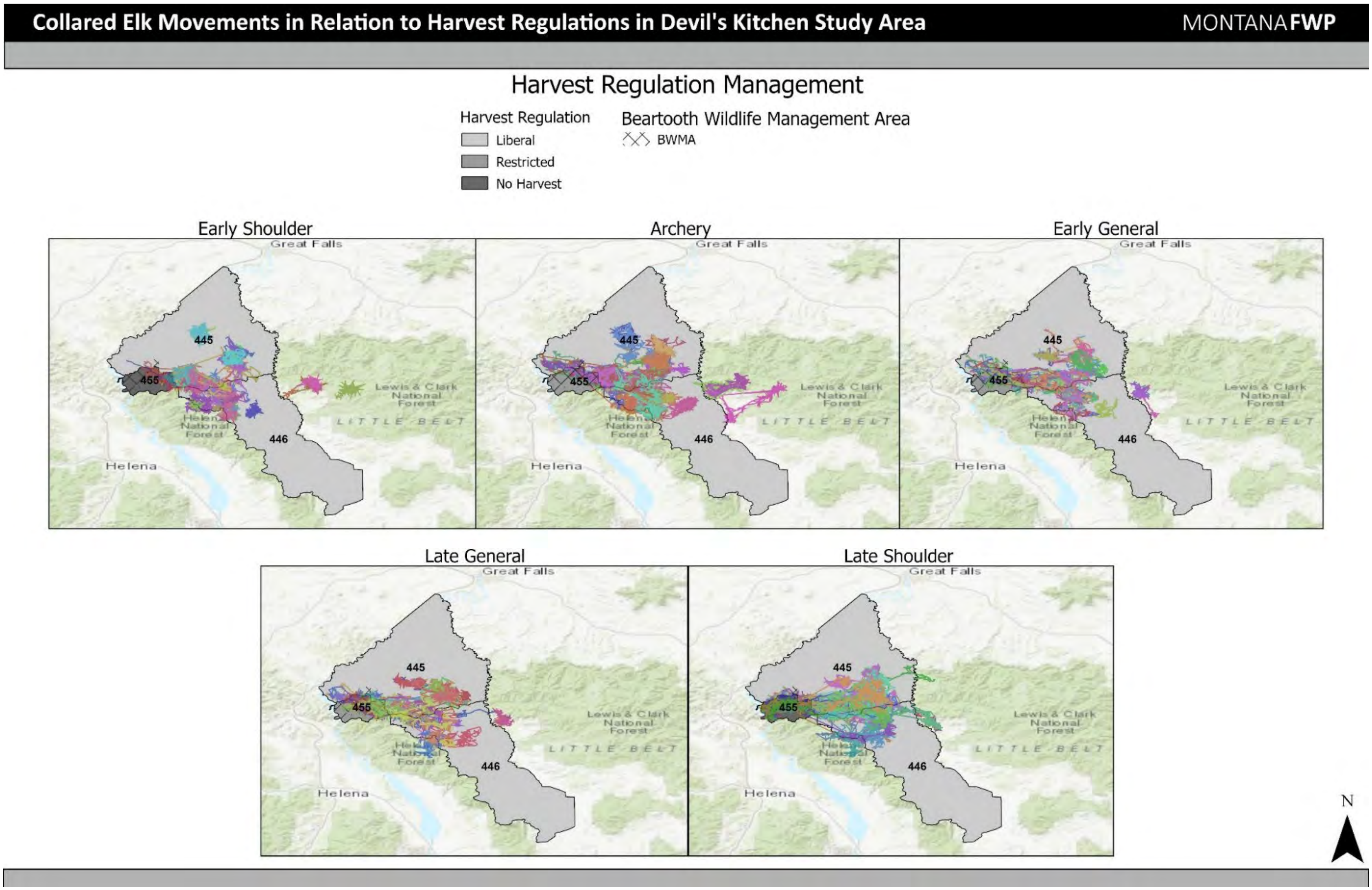

Figure 29. Movements of collared female elk in relation to harvest regulation classes (see Table 4) across the five hunting periods in the Devil's Kitchen study area, central Montana, USA, 2020—2023.

RESULTS

Elk movements between hunter access management strategies

Elk demonstrated all 9 possible transitions between access strategies in every hunting period (Tables 5-8). The total number of daily transitions varied between hunting periods due to differences in the length of period and number of animals monitored. Overall, daily transitions originating and ending in the same access strategy were most common. In the early shoulder season, limited to moderate was the most common transition between strategies and limited to open was the least common (Table 5). More daily transitions began in open access than ended in open access, more daily transitions ended in moderate access than began in moderate access, and about the same number of daily transitions started and ended in limited access. In the archery season, moderate to limited was the most common transition between strategies and limited to open was the least common (Table 6). Slightly more daily transitions ended in moderate and limited access than began in moderate and limited access, and about the same number of daily transitions started and ended in open access. In the general season, moderate to open was the most common transition between strategies and open to limited was the least common (Table 7). More daily transitions ended in open and moderate access than began in open and moderate access, and about the same number of daily transitions started and ended in limited access. In the late shoulder season, moderate to limited was the most common transition between strategies and open to moderate was the least common (Table 8). More daily transitions ended in limited access than began in limited access, fewer daily transitions ended in moderate access than started in moderate access, and about the same number of daily transitions started and ended in open access.

The top-performing model in our candidate suite included hunting period as the explanatory variable (Table 9). Estimates from this model showed that the probability that an elk on day t would be located in the same access strategy on day t+1 was much greater than the probability that an elk transitioned to an area with a different access strategy on day t+1. This general pattern was consistent across all access strategies and all hunting periods, (Figure 30) but was weaker during the general season. Elk appeared to behave in similar ways during the early shoulder and archery hunting periods, demonstrating considerable probabilities of moving from open access to moderate access (Figure 30). Elk in open access had a 28.53% probability (95% CI = 24.20%, 32.96%) of transitioning to moderate access in the early shoulder season and a 26.57% probability (95% CI = 23.61%, 29.68%) in the archery season.

In the general rifle season, elk already present in open access had an 84.05% probability (95% CI = 82.54%, 85.50%) of remaining in open access; the highest probability of remaining in open access found in any hunting period. We found a 23.24% probability (95% CI = 20.86%, 25.74%) that elk transitioned from limited access to moderate access and a 7.51% probability (95% CI = 6.59%, 8.46%) that elk transitioned from moderate to limited access. During the general rifle period, elk were more likely to transition from limited to open access (6.21% probability, 95% CI = 4.90%, 7.62%) and from moderate to open access (9.48% probability, 95% CI = 8.45%, 10.57%) as compared to other hunting periods. The general rifle period had the lowest estimated probability of remaining in limited access (70.56% probability, 95% CI = 67.85%, 73.20%) as compared to other hunting periods, though it should be noted that most elk that began the general rifle season in limited access remained in limited access.

During the late shoulder season, the probability that an elk transitioned from open access to limited access was 48.44% (95% CI = 43.41%, 53.43%); the highest estimated probability of transitioning across access strategies found in this study (Figure 30). Correspondingly, the probability that elk already present in limited access remained in limited access was 92.11% (95% CI = 91.52%, 92.72%); the highest estimated probability of remaining in limited access across all hunting periods. Finally, the probability that an elk remained in open access was 47.93% (95% CI = 42.88%, 53.01%), the lowest of any hunting period.

Table 5. Observed daily transitions between categories of hunter access management during the early shoulder season hunting period in the Devil's Kitchen study area in central Montana, USA. Daily transitions occur from day *t* represented in rows to day *t+1* represented in columns.

	Open	**Moderate**	**Limited**	**Total**
Open	179	81	23	283
Moderate	68	1138	86	1292
Limited	16	94	806	916
Total	263	1313	915	2491

Table 6. Observed daily transitions between categories of hunter access management during the archery season hunting period in the Devil's Kitchen study area in central Montana, USA. Daily transitions occur from day *t* represented in rows to day *t+1* represented in columns.

	Open	**Moderate**	**Limited**	**Total**
Open	374	152	34	560
Moderate	155	3990	163	4308
Limited	30	161	1155	1346
Total	559	4303	1352	6214

Table 7. Observed daily transitions between categories of hunter access management during the general season hunting period in the Devil's Kitchen study area in central Montana, USA. Daily transitions occur from day *t* represented in rows to day *t+1* represented in columns.

	Open	**Moderate**	**Limited**	**Total**
Open	1376	180	37	1593
Moderate	202	1711	151	2064
Limited	49	185	567	801
Total	1627	2076	755	4458

Table 8. Observed daily transitions between categories of hunter access management during the late shoulder season hunting period in the Devil's Kitchen study area in central Montana, USA. Daily transitions occur from day *t* represented in rows to day *t+1* represented in columns.

	Open	**Moderate**	**Limited**	**Total**
Open	128	9	130	267
Moderate	11	2820	306	3137
Limited	127	292	4919	5338
Total	266	3121	5355	8742

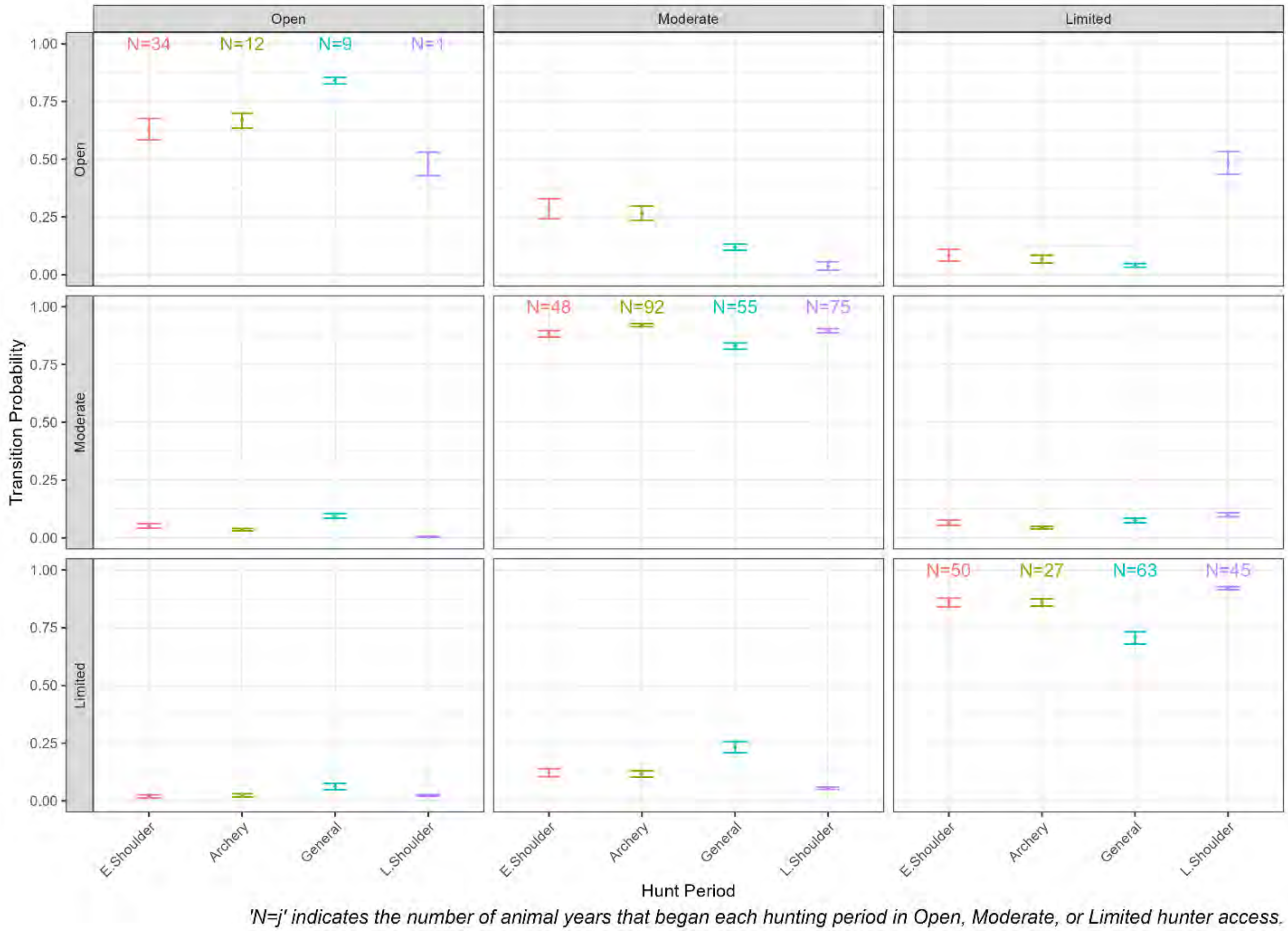

Figure 30. Results from the top performing model investigating the probability of transitioning across hunter access management strategies during the fall hunting season in the Devil's Kitchen study area in central Montana, USA. The plotted posterior means with 95% credible intervals show the estimated probability of transitioning from an access strategy on day **t** (rows) to an access strategy on day **t + 1** (columns) in each of the 4 hunting periods of interest. Numbers listed above within-category transition probabilities represent the number of individuals in that access strategy on the first day of the hunting period.

Table 9. Results of Watanabe-Akaike information criterion (WAIC) comparison of candidate multi-state models. ΔWAIC values indicate the difference between each candidate model's WAIC score and that of the top performing model.

Model	WAIC	ΔWAIC
Hunting Period	19242.60	0.00
Harvest Regulation	19564.76	-322.16
Snow Water Equivalent	20144.18	-901.58
Migratory Status	20338.34	-1095.74
Constant/Null	20371.53	-1128.93

Elk habitat selection

Availability remained constant for landcover and terrain covariates, which did not vary through time. Availability varied by hunting period for harvest regulation, security habitat, and hunter access management, as harvest regulations changed between periods, security recommendations varied by hunting period, and individual landowners made different hunter access management decisions for their properties for different periods of the hunting season. Availability varied throughout time for the snow water equivalent (SWE) covariate, which was a daily measurement.

Pooled across the five hunting periods, 86% of the available locations had liberal harvest, 7% had restricted harvest, and 7% had no harvest. In comparison, 71% of elk used locations occurred in areas with liberal harvest, 9% occurred in restricted harvest areas, and 20% occurred in no harvest areas, demonstrating that elk used no harvest areas in greater proportion and liberal harvest areas in lesser proportion than available. Across the five hunting periods, elk use of liberal harvest areas was high in comparison to availability in the early shoulder season, then steadily decreased through time during the rest of the hunting season. Elk use of restricted and no harvest areas increased throughout the hunting season in comparison to availability (Figure 31). Elk use of liberal harvest areas shifted from higher than availability to lower than availability between the archery and early general hunting periods, which aligned with the beginning of the general rifle season.

Pooled across the five hunting periods, 14% of the available locations were classified as open hunter access, 53% was moderate access, and 33% was limited access. In comparison, 12% of elk used locations occurred in open access, 52% occurred in moderate access, and 36%

occurred in limited access, demonstrating that elk only slightly used moderate and limited areas in greater proportion and open access areas in lesser proportion to availability. Across the five hunting periods, elk use of open access areas was low, and use of moderate access was high in comparison to availability in the early shoulder and archery seasons, then use of open access was higher than availability in early and late general hunting periods (Figure 32). Finally, elk ended the hunting season in the late shoulder period with comparatively high use of limited access and low use of open access, aligning with their high use of the BTWMA.

Pooled across the five hunting periods, available locations were 53% liberal harvest-moderate access, 29% liberal harvest-limited access, 7% restricted harvest-open access, 4% liberal harvest-open access, 4% no harvest-limited access, and 3% no harvest-open access (Figure 33). In comparison, elk used locations were 52% liberal harvest-moderate access, 19% liberal harvest-limited access, 9% restricted harvest-open access, 1% liberal harvest-open access, 18% no harvest-limited access, and 2% no harvest-open access. In comparison to the available landscape, elk used less liberal harvest-open access and liberal harvest-limited access. Elk used much more no harvest-limited access than available, reflecting heavy use of the BTWMA. When examining trends across the five hunting periods, some regulation-access categories show a consistent trend through the hunting season, while others are used differently in different periods (Figure 34). Liberal harvest-open access and liberal harvest-limited access were used by elk less than their availability through all five periods. Liberal harvest-moderate access was used more than its availability for the first two periods, then less than its availability for early and late general and late shoulder seasons. The remaining three categories representing the BTWMA (restricted and no harvest categories) showed a pattern of lower use than availability during early shoulder and archery seasons, then higher and increasing use during the last three hunting periods of the season.

Pooled across hunting periods, 18% of the available locations were defined as security habitat and 21% of locations used by elk were defined as occurring in security habitat. Across the five hunting periods, elk used security habitat slightly more during early shoulder season, much more during archery season, approximately equal during early general season, slightly more during late general season, and much less during late shoulder season (Figure 35).

Available locations were classified as 50% grassland, 33% conifer woodland, 10% sagebrush steppe, 5% shrubland, 2% riparian, 1% agriculture, and 0.3% nonhabitat. Pooled across individuals and seasons, elk used 48% grassland, 35% conifer woodland, 12% sagebrush steppe, 4% shrubland, 1% riparian, 0.2% agriculture, and 0.2% nonhabitat. Elk use varied slightly through the hunting season (Figure 36). Elk used more conifer woodland than availability during the early shoulder and archery periods, then used less conifer woodland than availability during the shoulder season. Elk use of grassland, sagebrush steppe, and shrubland increased to greater than availability during the late shoulder season. Across all periods, elk used very low amounts of riparian, agriculture, and nonhabitat. Due to low availability and use, riparian and agriculture locations were reclassified as grassland and nonhabitat locations were excluded for the RSF analysis.

The mean vector ruggedness measure was 0.004 for available locations (range = 0 - 0.193, SD = 0.0074) and 0.003 for used locations (range = 0 - 0.132, SD = 0.0055), and elk use did not vary much throughout the season. The mean terrain ruggedness index value was 17.1 for available locations (range = 0 – 147, SD = 10.4)) and 17.8 for used locations (range = 0 – 86, SD = 8.8), and elk use did not vary much throughout the hunting season. The mean slope value was 13.8% for available locations (range = 0% – 62%, SD = 7.8%) and 14.5% for used locations (range = 0% – 49%, SD = 6.7%), and elk use did not vary much throughout the hunting season. The mean aspect value was 0.097 for available locations (range = -1 – 1, SD = 0.72) and 0.19 for used locations (range = -1 – 1, SD = 0.70). Elk used north-facing slopes more than available in early shoulder and archery season, then shifted towards more southerly slopes for the remainder of the season. Pooled across the hunting season, the mean snow water equivalent (SWE) value was 11.5 kg/m^2 for available locations (range = 0 – 161 kg/m^2, SD = 21.4 kg/m^2) and 10.1 kg/m^2 for elk used locations (range = 0 – 104 kg/m^2 , SD = 17.5 kg/m^2). SWE values varied throughout the hunting period, increasing from zero in early shoulder season to their peak in late shoulder season. Elk tended to use lower and less extreme values than availability on the landscape.

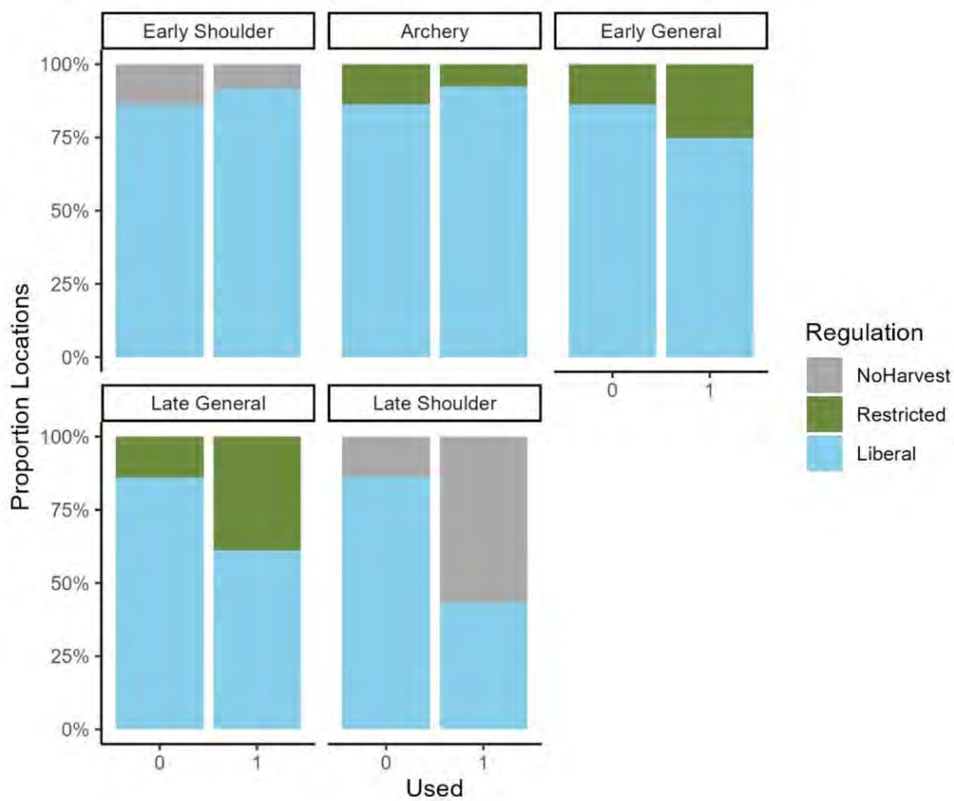

Figure 31. Proportions of used elk locations (Used = 1) and available locations (Used = 0) in fall/winter elk range falling into three harvest regulation classes across the five hunting periods. Devil’s Kitchen study area, central Montana, USA, 2020-2023.

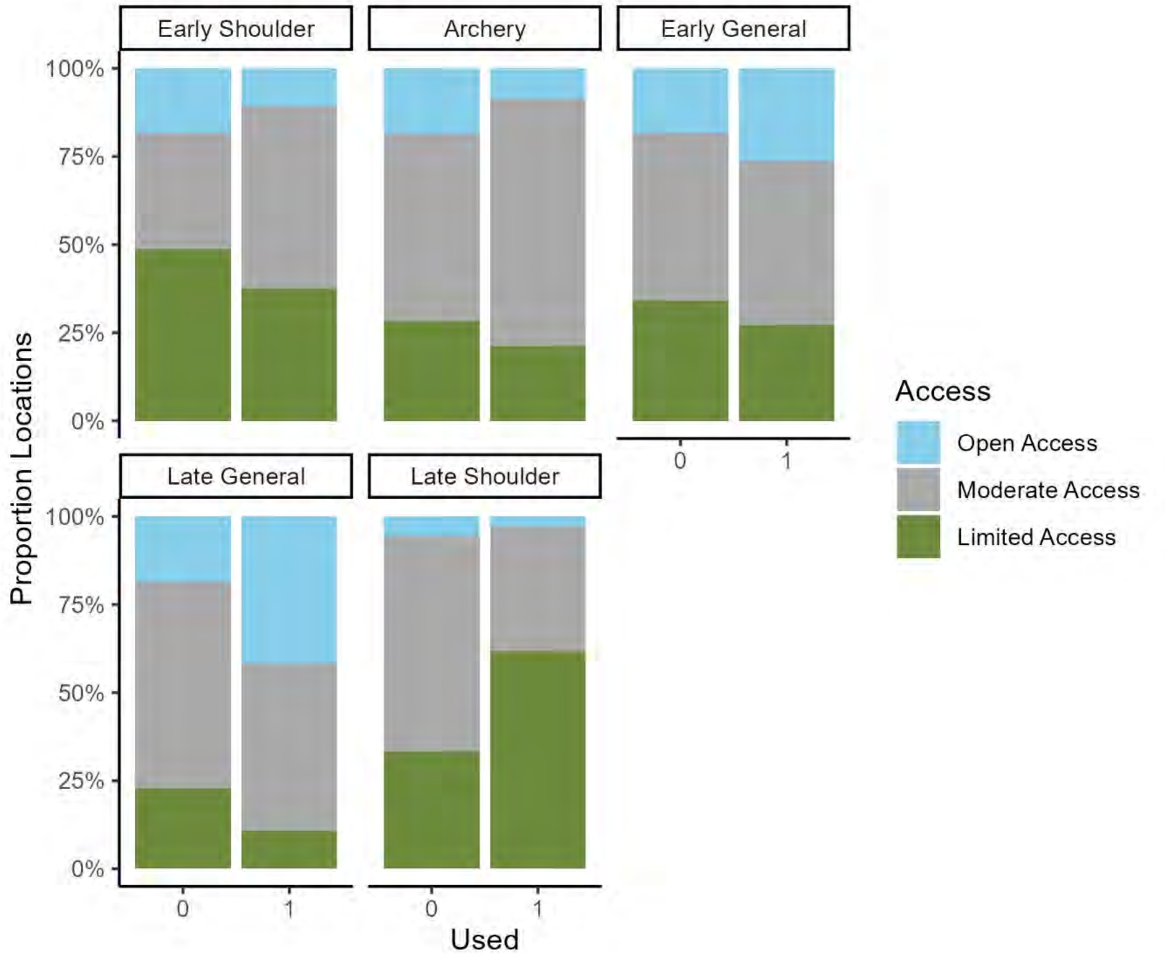

Figure 32. Proportions of used elk locations (Used = 1) and available locations (Used = 0) in fall/winter elk range falling into three hunter access management strategies across the five hunting periods. Devil's Kitchen study area, central Montana, USA, 2020-2023.

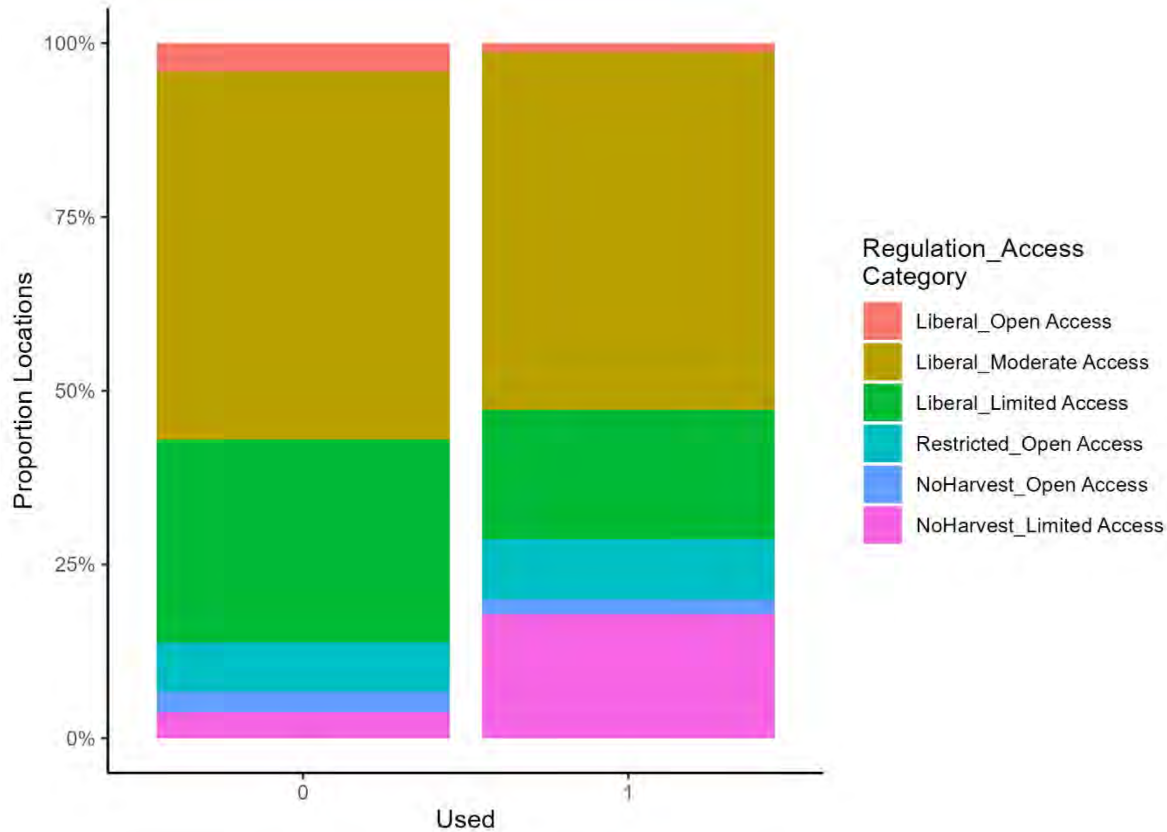

Figure 33. Proportions of used elk locations (Used = 1) and available locations (Used = 0) in fall/winter elk range falling into six possible combinations of three harvest regulation categories and three hunter access management strategies. Devil's Kitchen study area, central Montana, USA, 2020-2023.

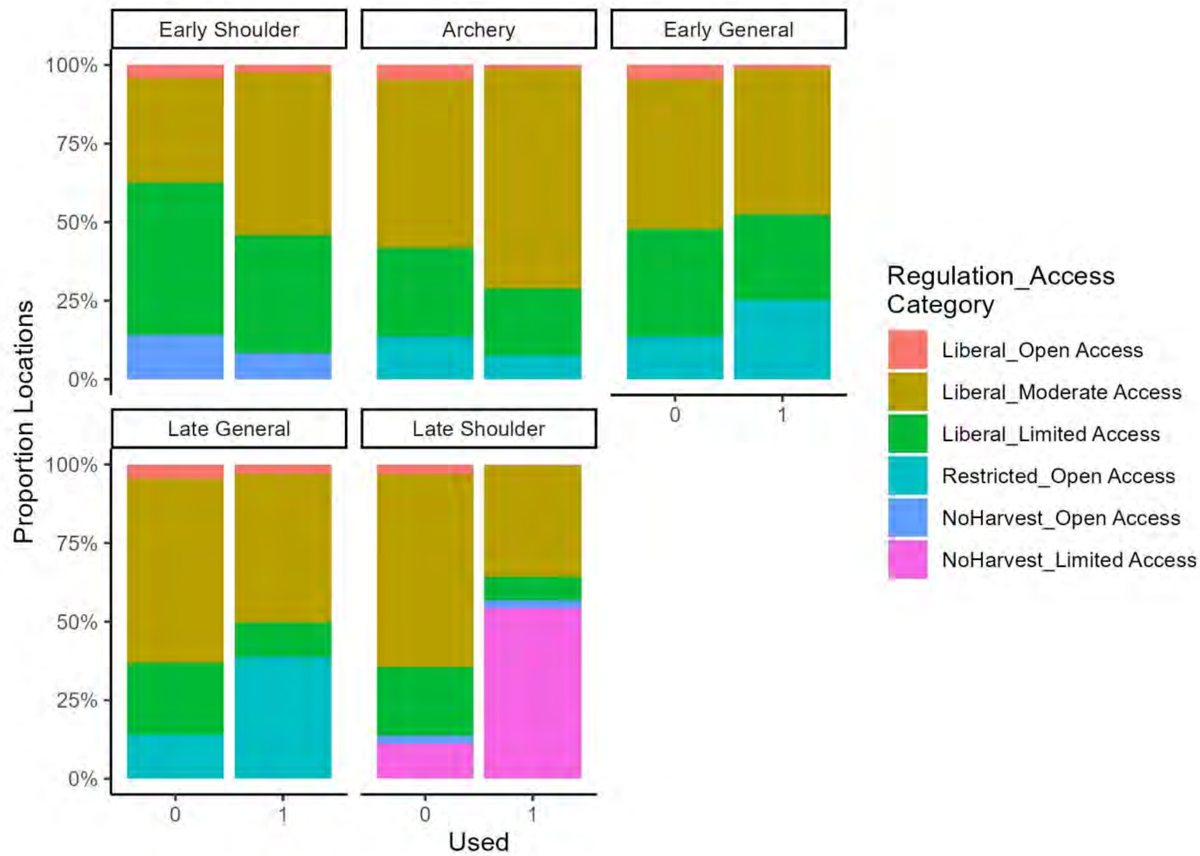

Figure 34. Proportions of used elk locations (Used = 1) and available locations (Used = 0) in fall/winter elk range falling into six possible combinations of three harvest regulation categories and three hunter access management strategies across the five hunting periods. Devil's Kitchen study area, central Montana, USA, 2020—2023.

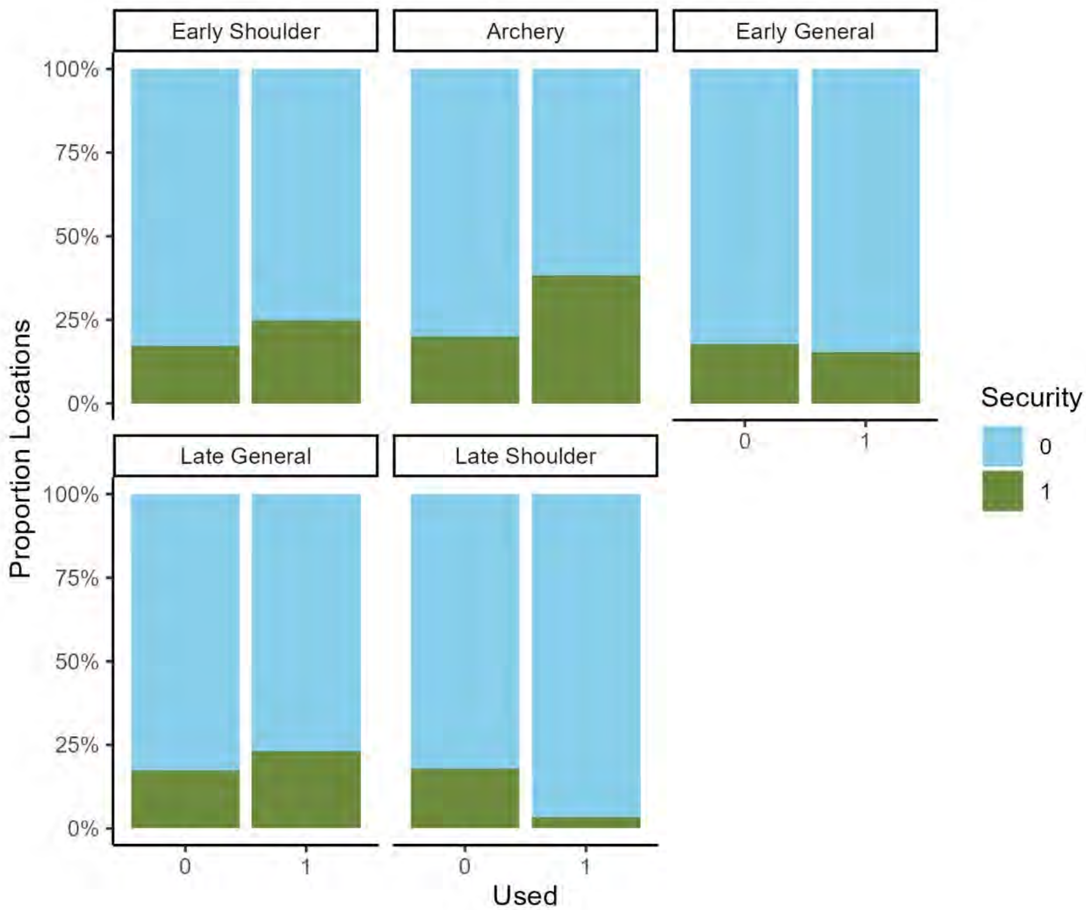

Figure 35. Proportions of used (Used = 1) and available elk locations (Used = 0) in fall/winter elk range defined as security habitat across the five hunting periods. Devil's Kitchen study area, central Montana, USA, 2020-2023.

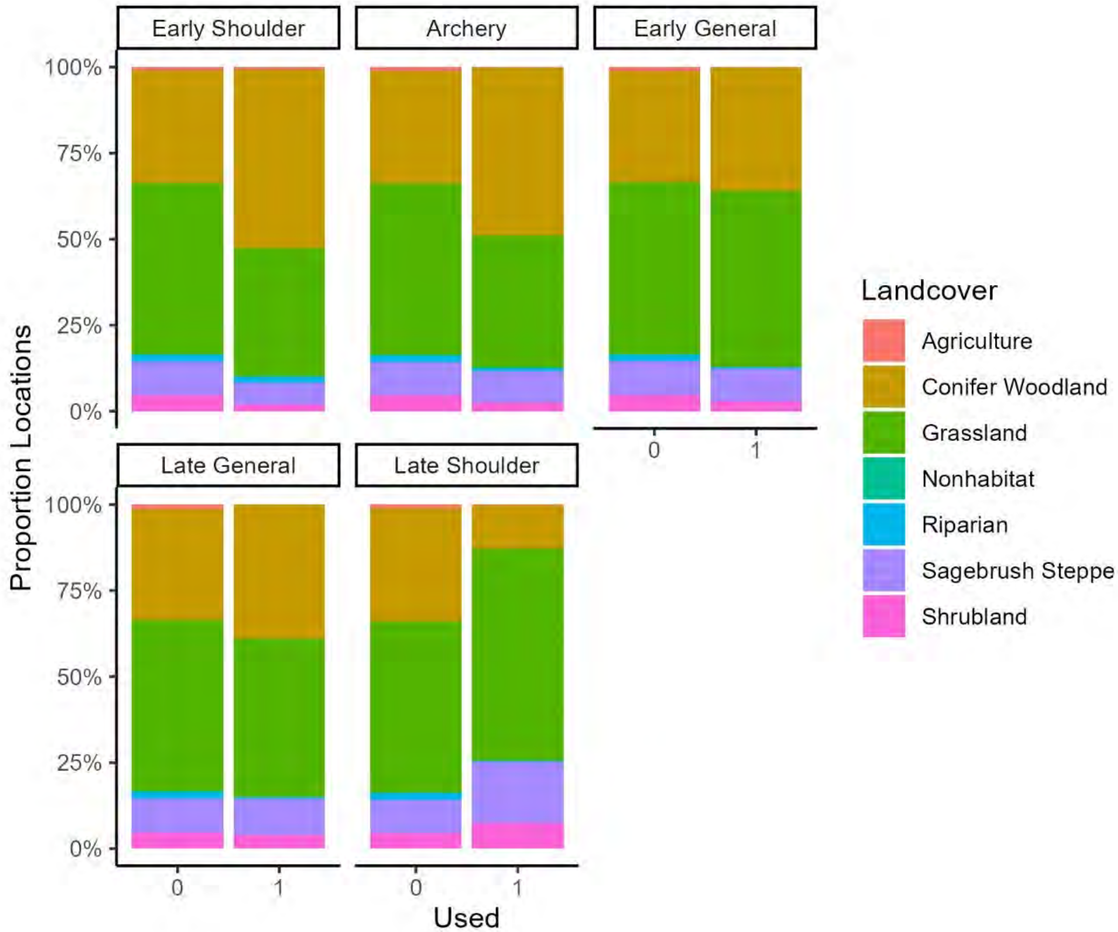

Figure 36. Proportions of used (Used = 1) and available elk locations (Used = 0) in fall/winter elk range in seven landcover categories across the five hunting periods. Devil's Kitchen study area, central Montana, USA, 2020-2023.

The resource selection function (RSF) analysis of the complete dataset pooled across hunting periods included 88,089 locations from 58 individuals. The mean number of locations per individual was 1,519 (range 24 – 2,218). The covariate terrain ruggedness index (TRI) was removed from analysis because it was highly correlated with slope. In step 1 of model selection, the pseudothreshold functional form of slope was selected and all other functional forms selected were linear (Appendix A, Table A1). In step 2 of model selection, the top landscape model included all six landscape covariates (landcover, terrain ruggedness, aspect, slope, security habitat, SWE, Appendix A, Table A2). In step 3 of model selection, the final top model was the interactive combination of hunter access management and harvest regulation (Tables 10 and 11, Figure 37). The final pooled top model demonstrated strong predictive performance with Spearman rank correlations ranging from 0.93 to 0.99 amongst the five iterations and a correlation coefficient of 0.99 for the average frequencies. Predictive performance based on Spearman rank correlation coefficients remained strong when the final top model was fit to each hunting period: for the early shoulder period, Spearman rank correlation coefficients ranged from

0.93 to 0.99 amongst the five iterations and the correlation coefficient was 1.0 for the average frequencies; for the archery season period, correlation coefficients ranged from 0.83 to 0.99 amongst the five iterations and the correlation coefficient was 0.95 for the average frequencies; for the general season period, correlation coefficients ranged from 0.71 to 0.99 amongst the five iterations and the correlation coefficient was 0.98 for the average frequencies; and for the late shoulder season period, correlation coefficients ranged from 0.78 to 0.96 amongst the five iterations and the correlation coefficient was 0.96 for the average frequencies.

Based on our hunting period-specific models, elk responded to regulation-access in varying ways across the hunting periods. In comparison to the reference category of liberal harvest-open access, elk demonstrated positive selection for liberal harvest-moderate access across all models, with the weakest response in the general season model, followed by early shoulder season, late shoulder season, and the strongest response in the archery season model (Figure 37). In comparison to liberal harvest-open access, elk demonstrated positive selection for liberal harvest-limited access across all models, with the weakest response in the general season model, followed by early shoulder season, late shoulder season, and the strongest response in the archery season model. Across all models, selection for liberal harvest-limited access was weaker, respectively, than selection for liberal harvest-moderate access. In comparison to liberal harvest-open access, elk demonstrated positive selection for restricted harvest-open access, with the weakest response in the archery season model, and the strongest response in the general season model (restricted harvest-open access did not occur in the early or late shoulder seasons). In comparison to liberal harvest-open access, elk demonstrated positive selection for no harvest-open access, with the weakest response in the early shoulder season model, and the strongest response in the late shoulder season model (no harvest-open access did not occur during the archery and general seasons). In comparison to liberal harvest-open access, elk demonstrated strong and positive selection for no harvest-limited access in the late shoulder season model, representing the strongest selection for any covariate in any model (no harvest-limited access did not occur in the early shoulder, archery, or general seasons).

Table 10. Model selection results from the third step of model selection where combinations of hunter access management and harvest regulation were added to the top performing landscape model evaluating female elk habitat selection during hunting season in the Devil's Kitchen study area in central Montana, USA. Akaike's information criterion adjusted for small sample size (AICc) was used to select the most-supported model. SWE represents snow-water equivalent.

Model Structure	**K**	**Delta AICc**	**AICc Weight**
Landcover + Terrain ruggedness + Aspect + Slope + Security + SWE + Regulation-Access	15	0	1.0
Landcover + Terrain ruggedness + Aspect + Slope + Security + SWE + Access + Regulation	14	908	0
Landcover + Terrain ruggedness + Aspect + Slope + Security + SWE + Regulation	12	10848	0
Landcover + Terrain ruggedness + Aspect + Slope + Security + SWE + Access	12	31494	0
Landcover + Terrain ruggedness + Aspect + Slope + Security + SWE	10	33131	0

Table 11. Standardized selection coefficients and 95% confidence intervals from the top-performing pooled hunting season model fit to four hunting periods examining female elk habitat selection during the hunting season in the Devil's Kitchen study area in central Montana, USA. Covariates labeled RA are categorical levels of Regulation-Access and covariates labeled LC are categorical levels of Landcover. Coefficients for categorical variables are relative to the reference category of Conifer for Landcover and Liberal-Open for Regulation-Access.

Covariate	**Pooled**	**Early Shoulder**	**Archery**	**General**	**Late Shoulder**
Terrain Ruggedness	-0.258 (-0.269, -0.248)	-0.254 (-0.287, -0.222)	-0.200 (-0.219, -0.181)	-0.244 (-0.266, -0.222)	-0.306 (-0.324, -0.289)
Slope	0.0958 (0.0874, 0.104)	0.156 (0.130, 0.182)	0.190 (0.173, 0.207)	0.207 (0.187, 0.227)	-0.0683 (-0.0815, -0.0552)
Aspect	0.112 (0.104, 0.120)	0.287 (0.264, 0.311)	0.204 (0.189, 0.219)	0.0534 (0.0367, 0.0702)	0.0400 (0.0274, 0.0526)
SWE	-0.152 (-0.161, -0.144)		0.194 (0.0951, 0.293)	0.140 (0.111, 0.169)	0.0327 (0.0215, 0.0439)
Security Habitat	0.128 (0.104, 0.151)	-0.120 (-0.178, -0.0619)	0.652 (0.611, 0.693)	-0.0321 (-0.0812, 0.0170)	-1.270 (-1.336, -1.203)
LC Grassland	-0.113 (-0.135, -0.0907)	-0.692 (-0.750, -0.634)	-0.296 (-0.340, -0.252)	-0.195 (-0.241, -0.149)	0.371 (0.330, 0.413)
LC Sagebrush Steppe	-0.00746 (-0.0363, 0.0213)	-0.713 (-0.806, -0.621)	0.130 (0.0732, 0.187)	-0.349 (-0.413, -0.285)	0.387 (0.338, 0.436)
LC Shrubland	-0.285 (-0.324, -0.247)	-1.117 (-1.263, -0.971)	-0.471 (-0.560, -0.383)	-0.635 (-0.726, -0.544)	0.280 (0.221, 0.338)
RA Liberal-Moderate	1.08 (1.020, 1.141)	1.151 (1.020, 1.281)	1.785 (1.671, 1.900)	0.561 (0.460, 0.662)	1.296 (1.125, 1.466)
RA Liberal-Limited	0.662 (0.601, 0.723)	0.425 (0.294, 0.556)	1.163 (1.046, 1.279)	0.266 (0.162, 0.370)	0.925 (0.752, 1.099)
RA Restricted-Open	1.470 (1.406, 1.534)		0.833 (0.710, 0.957)	1.621 (1.518, 1.724)	
RA NoHarvest-Open	0.929 (0.852, 1.007)	0.295 (0.148, 0.441)			2.269 (2.083, 2.455)
RA NoHarvest-Limited	2.906 (2.843, 2.968)				3.623 (3.451, 3.794)

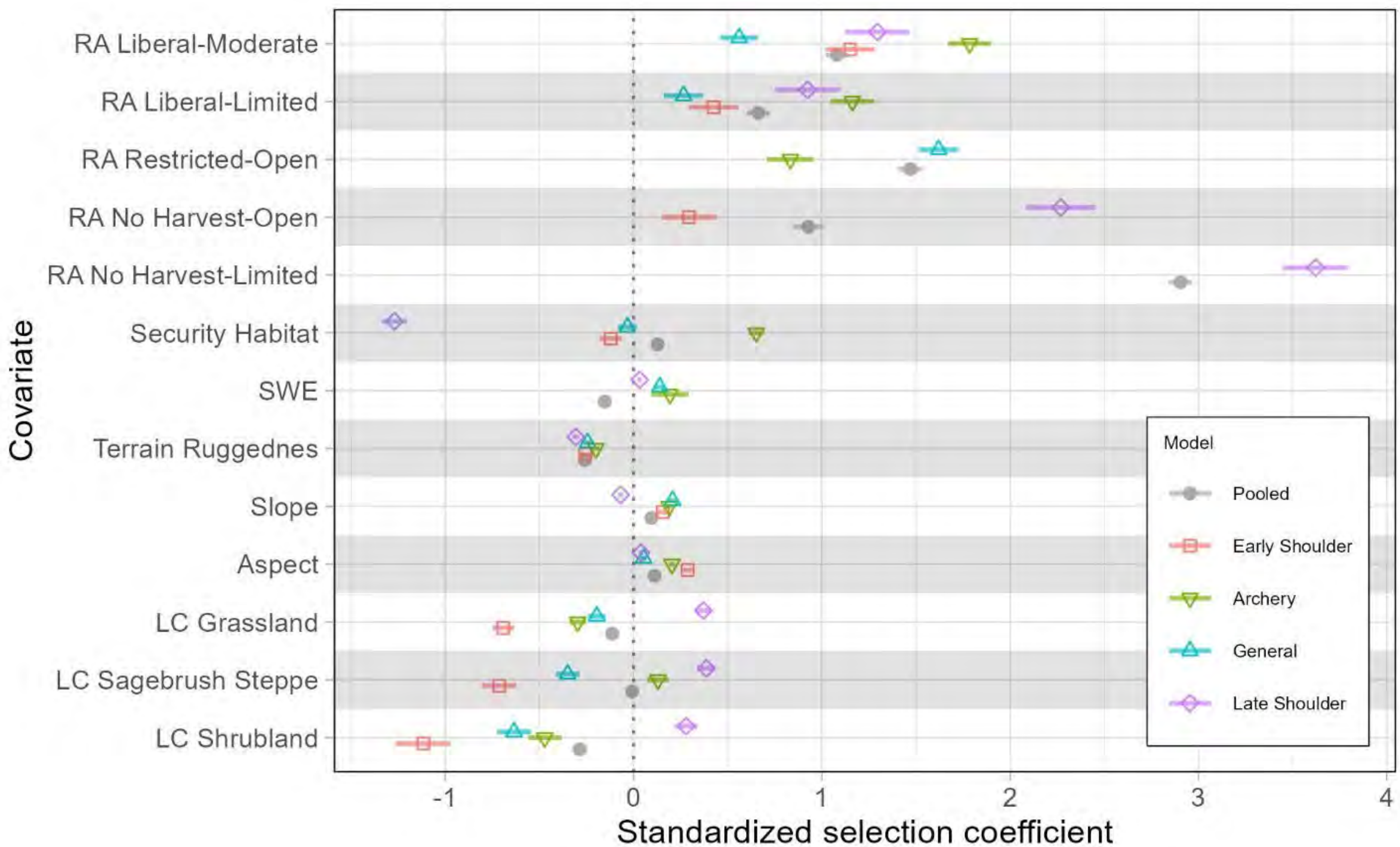

Figure 37. Standardized selection coefficients and 95% confidence intervals from the top-performing pooled hunting season model (gray estimates) fit to four hunting periods (colored estimates) examining female elk habitat selection during the hunting season in the Devil's Kitchen study area in central Montana, USA. Covariates labeled RA are categorical levels of Regulation-Access and covariates labeled LC are categorical levels of Landcover. Coefficients for categorical variables are relative to the reference category of Liberal-Open for Regulation-Access and Conifer for Landcover.

In the early shoulder season model, elk selected positively for all regulation-access categories in comparison to liberal harvest-open access, with response strength lowest for no harvest-open access, followed by liberal harvest-limited access, and the strongest response to liberal harvest-moderate access (Figure 37). Based on coefficient estimates from the early shoulder season model, the odds of elk selecting no harvest-open access were 34% higher (95% CI = 16%, 55%) in comparison to the reference category of liberal harvest-open access; 53% higher (95% CI = 34%, 74%) for liberal harvest-limited access, and 216% higher (95% CI = 177%, 260%) for liberal harvest-moderate access.

In the archery season model, elk selected positively for all regulation-access categories in comparison to liberal harvest-open access, with response strength lowest for restricted harvest-open access, followed by liberal harvest-limited access, and the strongest response to liberal harvest-moderate access (Figure 37). Based on coefficient estimates from the archery season model, the odds of elk selecting restricted harvest-open access were 130% higher (95% CI = 103%, 160%) in comparison to the reference category of liberal harvest-open access; 220% higher (95% CI = 185%, 259%) for liberal harvest-limited access, and 496% higher (95% CI = 432%, 568%) for liberal harvest-moderate access.

In the general season model, elk selected positively for all regulation-access categories in comparison to liberal harvest-open access, with response strength lowest for liberal harvest-limited access, followed by liberal harvest-moderate access, and the strongest response to restricted harvest-open access (Figure 37). Based on coefficient estimates from the general season model, the odds of elk selecting liberal harvest-limited access were 30% higher (95% CI = 18%, 45%) in comparison to the reference category of liberal harvest-open access; 75% higher (95% CI = 58%, 94%) for liberal harvest-moderate access, and 406% higher (95% CI = 356%, 461%) for restricted harvest-open access.

In the late shoulder season model, elk selected positively for all regulation-access categories in comparison to liberal harvest-open access, with response strength lowest for liberal harvest-limited access, followed by liberal harvest-moderate access, no harvest-open access, and the strongest response to restricted harvest-open access (Figure 37). Based on coefficient estimates from the late shoulder season model, the odds of elk selecting liberal harvest-limited access were 152% higher (95% CI = 112%, 200%) in comparison to the reference category of liberal harvest-open access; 265% higher (95% CI = 208%, 333%) for liberal harvest-moderate access, 867% higher (95% CI = 703%, 1,064%) for no harvest-open access, and 3,644% higher (95% CI = 3,054%, 4,344%) for no harvest-limited access.

In the model pooled across hunting periods, elk selected positively for all regulation-access categories in comparison to the reference category of liberal harvest-open access, with response strength lowest for liberal harvest-limited access, followed by no harvest-open access, liberal harvest-moderate access, restricted harvest-open access, and the strongest response to no harvest-limited access (Figure 37). Based on coefficient estimates from the pooled model, the odds of elk selecting liberal harvest-limited access were 94% higher (95% CI = 82%, 106%) in comparison to the reference category of liberal harvest-open access; 153% higher (95% CI = 134%, 174%) for no harvest-open access, 195% higher (95% CI = 177%, 213%) for liberal harvest-moderate access, 335% higher (95% CI = 308%, 364%) for restricted harvest-open access, and 1,728% higher (95% CI = 1,617%, 1,845%) for no harvest-limited access.

Elk demonstrated weak selection for security habitat in the pooled model, weak selection against security habitat in the early shoulder season model, strong selection for security habitat in the archery season model, no significant response in the general season model, and strong selection against security habitat in the late shoulder season model (Figure 37). Elk selected against SWE in the pooled model, had no response in the early shoulder season model as there was no snow, and showed selection for SWE in the archery season model that decreased in the general and late shoulder season models. Across the pooled model and all individual hunting period models, elk selected against terrain ruggedness. Elk showed weak selection for slope in the pooled model, increasing selection for slope in the early shoulder season, archery season, and general season models, and weak selection against slope in the late shoulder season model. Elk demonstrated an overall positive response to aspect (indicating selection for northerly aspects), with strongest positive selection in the early shoulder and archery season models that decreased in the general and late shoulder season models. In reference to the conifer forest landcover category, elk demonstrated weak selection against grassland and shrubland landcover types and no response to sagebrush steppe landcover types in the pooled model. In the early shoulder season model, elk demonstrated strong selection against grassland, sagebrush steppe, and shrubland landcover in comparison to conifer forest. In the archery season model, selection remained negative for grassland and shrubland (but weaker) and was weakly positive for sagebrush steppe. In the general season model, selection was negative and moderate for grassland, sagebrush steppe, and shrubland in comparison to conifer forest. In the late shoulder season model, selection was moderate and positive for grassland, sagebrush steppe, and shrubland in comparison to conifer forest.

DISCUSSION

Overall, our results indicate that female elk generally avoided hunting pressure and the associated harvest risk by moving towards or selecting for areas with less hunter access and more restrictive harvest regulations, similar to elk responses to hunting pressure in other studies (Vieira et al. 2003, Proffitt et al. 2013, Proffitt et al. 2016, Ranglack et al. 2017). We found elk responses to hunter access management and harvest regulations varied throughout the hunting season. Elk responded strongly to hunter access management in the early shoulder and archery seasons, moving to less accessible private lands with the onset of hunting pressure. In the general and late shoulder seasons, elk responded more strongly to harvest regulations, selecting for the BTWMA. Although some elk responded to harvest risk by moving to less accessible lands, about a third of the population occupied less accessible lands all or almost all of the time. Elk responded strongly to the combination of no female harvest and no hunter access on the BTWMA in the late shoulder season, maintaining elk on public land and achieving a desirable elk distribution that reduces conflict with private landowners.

Responses of female elk to hunter access management and harvest regulations varied between hunting periods. The top model evaluating factors influencing the probability that an elk transitioned between hunter access management strategies included hunting period as an explanatory variable, likely capturing various temporally-linked changes on the landscape, including changes in hunter access management and harvest regulations. The top model describing female elk habitat selection included the interactive regulation-access covariate, and selection for each regulation-access category differed between hunting periods. Both top models together highlight the dynamic behavior of female elk throughout the hunting season. For example, during the archery and general seasons, elk were exposed to the same four regulation-access categories: liberal harvest-open access, liberal harvest-moderate access, liberal harvest-limited access, and restricted harvest-open access. Selection was lowest for the reference category of liberal harvest-open access in both periods. In archery season, the order of selection strength from low to high was restricted harvest-open access, liberal harvest-limited access, and liberal harvest-moderate access. However, in general season, the order of selection strength from low to high became liberal harvest-limited access, liberal harvest-moderate access, and restricted harvest-open access (Figure 37). This variation in response could derive from two sources: changes in elk response to the harvest risk conditions of a given regulation-access category or changes in the harvest risk conditions associated with a given regulation-access category. Female elk may have responded differently to the same regulation-access harvest risk conditions between hunting periods due to changing seasonal habitat preferences or a varying risk-response after repeated encounters with hunters. However, the amount and type of hunting pressure clearly changed between hunting periods, with changes in hunter equipment and hunter harvest increasing from early shoulder season through the general season and declining in the late shoulder season (Appendix B, Table B1). These changes through time suggest that a given regulation-access category is associated with different levels of harvest risk depending on the hunting period, contributing to variations in elk responses. These dynamic responses underscore the complexity of this system, with many factors influencing elk behavior throughout the hunting season.

Female elk responded to harvest risk by shifting towards less accessible private lands in the early shoulder and archery seasons and inaccessible public lands in the late shoulder season, but did not shift towards less accessible lands during the general season. Together, the predicted transition probabilities between access strategies and changes in elk selection responses to the regulation-access covariate demonstrated that at least some elk changed their behavior in response to hunting pressure and harvest risk. Movements from open access lands to less accessible lands were most likely to occur in the early shoulder and archery seasons and open to limited access transitions were most likely to occur in the late shoulder season (Figure 30). The estimated probability of transitioning from open access to limited access during the late shoulder season was the highest probability of any transition between access strategies. However, overall transitions between access strategies were most likely to occur during the general season, but not towards less accessible lands (i.e. moderate and limited access). The probability of remaining in open access was highest during the general season as well as the probability of transitioning from moderate or limited access to open access (Figure 30). These high transition probabilities may indicate that the high hunting pressure of the general season resulted in more dynamic elk movements, but not movement from accessible lands to less accessible lands. The increase of movement across access strategies and dynamism of the general season is also reflected by the relatively small selection coefficients for regulation-access in the habitat selection model. The lack of movement towards less accessible lands during the general season may also be partially explained by the considerable movements to less accessible lands in the early shoulder and archery seasons, setting up the elk distribution going into the general rifle season. In accordance with our findings, the onset of an archery or early season has been demonstrated to induce elk movement to private lands in other studies as well (Conner et al. 2001, Vieira et al. 2003). Additionally, a large portion of the open access lands during the general season occurred on the BTWMA, which had restricted harvest regulations, resulting in decreased harvest risk and encouraging elk to remain on those open access lands.

Despite some elk responding to harvest risk by moving to less accessible lands, female elk were generally more likely to remain within the hunter access management strategy in which they already resided. The predicted probabilities of elk remaining in the same access strategy (probability range: 47.93% - 92.11%) were much higher than the probabilities of elk moving between strategies (probability range: 0.38% - 48.44%). This lack of movement may indicate that some elk have established home ranges entirely or mostly on less accessible lands, potentially due in part to the large parcel size in this study area. Of the 58 elk included in this analysis, 4 individuals remained entirely on less accessible lands during all hunting periods and years, and an additional 10 individuals remained on less accessible lands over 97% of the time during hunting season. Of the 130 animal-years available, 21 animal-years remained entirely on less accessible lands and an additional 22 animal-years remained on less accessible lands over 97% of the time during hunting season. These elk may still respond to hunting pressure by fleeing hunters but may do so within one access strategy. Elk with established home ranges on less accessible lands are not exhibiting a short-term behavioral response due to hunting pressure, rather, they occupy those lands as part of their normal movement. These elk may also still migrate but do so on less accessible lands. Of the 43 animal-years of less accessible residents who remained on less accessible lands over 97% of the time, 45% exhibited migratory behavior, which is 11 percentage points lower than the population proportion. Location data from these less accessible residents contribute to positive habitat selection coefficients for less accessible lands, but these selection coefficients do not necessarily represent movement to less accessible lands from open access lands. Additionally, these ingrained home ranges on less accessible lands may be much more difficult to influence than animals who make movements to less accessible lands during hunting season as a response to harvest risk.

Hunter access management appeared most influential on elk movement and habitat selection during the early shoulder and archery seasons, whereas harvest regulations appeared more influential during the general and late shoulder seasons. During the early shoulder and archery seasons, predicted transition probabilities indicated elk avoided harvest risk by leaving open access lands. Female elk selected more strongly for less accessible private lands with liberal harvest than more restrictive harvest regulations on the BTWMA. This strong selection for less accessible lands in early seasons echoes previous research in central-eastern Montana that found selection against hunter access was stronger during the archery season than the general season (Proffitt et al. 2016), but other studies from southwest Montana found increasing selection against hunter access from archery to general season (Proffitt et al. 2013, Ranglack et al. 2017). During the general season, elk responses strongly shifted from the archery season: the probability of remaining in open access and the probabilities of transitioning into open access were highest, while the probabilities of remaining in moderate and limited access were lowest. In the general and late shoulder seasons, female elk selected more strongly for more restrictive harvest categories on the BTWMA than less accessible private lands. The shift from hunter access management-driven responses to harvest regulation-driven responses may have been caused by the increase in hunting pressure and harvest success that occurred during the general season (Appendix B, Table B1) as well as the change in hunting approaches from archery equipment to firearms. This change in hunting pressure may equalize the difference in risk between open access and less accessible lands, making the difference in risk caused by harvest regulations more important. However, seasonal changes in habitat preferences may also contribute to the apparent shift as many elk make migratory movements to the BTWMA where harvest regulations are more restrictive. These movements may be driven by pre-existing cultural knowledge of the migratory route and seasonal habitat preferences for winter range. However, this elk population is only partially migratory, with largely overlapping summer and winter ranges and a moderate amount of migratory switching, so migratory movements could also be considered largely a behavioral choice. In this context, migratory behavior may influence elk responses to harvest risk, but harvest risk may also impact elk migratory behavior and seasonal movement patterns. With this complexity in mind, the observed movement of elk to the BTWMA is likely caused by a combination of both factors.

The BTWMA concentrated elk over the course of the hunting season with restrictive female harvest and limited hunter access in the late shoulder season, producing desirable elk distributions but potentially limiting harvest. The BTWMA represents its own hunting district, HD 455, and was classified as no harvest-open access during early shoulder season, restricted harvest-open access during archery and general season, and a combination of no harvest-open access and no harvest-limited access during late shoulder season (due to mixed state and federal landownership). The BTWMA was the only area in the study where no harvest and restricted harvest occurred. Elk selection strength for the BTWMA steadily increased throughout the hunting season, beginning relatively low in the early shoulder season (no harvest-open access, odds of selection 34% higher than reference of liberal harvest-open access), increasing in archery season (restricted harvest-open access, odds of selection 130% higher than reference), increasing further in general season (still restricted harvest-open access, odds of selection 406% higher than reference), and increasing in late shoulder season to the two largest selection coefficients of any model (no harvest-open access and no harvest-limited access, odds of selection 867% and 3,644% higher than reference, respectively). Additionally, the estimated transition probability of moving from open access to limited access increased to 48.44% (95% CI = 43.41%, 53.43%), the highest probability of any transition between categories. Interestingly, other research has found reducing hunter numbers by 50% did not reduce elk movement to private (inaccessible) land (Vieira et al. 2003), but it appears the restricted harvest regulations on the BTWMA effectively maintained elk on or attracted elk to public lands. As discussed above, seasonal habitat preferences may have also contributed to this effect. The BTWMA concentrated elk more and more throughout the hunting season, serving as a winter elk refuge on public lands and achieving a desirable elk distribution. The current consensus from managers and landowners in the area prioritizes the role of the BTWMA to reduce conflict with agricultural producers, so our results support that those objectives are being met. However, the use of the BTWMA by large numbers of elk may make it more difficult to achieve hunter harvest goals and meet population objectives for this area as outlined in the state elk management plan. If objectives for elk management in the area change, the role of the BTWMA may need to be considered.

A wide variety of land management practices and decisions made by individual landowners may have had large impacts on elk behavior. The Devil's Kitchen study area was composed of very large land parcels, meaning individual landowners may effectively set their own harvest regulations on large parcels of land if they manage harvest more restrictively than the state regulations, complicating the interpretation of our results, which only account for the official state regulations. Other land management practices that landowners implement may impact habitat quality in positive or negative ways that influence elk movement, potentially impacting our results as well. Counter-intuitively, female elk selected more strongly for liberal harvest-moderate access than liberal harvest-limited access throughout all hunting periods. This unexpected result may have been caused by a mismatch between our classifications and actual hunting pressure (i.e. limited access parcels had higher hunting pressure than moderate access parcels) or potentially by other unrelated factors such as habitat quality. Additionally, we classified harvest regulation based on harvest options for female elk (i.e. actual harvest risk), but elk may perceive hunting pressure differently. For example, female elk may avoid hunters who are only permitted to hunt male elk, hunters targeting other species of game, or other recreators who are not hunting. In such a complex and dynamic landscape, an experimental study design may be necessary to solidify cause-and-effect relationships.

Management Implications

Our results demonstrate that female elk responded to harvest risk by moving to areas with less hunter access and more restrictive harvest regulations. The considerable movement of elk to less accessible private lands in the early shoulder and archery seasons indicate that hunting pressure during those early hunting periods is significant enough for elk to respond with avoidance, shaping elk distributions ahead of the general rifle season. Because hunter access management on private lands is determined by individual landowners, these movements may be challenging for wildlife managers to influence. Our study area included a large tract of public land, the BTWMA, where hunter access and harvest regulations were both managed by the state wildlife agency, providing a unique tool for managers to influence elk harvest risk. Female elk demonstrated increasingly strong selection for the BTWMA during the general and especially late shoulder seasons, responding to the favorable combination of no female harvest and no hunter access during the late shoulder season. These responses to harvest risk may limit hunter harvest and make it more difficult to achieve population objectives, but conversely, heavy late shoulder season use of the BTWMA achieves a desirable elk distribution, meeting key objectives in the BTWMA management plan. In this area, managers and landowners prioritize reducing conflict on private lands by providing secure winter elk habitat on public lands. However, priorities vary between areas and this approach may not be acceptable in other contexts, highlighting the need to thoroughly understand stakeholder priorities and make decisions accordingly. In complex landscapes of public and private ownership, managers and stakeholders may have to prioritize management objectives for elk populations and identify appropriate management actions.

3.2 Custer Forest and Missouri Breaks Analysis

Throughout the last century, elk distributions have occurred primarily in forested and montane environments in the western United States, and elk habitat selection and behavior in response to hunting pressure are well-understood in these systems (Skovlin et al. 2002). Consequently, conventional management strategies for providing security habitat have often focused on preserving blocks of hiding cover far from motorized routes, while also considering vegetation density, topography and hunter-use patterns (Hillis et al. 1991). However, little is known about elk habitat selection, movement patterns, and responses to hunting pressure in prairie environments. Only two published papers have evaluated elk-habitat relationships during hunting in prairies (Millspaugh et al. 2000, Proffitt et al. 2016), and only Proffitt et al. (2016) assessed the effects of hunter access. While this work established that access was an important factor influencing population distributions (Proffitt et al. 2016), little is known about how elk select for security features other than access in prairie environments. Prairies are characterized by limited tree cover and milder elevational and topographical gradients, making them more homogenous than the forested, mountainous landscapes typical of most studies. Such differences in available habitat likely carry implications for habitat selection during hunting seasons and location-appropriate definitions of security habitat. Further, extrapolating results of habitat selection models developed for other elk populations, especially those with drastic differences in habitat or that are geographically distant, can be problematic (Ranglack et al. 2022).

In landscapes with mixed ownership and variable hunter access, varying exposure to harvest risk could be associated with changes in the strength or direction of elk-habitat relationships (i.e. functional responses) at the population- or individual-level (Mysterud and Ims 1998, Hebblewhite and Merrill 2008, Mabille et al. 2012). For instance, Ranglack et al. (2017) established that responses to harvest risk increase as risk increases for elk populations, while other recent work also highlighted significant variation in how individual elk respond to predation risk (Paterson et al. 2022). Further, selection patterns may vary in direction and strength depending on exposure to harvest risk at the individual level (DeVoe et al. 2019). More work is needed to understand if and how selection for security features changes across the gradient of harvest risk experienced by individual elk, and the consequences of such risk-related responses for managing harvest and security habitat.

Recent increases in elk populations and changes in distributions in eastern Montana further emphasize the need for information about habitat selection in prairie regions. The Missouri Breaks and Custer Forest elk populations are characterized by a mix of public and private lands with a range of hunting access management strategies. Both populations have distributions that are gradually expanding into available habitat and areas with varied landowner opinion and tolerance. The general lack of information makes managing elk habitat and harvest in these populations difficult, especially when coupled with other management challenges.

To improve our understanding of elk-habitat relationships in prairie environments during the hunting season, we evaluated resource selection during the archery and rifle seasons for male and female elk in these eastern Montana elk populations. Specifically, our analysis included the following objectives: (1) evaluate relationships between resource selection and landscape and environmental factors that may influence population distributions, (2) assess individual variability in risk-related selection patterns and examine functional responses between individual selection and the gradient of harvest risk, and (3) identify and map security habitat metrics to provide recommendations for security habitat management in prairie landscapes.

METHODS

Covariate data

We assessed evidence for potential relationships between elk habitat selection and six covariates: canopy cover, distance to motorized routes, terrain ruggedness, herbaceous biomass, snow water equivalent (SWE), and hunter access. We used the Rangeland Analysis Platform (https://rangelands.app/) vegetation cover product for annual percent tree cover to represent canopy cover (Allred et al. 2021). The TIGER system for all roads (U.S. Census Bureau 2018) was used to define most motorized routes. We defined additional routes on public lands using the following sources: a U.S. Forest Service (USFS) layer for existing open roads and motorized trails and to exclude permanently and seasonally closed routes on USFS lands, a U.S. Fish and Wildlife layer for the Charles M. Russell National Wildlife Refuge (CMR), and a local BLM layer for BLM lands. Because of motorized boat access, we also included the shoreline of Fort Peck Lake (U.S. Geological Survey 2023a) as a road. We produced and tested two versions of the distance to motorized routes covariate in our analysis: (1) distance to all motorized routes, regardless of public accessibility, and (2) distance to public motorized routes, which excluded private routes and routes with unknown public access. We used a 30-m digital elevation model (U.S. Geological Survey 2023b) to estimate a terrain ruggedness index, calculated as the amount of elevation difference between a given pixel of the digital elevation model and its neighbors (Riley et al. 1999). To represent average herbaceous biomass for elk during the rifle season, we used the Rangeland Analysis Platform annual vegetation biomass products and calculated mean aboveground herbaceous biomass (kg/ha) for each pixel across the most recent five years for which the product was available (2018-2022). Similarly, we obtained daily SWE data at a 1 km resolution from Daymet (Thornton et al. 2022) and calculated mean SWE (kg/m2) for each pixel across all days of the rifle season for the most recent five years for which the product was available (2019-2023) to represent typical snowpack conditions.

Hunter access was a binary covariate designed to reflect the expected level of hunting pressure associated with various access management strategies: open access and restricted access. Open access areas are accessible to public hunting (i.e., can be reached via a public access point), and include public lands as well as private lands enrolled in the State of Montana’s Block Management Program and designated as Type I Block Management Areas. Restricted access areas are characterized by varying hunting access restrictions and include public lands that are inaccessible (i.e., landlocked by private lands), Type 2 Block Management Areas that require a reservation to hunt, and other privately owned lands that may employ a range of hunting access management strategies. Privately owned lands in this category may allow free hunting for select members of the public or to friends and family, may charge an access fee or be outfitted, or may prohibit hunting all-together. More information on covariate data sources and development steps can be found in Appendix D, as well as information on hypothesized direction of selection for each covariate in Table D1.

Resource selection modeling

To evaluate factors associated with elk habitat selection during the archery and rifle seasons, we used a resource selection function (RSF) approach with a use-available design (Manly et al. 2002). Because we were interested in factors affecting fine-scale elk distributions within the population range, we conducted this investigation between the second and third orders of selection (Johnson 1980) by comparing GPS locations collected from radio collared elk to available locations sampled from within the population range. Analyses were conducted separately for the archery and rifle seasons.

We developed the sample of used locations through the following steps. First, we omitted data from individuals that did not occupy the study area during the period of interest or had an insufficient amount of GPS location data, which we defined as fewer than 70 total locations or less than 14 days with at least one location during the hunting season. We then subset GPS location data by removing locations that occurred outside legal shooting times. Finally, we broke the daily legal shooting period into four equal time blocks and randomly sampled one location from each block from each individual to reduce autocorrelation, resulting in up to 4 locations per elk per day.

To develop the sample of available locations, we pooled data from all years of archery and rifle season and both sexes and estimated population-specific archery and rifle season ranges by randomly selecting 4 locations per individual per day and building a 99% kernel density estimator (KDE) contour using the “kernelUD” function in the “adehabitat” package (Worton 1989) in Program R (R Core Team 2024). For each used location, we randomly sampled five available locations from within the population range (approximately 1:5 used:available).

We split the data into study area and sex-specific datasets so that modeling could be conducted separately for each. To facilitate interpretation of coefficients, each continuous covariate was standardized by subtracting the mean and dividing by the standard deviation prior to analysis. We then calculated Pearson’s correlation coefficients for all pairs of continuous covariates: collinear covariates ($|r| > 0.7$) were not included together in the same model (Dormann et al. 2013). Additionally, we calculated variance inflation factors to check for multicollinearity among continuous covariates. All models were fit as generalized linear mixed models with a logit link using the “glmer()” function in the “lme4” R package. To account for lack of independence among observations from the same animal and differences in used to available ratios, all models included a random intercept for individual (Gillies et al. 2006).

To address our first objective, we employed a global modeling approach to identify the best-supported version of the distance to motorized route variable and evaluate potential non-linear relationships between each continuous covariate and resource selection. Therefore, all rifle season candidate models included hunter access and either a linear or psuedothreshold (log-transformed) functional form of canopy cover, terrain ruggedness, distance to motorized routes, snow water equivalent, and herbaceous biomass. The same covariates were included in archery season candidate models except for snow water equivalent as there was little to no snowfall during the archery time period. Candidate models also included either the all routes or public-only routes version of the distance to motorized route covariate. This process resulted in a set of 64 candidate models containing all combinations of linear or pseudothreshold forms on continuous covariates and either the all- or public-routes distance to route variable. We used Akaike's information criterion corrected for sample size (AICc, Burnham and Anderson 2002) to compare models and selected a model structure for each sex and population that we advanced to the next step.

To account for individual heterogeneity in habitat selection, we used the model structure identified in the previous step and fit a more complex model with individual random coefficients for each of the covariates representing different forms of elk security: canopy cover, distance to motorized routes and terrain ruggedness. We did not include a random effect on the hunter access covariate as we later investigated the functional relationship between individual selection for security attributes and exposure to harvest risk. Herbaceous biomass and snow water equivalent also remained in the model as fixed effects to account for their influences while assuming that selection for these factors would be similar across individuals. We used these models, henceforth referred to as final models, to (1) make inferences about habitat factors affecting elk population distributions based on estimates of the fixed effects and (2) evaluate the size of variance components on the random effects and plot predicted relationships between individual selection and continuous covariates to assess variation among individuals (Gillies et al. 2006, Muff et al. 2020).

We validated final models using k-folds cross validation with five folds. Data was clustered based on the individual elk it originated from, and each elk was then assigned to one of the five folds. Using an iterative process, we fit a RSF using the model structure described in the previous step to data from four of the five folds, then predicted the fitted values for the data in the withheld fold (Boyce et al. 2002). We generated 10 equal-area RSF bins, counted the number of used locations within each bin, and evaluated the correlation between frequency of occurrence and the relative RSF score with Spearman's rank correlation (Boyce et al. 2002). Models that perform well have adjusted frequencies that are highly correlated with the relative RSF (Boyce et al. 2002).

Individual variation and functional responses to harvest risk

To address our second objective, we assessed individual variability in risk-related selection patterns and examined potential functional responses between individual selection and the gradient of harvest risk experienced by individual elk. We used estimates of individual selection coefficients from the final model as the individual's selection and defined harvest risk for each individual as the proportion of an elk's used on locations that occurred on open access lands during the archery or rifle season, respectively. We fit univariate linear models with individual selection as the dependent variable and harvest risk as the explanatory variable. We interpreted the slope value to represent the effect of harvest risk on elk selection (Hebblewhite and Merrill 2008), where positive or negative slope values with 95% confidence intervals that did not overlap zero indicated a functional response to harvest risk. Conversely, slope values with 95% confidence intervals that included zero suggest limited support for a functional response to harvest risk. Based on our hypothesis that elk exposed to higher levels of harvest risk would exhibit increasing selection strength for more secure habitat features, we expected to find positive slope estimates with 95% confidence intervals that did not overlap zero for the relationship between harvest risk and canopy cover, distance to motorized routes, and terrain ruggedness individual selection coefficients.

Security thresholds

To provide recommendations for managing elk security, we followed methods established by Lowrey et al. (2020) which used covariate values associated with 75% and 50% of the cumulative area under the curve in their RSF models to represent security and preferred security thresholds, respectively. For each sex and population, we first removed observations where covariate values were beyond -/+ 1.5 times the interquartile range from the use-available dataset to better target the covariate values typical of the study areas and remove the influence of large outliers in subsequent calculations. We then calculated cumulative area under the curve to represent cumulative elk use and identified the range of values for the canopy cover, terrain ruggedness and distance to motorized route covariates associated with the upper 75% and 50% of the area under the curve. The minimum values within these ranges were used to define the security and preferred security thresholds. We did not report thresholds for a habitat feature if the associated final model provided 95% confidence intervals on the coefficient estimate that widely overlapped zero because we couldn't draw reasonable conclusions about the strength or direction of the relationship between the habitat feature and elk selection. Finally, we used ArcGIS Pro (version 3.4.3) to produce maps identifying areas that met all applicable security and preferred security thresholds for each season, study area, and sex.

Table 12. Harvest regulations effective in the Missouri Breaks study area, HD 700, eastern Montana, USA, 2022-2024. Limited permits and licenses to hunt elk were allocated through drawings and were only valid with a General License. Elk B-Licenses were only valid for the harvest of antlerless elk. An annual quota of 700 B-license 700-00 and 800 B-License 007-00, which were not valid on USFS or the CMR, were available during the study period. In 2022 and 2024, quotas of 250 Permit 700-20 and 800 Permit 700-21 were available, and 2023 they were reduced to 200 and 660 permits, respectively.

Year	Hunting Period	License Type	Harvest Regulation	Restrictions
2022 - 2024	Early Season	-	No Harvest	-
	Archery	Permit 700-20	Either-sex	-
		Permit 700-21	Either-sex	-
		B-License 700-00	Antlerless	-
		B-License 007-00	Antlerless	Valid all Region 7
	Rifle	Permit 700-20	Either-sex	-
		B-License 700-00	Antlerless	-
		B-License 007-00	Antlerless	Not valid on USFS or CMR
	Late Shoulder	-	No Harvest	-

Table 13. Harvest regulations effective in the Custer Forest study area, HD 704, eastern Montana, USA, 2021-2023. General licenses were valid across the state for the harvest of one elk depending on unit-specific regulations. Individuals could only purchase a single general license each year but there was no quota on the total number available for purchase by resident hunters. Elk B-Licenses were only valid for the harvest of antlerless elk. An annual quota of 700 B-license 700-00, 600 B-License 799-00, and 800 B-License 007-00 were available during the study period. Elk permits were only valid with a General License and were allocated through a drawing. A quota of 225-280 Permit 799-20, 4,000 Permit 900-20, and 1,000 Permit 799-21 were available annually during the study period.

Year	Hunting Period	License Type	Harvest Regulation	Restrictions
2021	Early Season	-	No Harvest	-
	Archery	General License	Spike Bull or Antlerless	-
		Permit 799-20	Either-sex	-
		Permit 900-20	Either-sex	-
		B License 799-00	Antlerless	-
		B License 007-00	Antlerless	Valid all Region 7
	Rifle	General License	Spike Bull or Antlerless	Not valid on USFS
		Permit 799-20	Either-sex	-
		B License 799-00	Antlerless	-

		B License 007-00	Antlerless	Not Valid on USFS or CMR
	Late Season	-	No Harvest	
2022 & 2023	Early Season	-	No Harvest	-
	Archery	General License	Spike Bull or Antlerless	-
		Permit 799-20	Either-sex	-
		Permit 799-21	Either-sex	-
		B-License 799-00	Antlerless	-
		B-License 007-00	Antlerless	Valid all Region 7
	Rifle	General License	Spike Bull or Antlerless	Not valid on USFS
		Permit 799-20	Either-sex	-
		B-License 799-00	Antlerless	-
		B-License 007-00	Antlerless	Not Valid on USFS or CMR
	Late Season	General License	Antlerless	Only on private land
		B-License 700-00	Antlerless	Only on private land
		B-License 799-00	Antlerless	Only on private land
		B-License 007-00	Antlerless	Only on private land

RESULTS

After accounting for mortalities and collar failures and censoring individuals we identified as having insufficient data, the archery season analysis included location data from 44 female and 25 male elk in the Custer Forest and 53 females and 29 males in the Missouri Breaks. For the rifle season, we retained location data from 44 female and 22 male elk in the Custer Forest and 49 female and 19 male elk in the Missouri Breaks. In addition to the animals that were excluded for having insufficient data, we censored a Custer Forest male after he dispersed outside the study area. Summaries of proportions of used locations on public lands can be found in Tables 17-18 and Figures 42-43. Additionally, statistical summaries of covariate data can be found in Appendix E, Table E1-E3.

Population-level resource selection

Archery season

During archery season in the Custer Forest, the global modeling procedure demonstrated clear support ($\Delta AIC_c = 52.88$) for a female resource selection model that included a linear form for canopy cover and psuedothreshold forms for distance to all motorized routes, terrain ruggedness and herbaceous biomass. For female elk in the Custer Forest, the final model with the addition of random coefficients for canopy cover, terrain ruggedness and distance to motorized routes, indicated that elk were more likely to use areas as canopy cover, distance to routes, terrain ruggedness, and herbaceous biomass increased. The hunter access estimate ($\beta = 0.006$, 95% CI = -0.032, 0.044) was very close to and had a confidence interval that overlapped zero, suggesting that this group of elk did not display selection among areas with different access regimes at the population level (Table E4 and Figure 38).

For male elk in the Custer Forest, the best-supported resource selection model had the same structure as the female top model and included linear forms of canopy cover and psuedothreshold forms for distance to all motorized routes, terrain ruggedness, and herbaceous biomass. The second-best model of the candidate set had a $\Delta AIC_c = 60.49$. The final model with added random coefficients indicated that male elk preferred areas with restricted access over open access, as well as higher values of canopy cover, greater distances from routes, more rugged terrain, and greater herbaceous biomass (Table E5 and Figure 38).

During archery season in the Missouri Breaks, the top female resource selection model (second-best model $\Delta AIC_c = 8.75$) contained linear forms only and the public routes only version of distance to motorized routes. The final model for this group demonstrated elk selection for restricted access, canopy cover, terrain ruggedness and herbaceous biomass. The distance to motorized routes coefficient and associated confidence intervals from the final model ($\beta = 0.037$, 95% CI = -0.222, 0.148) indicated no consistent relationship between female elk selection and public route distance at the population level (Table E6 and Figure 39).

For male elk in the Missouri Breaks, the top model from the candidate set included linear canopy cover, terrain ruggedness, and herbaceous biomass, but psuedothreshold distance to all motorized routes. The second-best model had a $\Delta AIC_c = 133.56$. The final model demonstrated elk preference for restricted access, as well as increasing values of canopy cover, distance to all motorized routes, ruggedness and herbaceous biomass (Table E7 and Figure 39).

Plots of predicted relative RSFs using population-level fixed effects can be found in Appendix E, Figures E1-E8, and of predicted relative RSFs based on individual-level random effects in Figures E9-16.

Rifle season

In the Custer Forest, the global modeling approach revealed clear support ($\Delta AIC_c = 196.91$) for a rifle season female resource selection model that included linear forms of canopy cover, distance to all motorized routes, and SWE, and pseudothreshold functional forms of terrain ruggedness and herbaceous biomass. For female elk in the Custer Forest, the final model indicated that elk selected for areas that restricted hunter access over those with open access. Additionally, elk were more likely to use areas as canopy cover, distance to routes, terrain ruggedness, and herbaceous biomass increased, whereas elk use declined with increasing SWE (Table E8 and Figure 38).

For male elk in the Custer Forest, the best-supported resource selection model included linear forms for canopy cover and SWE and pseudothreshold forms for distance to all motorized routes, terrain ruggedness and herbaceous biomass. The second-best model of the candidate set had a $\Delta AIC_c = 29.71$. Similar to the female models, the final model with added random coefficients indicated elk preference for areas with restricted access, greater values for canopy cover, distance to motorized routes, terrain ruggedness and herbaceous biomass, and lower values for SWE (Table E9 and Figure 38).

In the Missouri Breaks during the rifle season, the top female resource selection model contained linear functional forms only and the public-only distance to motorized routes version. The next-best model had $\Delta AIC_c = 32.16$. The final model for female elk indicated that preference increased as canopy cover, terrain ruggedness and herbaceous biomass increased, and declined as SWE increased. Similar to the archery season, the distance to public motorized routes coefficient and associated confidence intervals from the final model ($\beta = -0.030$, 95% CI = -0.235, 0.175) indicated no clear relationship between female elk selection and route distance. Lastly, female elk also preferred areas with restricted hunter access (Table E10 and Figure 39).

For male elk in the Missouri Breaks during rifle, the top model from the candidate set was the same as females with all linear forms and public routes only. The second-best supported model of the candidate set had a $\Delta AIC_c = 12.60$. The final model for this group showed that males in the Missouri Breaks had general similarities and some notable differences in their estimated selection patterns compared to the other groups of elk (Table E11 and Figure 39). In general, males in the Missouri Breaks were more likely to select areas with greater values for canopy cover, distance to motorized routes, terrain ruggedness and herbaceous biomass, similar to patterns observed in females as well as with elk in the Custer Forest. In contrast, however, the hunter access estimate ($\beta = -0.180$, 95% CI = -0.288, -0.072) was negative, implying that elk preferred open access over restricted access areas. Like their female counterparts, male elk in the Missouri Breaks also did not show clear preference or avoidance of distance to routes ($\beta = 0.065$, 95% CI = -0.337, 0.467).

In all cases, the inclusion of individual random effects in the final model improved model fit. During archery season, increased model complexity from the inclusion of random effects reduced the AIC_c of the final model by 2,598.17 and 920.6 for Custer Forest females and males, and by 7,982.82 and 1,342.3 for Missouri Breaks females and males. For the rifle season, the increased model complexity reduced AIC_c by 1,993.7 and 978.45 for Custer Forest females and males, respectively, and by 5,265.78 and 1,782.72 for females and males in the Missouri Breaks. All final models demonstrated strong predictive performance, with the Spearman rank correlation coefficient from the k-folds cross validation averaging 0.75 for the Missouri Breaks males during archery and >0.91 over the five iterations across all remaining final models for the various seasons, study areas and sexes.

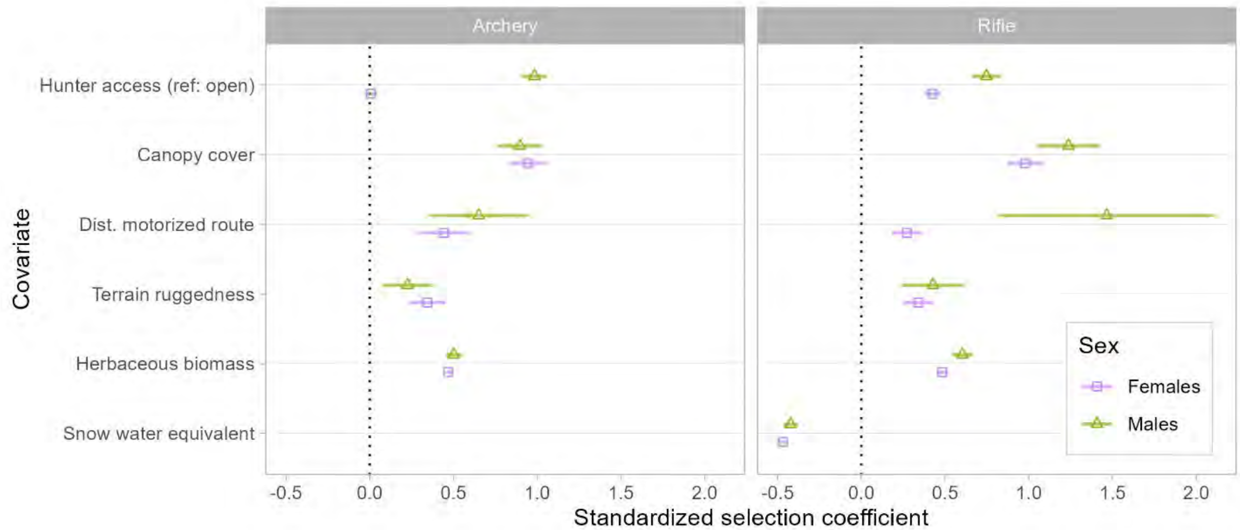

Figure 38. Population-level standardized resource selection coefficients from resource selection models for male and female elk during archery and rifle seasons in the Custer Forest study area, eastern Montana, 2021-2023.

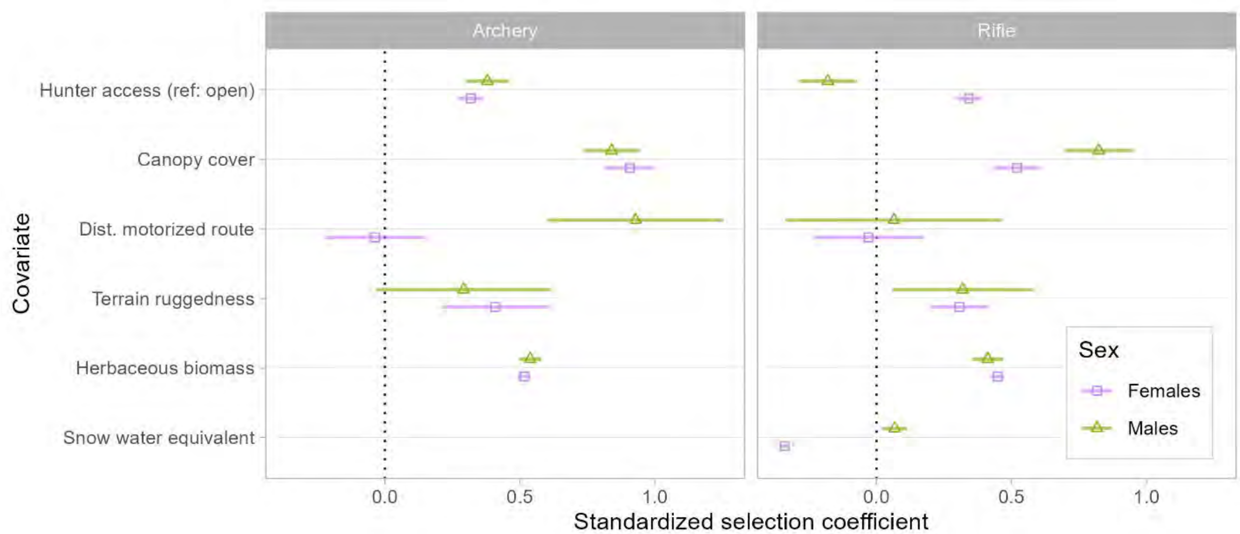

Figure 39. Population-level standardized resource selection coefficients from resource selection models for male and female elk during archery and rifle seasons in the Missouri Breaks study area, eastern Montana, 2021-2023.

Individual variation and functional responses to risk

Across study areas, sexes and seasons, estimates of random coefficients and their variance components suggested significant heterogeneity among individuals in relationships between selection and canopy cover, distance to motorized routes, and terrain ruggedness. The majority of the variability among individuals manifested as differences in selection strength for a given covariate, although the direction of selection switched for a subset of individuals (Figures

E10-E17). Summaries of functional response results can be found in Tables 14 and 15 for the Custer Forest and Missouri Breaks, respectively.

Archery season

Functional responses to harvest risk differed by study area, sex, and season. For Custer Forest females during archery season, we found moderate evidence that selection strength for canopy cover (β = 0.365, 95% CI = 0.063, 0.667) increased modestly with harvest risk, and no evidence of risk responses with distance to all motorized routes (β = 0.119, 95% CI = -0.323, 0.562) or terrain ruggedness (β = 0.066, 95% CI = -0.253, 0.386) (Table 14 and Figure 40). For male elk, harvest risk was again associated with increased selection strength for canopy cover (β = 0.639, 95% CI = 0.249, 1.030). Male elk also demonstrated suggestive but weak evidence of a risk response with terrain ruggedness (β = 0.411, 95% CI = -0.097, 0.919). There was no evidence of risk response with distance to any motorized route (β = -0.835, 95% CI = -1.867, 0.198) (Table 14 and Figure 40).

During archery season in the Missouri Breaks, female elk demonstrated a strong risk response with terrain ruggedness (β = 1.794, 95% CI = 1.317, 2.271) and weaker evidence for such a response with distance to public motorized routes (β = 0.595, 95% CI = -0.022, 1.208). However, there was no apparent risk relationship with canopy cover (β = -0.263, 95% CI = -0.567, 0.041) (Table 15 and Figure 41). For male elk in the Missouri Breaks, there was again no risk relationship with canopy cover (β = -0.133, 95% CI = -0.514, 0.249) but moderate to strong evidence with distance to any motorized route (β = 1.222, 95% CI = 0.085, 2.36) and terrain ruggedness (β = 2.021, 95% CI = 1.019, 3.024) (Table 15 and Figure 41).

Rifle season

For Custer Forest females, there was strong to very strong evidence that selection strength for canopy cover (β = 0.534, 95% CI = 0.277, 0.791) and distance to motorized routes (β = 0.390, 95% CI = 0.150, 0.630) increased with increasing harvest risk, and no evidence of changing selection for terrain ruggedness (β = 0.044, 95% CI = -0.2, 0.287) (Table 14 and Figure 40). For male elk, harvest risk was clearly associated with increased selection strength for more rugged terrain (β = 0.553, 95% CI = 0.057, 1.049). There was merely suggestive evidence for a risk relationship with canopy cover (β = 0.412, 95% CI = -0.147, 0.971), and no evidence of such a relationship with distance to routes (β = 0.679, 95% CI = -1.426, 2.784) (Table 14 and Figure 40).

During rifle season in the Missouri Breaks, we found strong to very strong evidence of relationships between female elk selection and risk with canopy cover (β = 0.471, 95% CI = 0.144, 0.798) and especially with terrain ruggedness (β = 1.178, 95% CI = 0.907, 1.448), and no support for this relationship with distance to routes (β = 0.533, 95% CI = -0.324, 1.390) (Table 15 and Figure 41). For male elk, there was weak evidence for a risk response with canopy cover (β = 0.503, 95% CI = -0.029, 1.035) and none with remaining covariates (Table 15 and Figure 41).

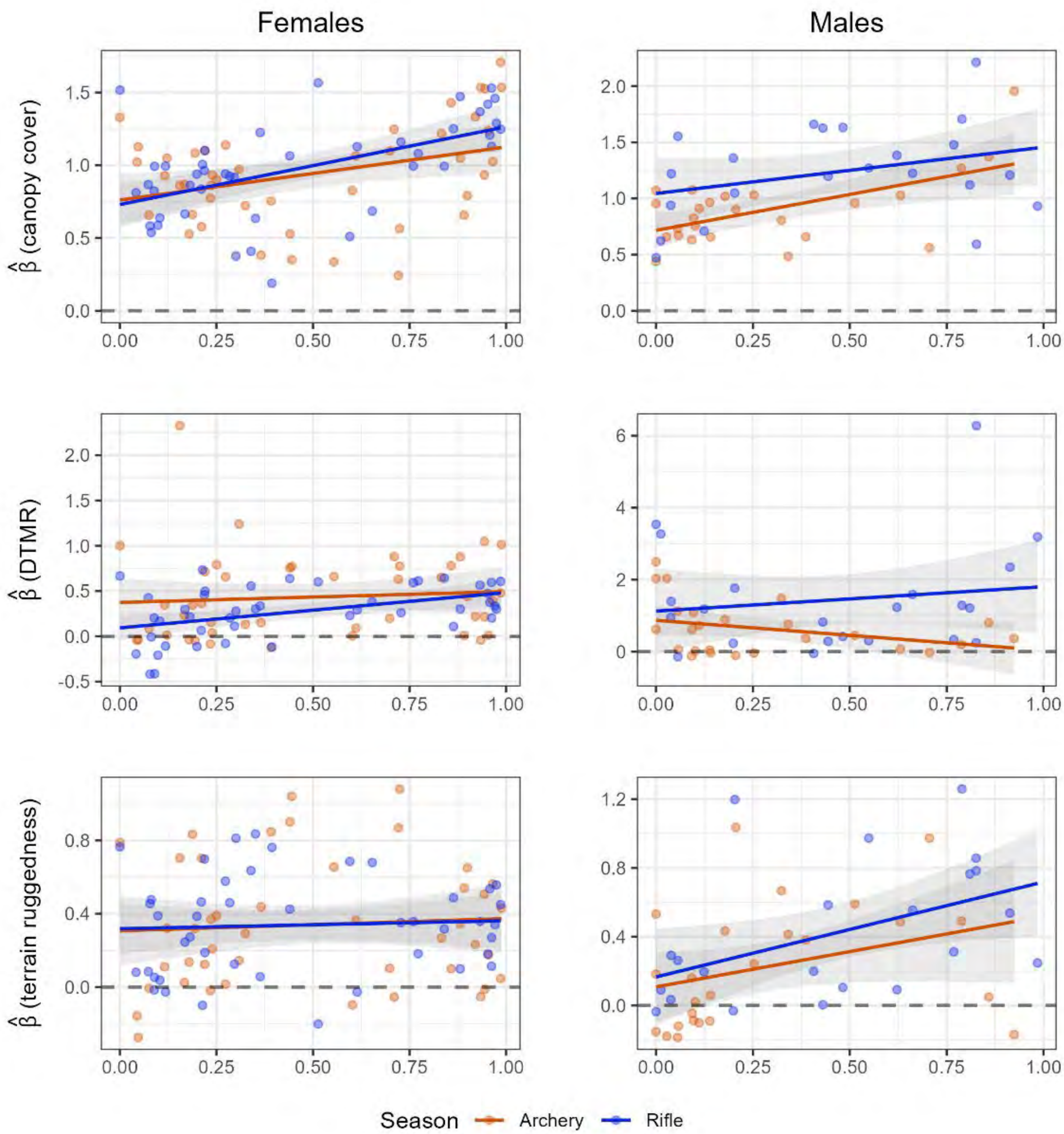

Figure 40. Functional responses between harvest risk (i.e., proportion open access) and individual resource selection for female and male elk in the Custer Forest study area, eastern Montana, 2021-2023. For female elk, instances with at least some statistical evidence for a risk response (p-value <0.1) include archery canopy cover, rifle canopy cover, and rifle distance to motorized routes. For males, such instances include archery canopy cover and rifle terrain ruggedness.

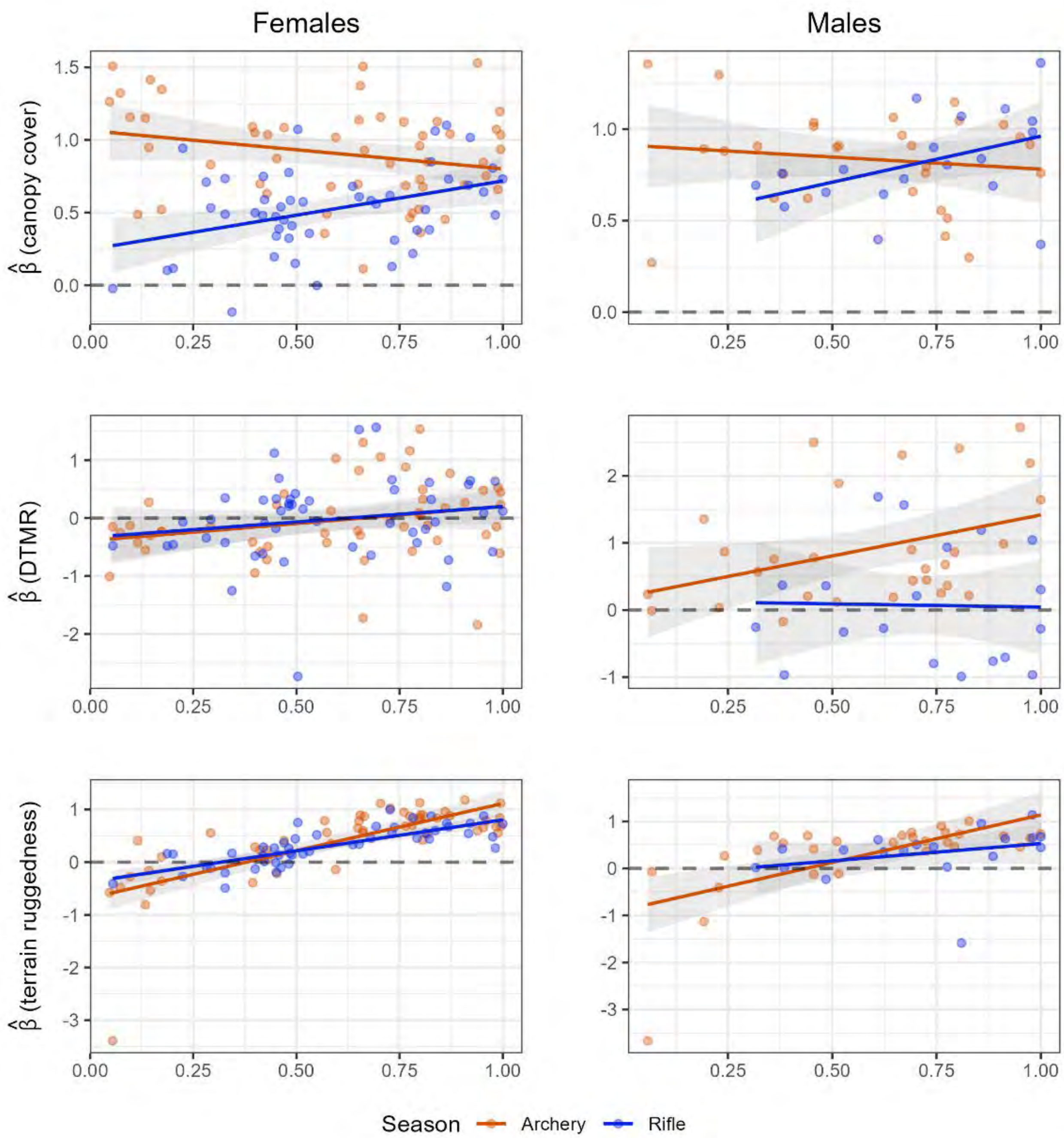

Figure 41. Functional responses between harvest risk (i.e., proportion open access) and individual resource selection for female and male elk in the Missouri Breaks study area, eastern Montana, 2022-2024. For female elk, instances with statistical evidence for a risk response (p-value <0.1) include archery season distance to routes and terrain ruggedness, as well as rifle season canopy cover and terrain ruggedness. For males, such instances include archery season distance to motorized routes and terrain ruggedness, as well as rifle season canopy cover.

Table 14. Results of univariate functional response models describing relationships between harvest risk and individual resource selection for elk in the Custer Forest study area, eastern Montana, USA, 2021-2023. Colors indicate strength of evidence based on p-values and color codes can be found in Table 16. Uncolored rows show instances with a lack of evidence for a risk response (p-values >0.1).

Risk coefficient estimate	P-value	95% CI	Security covariate	Study area	Sex	Season
0.365	0.019	(0.063, 0.667)	Canopy cover	Custer Forest	Females	Archery
0.119	0.589	(-0.323, 0.562)	DTMR	Custer Forest	Females	Archery
0.066	0.677	(-0.253, 0.386)	Terrain ruggedness	Custer Forest	Females	Archery
0.639	0.003	(0.249, 1.03)	Canopy cover	Custer Forest	Males	Archery
-0.835	0.108	(-1.867, 0.198)	DTMR	Custer Forest	Males	Archery
0.411	0.108	(-0.097, 0.919)	Terrain ruggedness	Custer Forest	Males	Archery
0.534	<0.001	(0.277, 0.791)	Canopy cover	Custer Forest	Females	Rifle
0.39	0.002	(0.15, 0.63)	DTMR	Custer Forest	Females	Rifle
0.044	0.719	(-0.2, 0.287)	Terrain ruggedness	Custer Forest	Females	Rifle
0.412	0.14	(-0.147, 0.971)	Canopy cover	Custer Forest	Males	Rifle
0.679	0.509	(-1.426, 2.784)	DTMR	Custer Forest	Males	Rifle
0.553	0.031	(0.057, 1.049)	Terrain ruggedness	Custer Forest	Males	Rifle

Table 15. Results of univariate functional response models describing relationships between harvest risk and individual resource selection for elk in the Missouri Breaks study area, eastern Montana, USA, 2022-2024. Colors indicate strength of evidence based on p-values and color codes can be found in Table 16.

Risk coefficient estimate	P-value	95% CI	Security covariate	Study area	Sex	Season
-0.263	0.088	(-0.567, 0.041)	Canopy cover	Missouri Breaks	Females	Archery
0.593	0.058	(-0.022, 1.208)	DTMR	Missouri Breaks	Females	Archery
1.794	<0.001	(1.317, 2.271)	Terrain ruggedness	Missouri Breaks	Females	Archery
-0.133	0.482	(-0.514, 0.249)	Canopy cover	Missouri Breaks	Males	Archery
1.222	0.036	(0.085, 2.36)	DTMR	Missouri Breaks	Males	Archery
2.021	<0.001	(1.019, 3.024)	Terrain ruggedness	Missouri Breaks	Males	Archery
0.471	0.006	(0.144, 0.798)	Canopy cover	Missouri Breaks	Females	Rifle
0.533	0.217	(-0.324, 1.39)	DTMR	Missouri Breaks	Females	Rifle
1.178	<0.001	(0.907, 1.448)	Terrain ruggedness	Missouri Breaks	Females	Rifle
0.503	0.062	(-0.029, 1.035)	Canopy cover	Missouri Breaks	Males	Rifle
-0.096	0.921	(-2.109, 1.917)	DTMR	Missouri Breaks	Males	Rifle
0.737	0.229	(-0.51, 1.983)	Terrain ruggedness	Missouri Breaks	Males	Rifle

Table 16. Legend providing color codes for statistically significant relationships between harvest risk and individual resource selection in Tables 14 and 15.

Color code, strength of evidence against null hypothesis
Very strong, p-value <0.001
Strong, p-value <0.01
Moderate, p-value <0.05
Weak, p-value <0.1

Security area thresholds

Archery season

Security and preferred security thresholds differed substantially between the study areas but were similar regardless of sex and season. Maps of security areas can be found in Figures 44-51. During archery season in the Custer Forest, female elk selected security and preferred security areas defined by canopy cover values ≥31.43 and ≥43.19%, ≥164.37 and ≥ 577.62 m from any motorized route, and ruggedness values ≥6.77 and ≥18.51 (Figure 44). Male elk in the Custer Forest had similar archery season security and preferred security thresholds at ≥21.23 and 31.31% canopy cover, ≥210.86 and 720.85 m from any motorized route, and ≥4.69 and ≥13.31 on the ruggedness index (Figure 46).

For the archery season in the Missouri Breaks, female elk selected security and preferred security areas with ≥3.66 and ≥6.28% canopy cover and values ≥15.50 and ≥24.69 on the terrain ruggedness index (Figure 48). Male elk in the Missouri Breaks selected security and preferred security thresholds ≥2.32 and ≥4.16% canopy cover, ≥303.79 and ≥939.31 m from any motorized route, and ≥13.34 and ≥22.75 on the terrain ruggedness index (Figure 50). The 95% confidence intervals for the estimated distance to motorized routes coefficient widely overlapped zero for females, suggesting this covariate was not strongly associated with selection during archery season.

Rifle season

During rifle season in the Custer Forest, female elk selected security and preferred security areas characterized by canopy cover values ≥28.60 and ≥39.46%, ≥515.12 and ≥891.37 m from any motorized route, and ruggedness values ≥7.00 and ≥19.21 (Figure 45). Male elk in the Custer Forest had comparable threshold values for security and preferred security areas at ≥27.67 and ≥36.62% canopy cover, ≥412.70 and ≥1010.59 m from any motorized route, and ≥7.33 and ≥18.44 on the ruggedness index (Figure 47).

In the Missouri Breaks during rifle season, female elk again selected security and preferred security areas with notably low canopy cover values at ≥2.09 and ≥3.91% and with ruggedness values ≥13.42 and ≥22.62 (Figure 49). Similarly, male elk in the Missouri Breaks selected security and preferred security areas with canopy cover ≥3.64 and ≥6.26% and values ≥14.17 and ≥23.68 on the ruggedness index (Figure 51). Similar to archery, the 95% confidence intervals for the estimated distance to motorized routes coefficient widely overlapped zero for both sexes, so we did not report threshold values for that covariate.

Table 17. Proportion of male and female elk locations occurring on USFS lands during shooting light during the hunting season in the Custer Forest study area, eastern Montana, 2021-2023. Animals who left the study area were censored. 'Deadweek' is included in the archery season.

Year	Sex	Season	PPN on USFS	# Animals
2021	Female	Preseason	0.47	38
2021	Female	Archery	0.41	38
2021	Female	Rifle	0.45	38
2021	Female	Postseason	0.45	38
2022	Female	Preseason	0.46	39
2022	Female	Archery	0.39	38
2022	Female	Rifle	0.38	36
2022	Female	Late Shoulder	0.49	37
2023	Female	Preseason	0.44	33
2023	Female	Archery	0.33	33
2023	Female	Rifle	0.25	32
2023	Female	Late Shoulder	0.32	31
2021	Male	Preseason	0.16	20
2021	Male	Archery	0.10	20
2021	Male	Rifle	0.26	18
2021	Male	Postseason	0.45	20
2022	Male	Preseason	0.29	9
2022	Male	Archery	0.31	9
2022	Male	Rifle	0.36	7
2022	Male	Late Shoulder	0.43	11
2023	Male	Preseason	0.05	5
2023	Male	Archery	0.09	5
2023	Male	Rifle	0.14	4
2023	Male	Late Shoulder	0	3

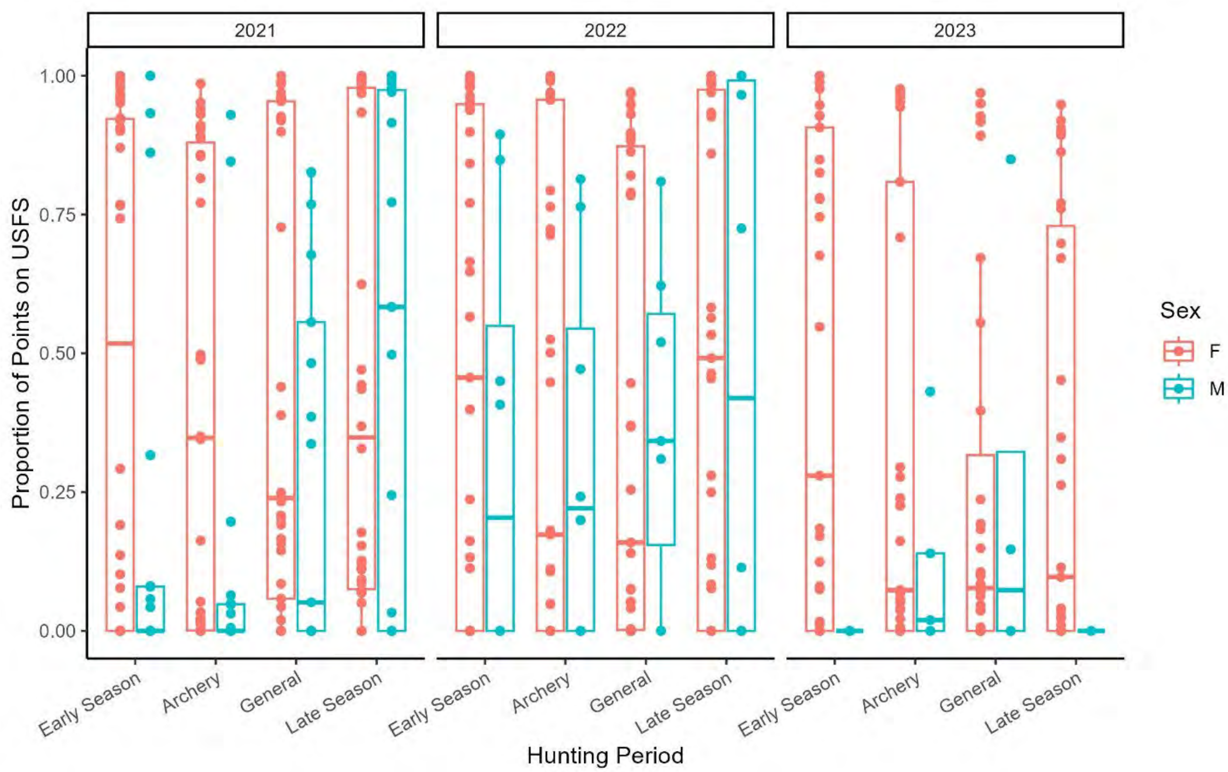

Figure 42. Proportion of each individual elk's locations occurring on USFS lands during shooting light during the hunting season in the Custer Forest study area, eastern Montana, 2021-2023. Animals who left the study area were censored. 'Deadweek' is included in the archery season. No hunting occurred in the Early Season during any year, and no hunting occurred during the Late Season in 2021. Note that circles representing individuals with the same value are plotted directly on top of one another.

Table 18. Proportion of male and female elk locations occurring on public lands during shooting light during the hunting season in the Missouri Breaks study area, 2022-2024. 'Deadweek' is included in the archery season.

Year	Sex	Season	PPN on Public	# Animals
2022	Female	Preseason	0.57	38
2022	Female	Archery	0.54	38
2022	Female	Rifle	0.61	38
2022	Female	Postseason	0.71	39
2023	Female	Preseason	0.60	37
2023	Female	Archery	0.57	36
2023	Female	Rifle	0.53	35
2023	Female	Postseason	0.62	41
2024	Female	Preseason	0.60	36
2024	Female	Archery	0.56	35
2024	Female	Rifle	0.57	34
2024	Female	Postseason	0.81	27

2022	Male	Preseason	0.43	17
2022	Male	Archery	0.43	17
2022	Male	Rifle	0.59	12
2022	Male	Postseason	0.75	18
2023	Male	Preseason	0.72	12
2023	Male	Archery	0.71	12
2023	Male	Rifle	0.75	8
2023	Male	Postseason	0.85	12
2024	Male	Preseason	0.78	10
2024	Male	Archery	0.56	10
2024	Male	Rifle	0.76	6
2024	Male	Postseason	0.96	6

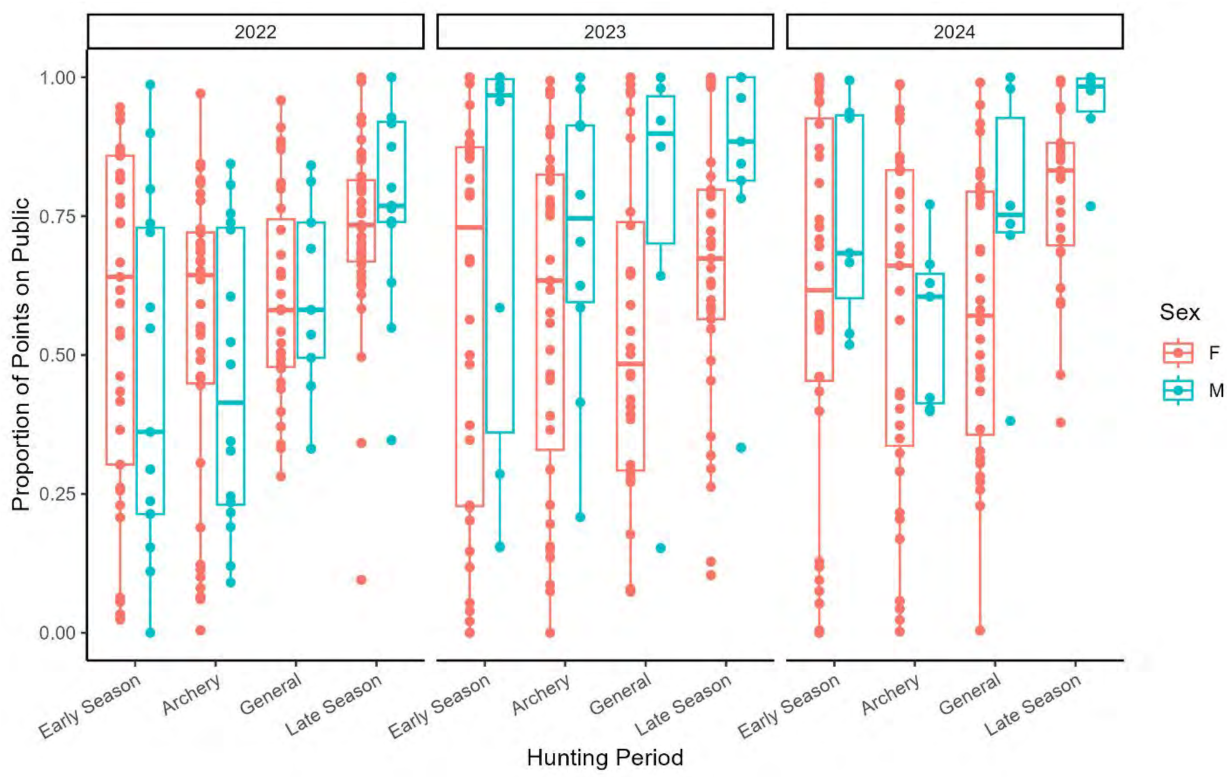

Figure 43. Proportion of each individual elk's locations occurring on public lands during shooting light during the hunting season in the Missouri Breaks study area, eastern Montana, 2022-2024. 'Deadweek' is included in the archery season. No hunting occurred in the Early Season or Late Season during any year. Note that circles representing individuals with the same value are plotted directly on top of one another.

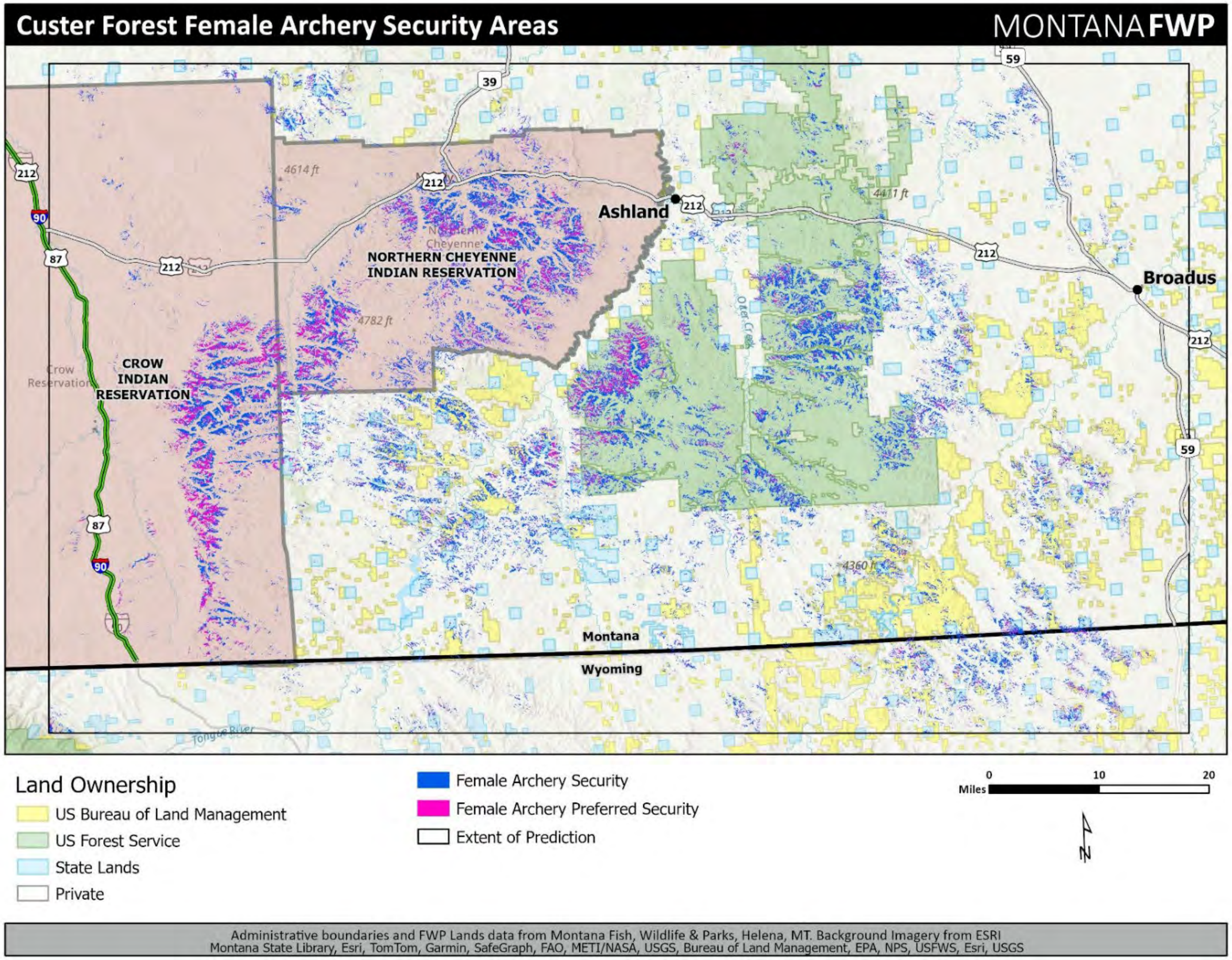

Figure 44. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for female elk during the archery season in the Custer Forest study area, eastern Montana, 2021-2023.

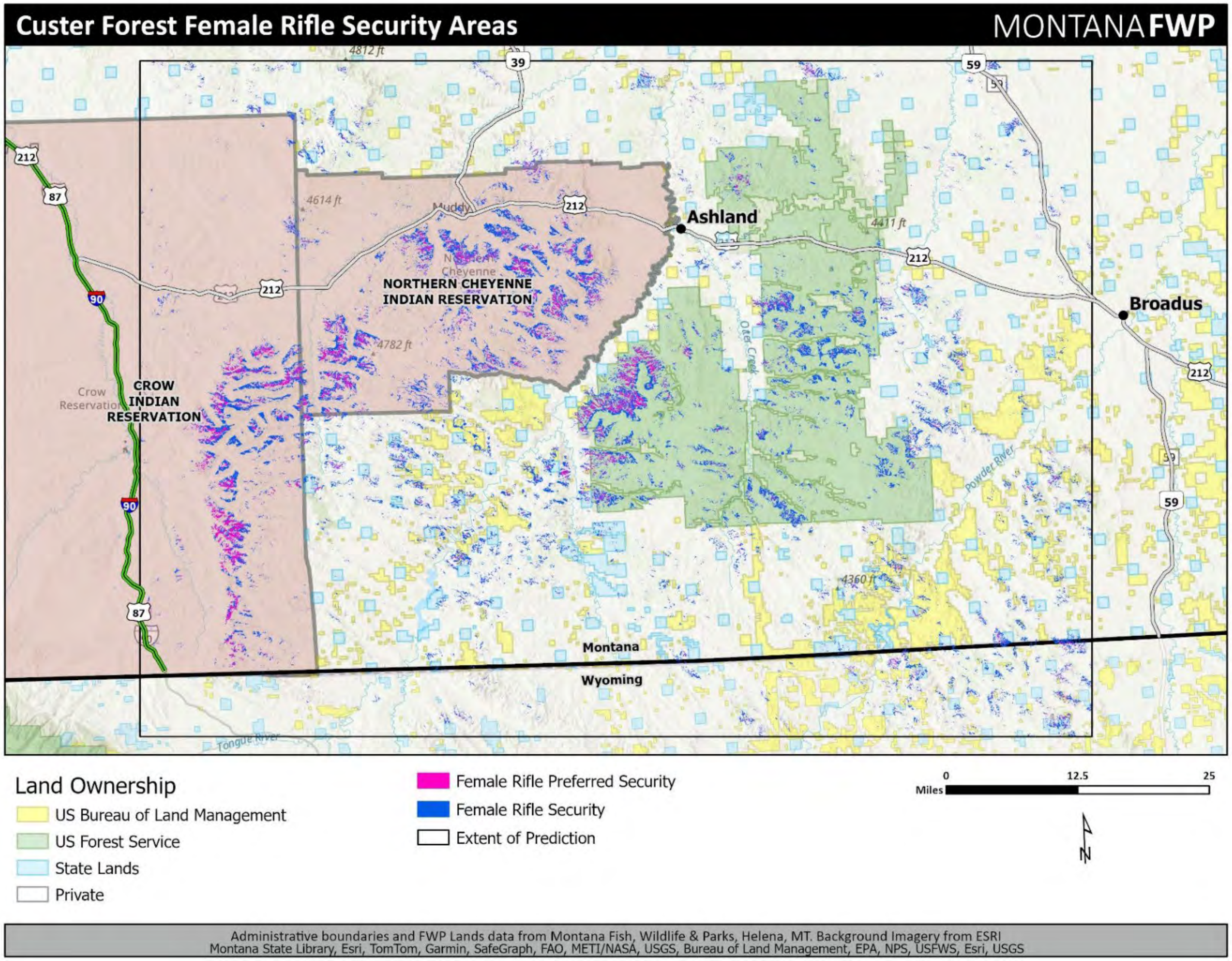

Figure 45. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for female elk during the rifle season in the Custer Forest study area, eastern Montana, 2021-2023.

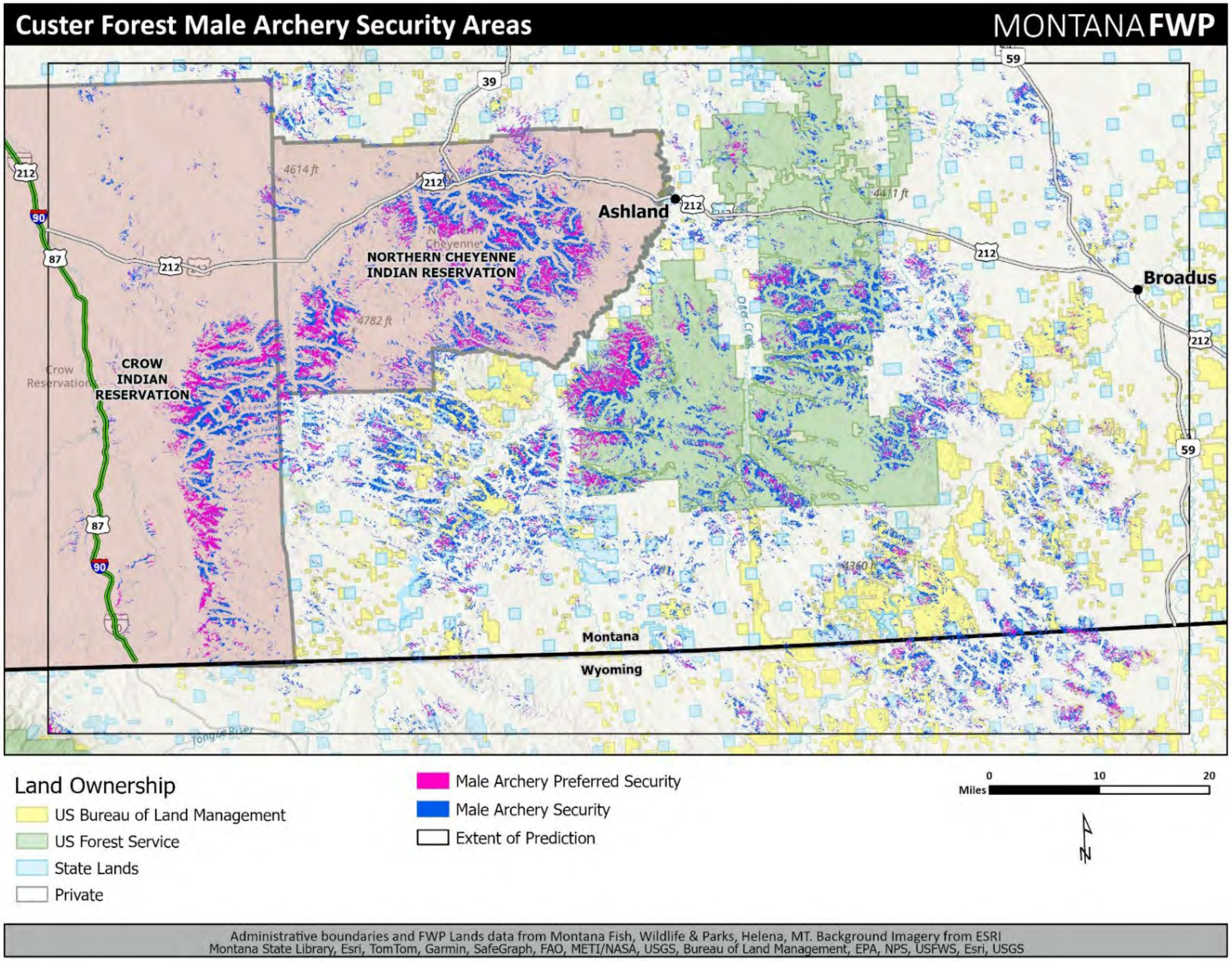

Figure 46. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for male elk during the archery season in the Custer Forest study area, eastern Montana, 2021-2023.

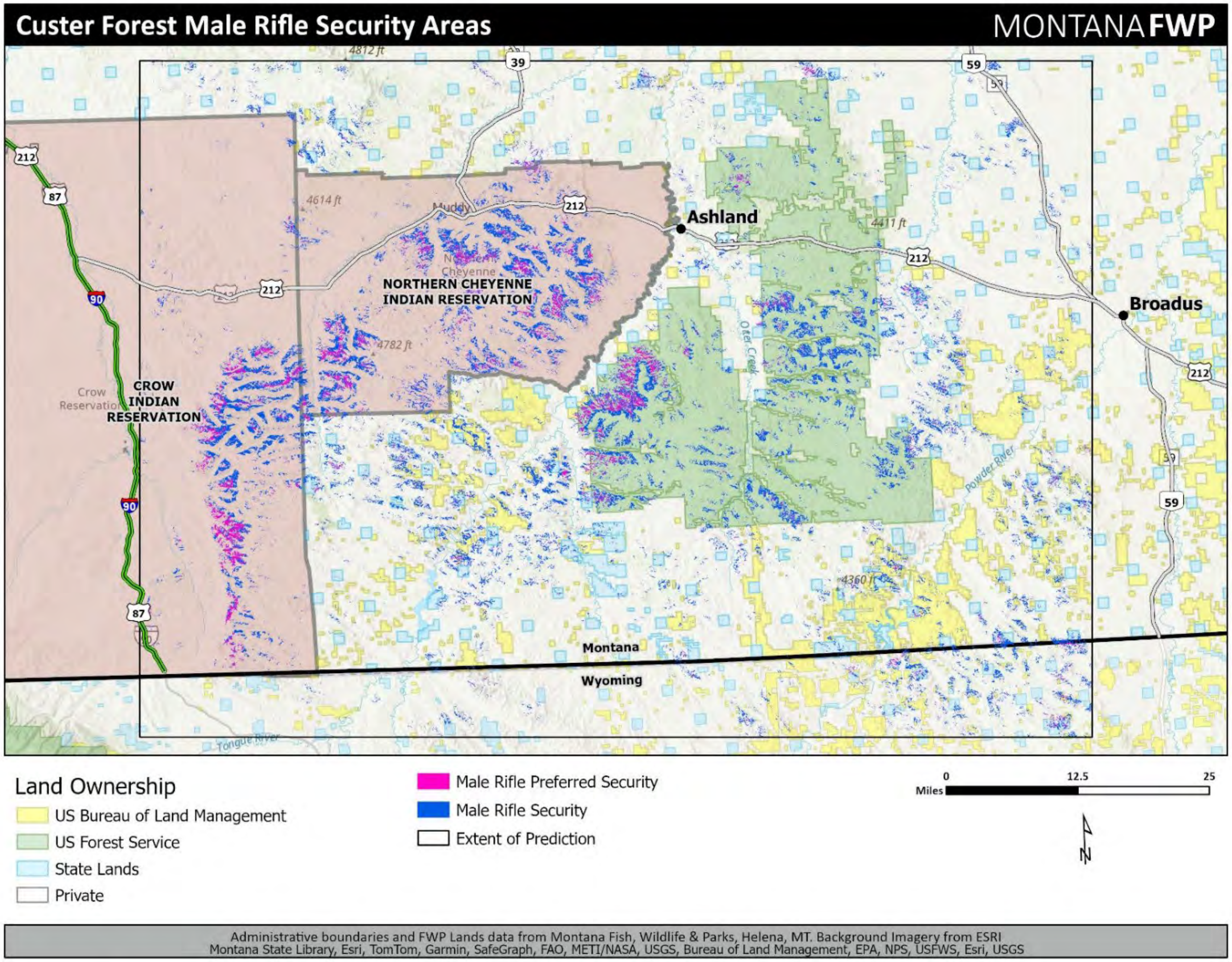

Figure 47. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for male elk during the rifle season in the Custer Forest study area, eastern Montana, 2021-2023.

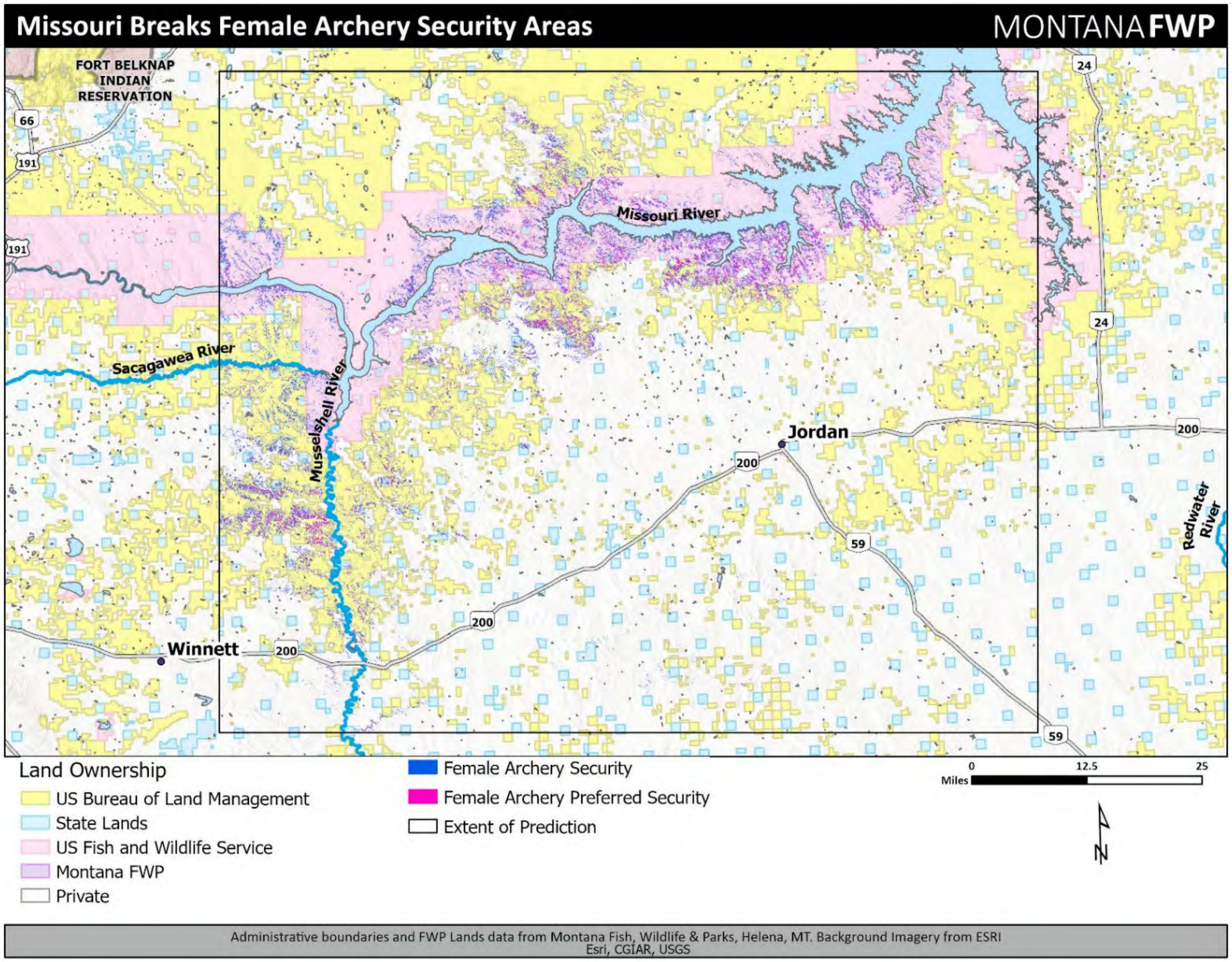

Figure 48. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for female elk during the archery season in the Missouri Breaks study area, eastern Montana, 2022-2024.

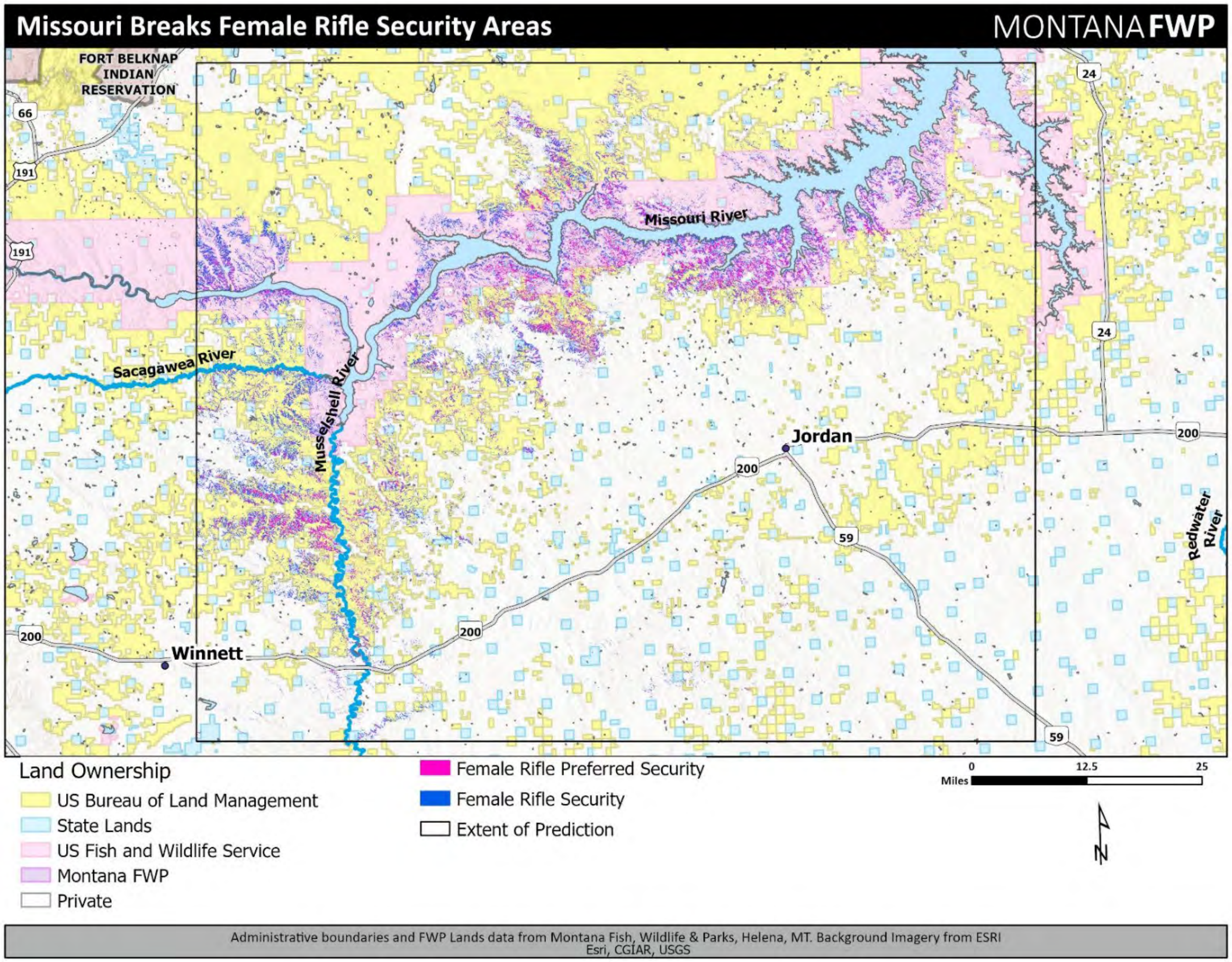

Figure 49. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for female elk during the rifle season in the Missouri Breaks study area, eastern Montana, 2022-2024.

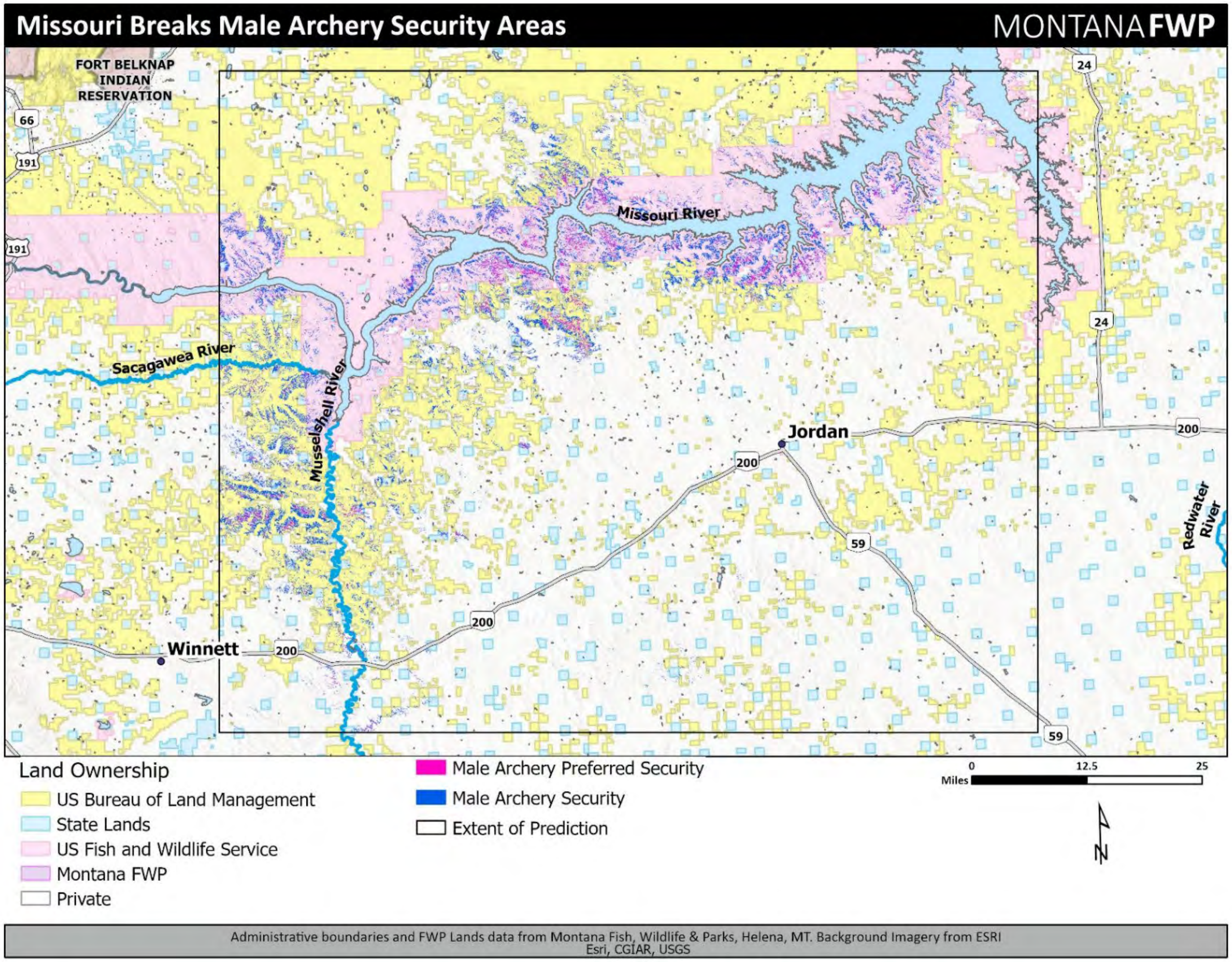

Figure 50. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for male elk during the archery season in the Missouri Breaks study area, eastern Montana, 2022-2024.

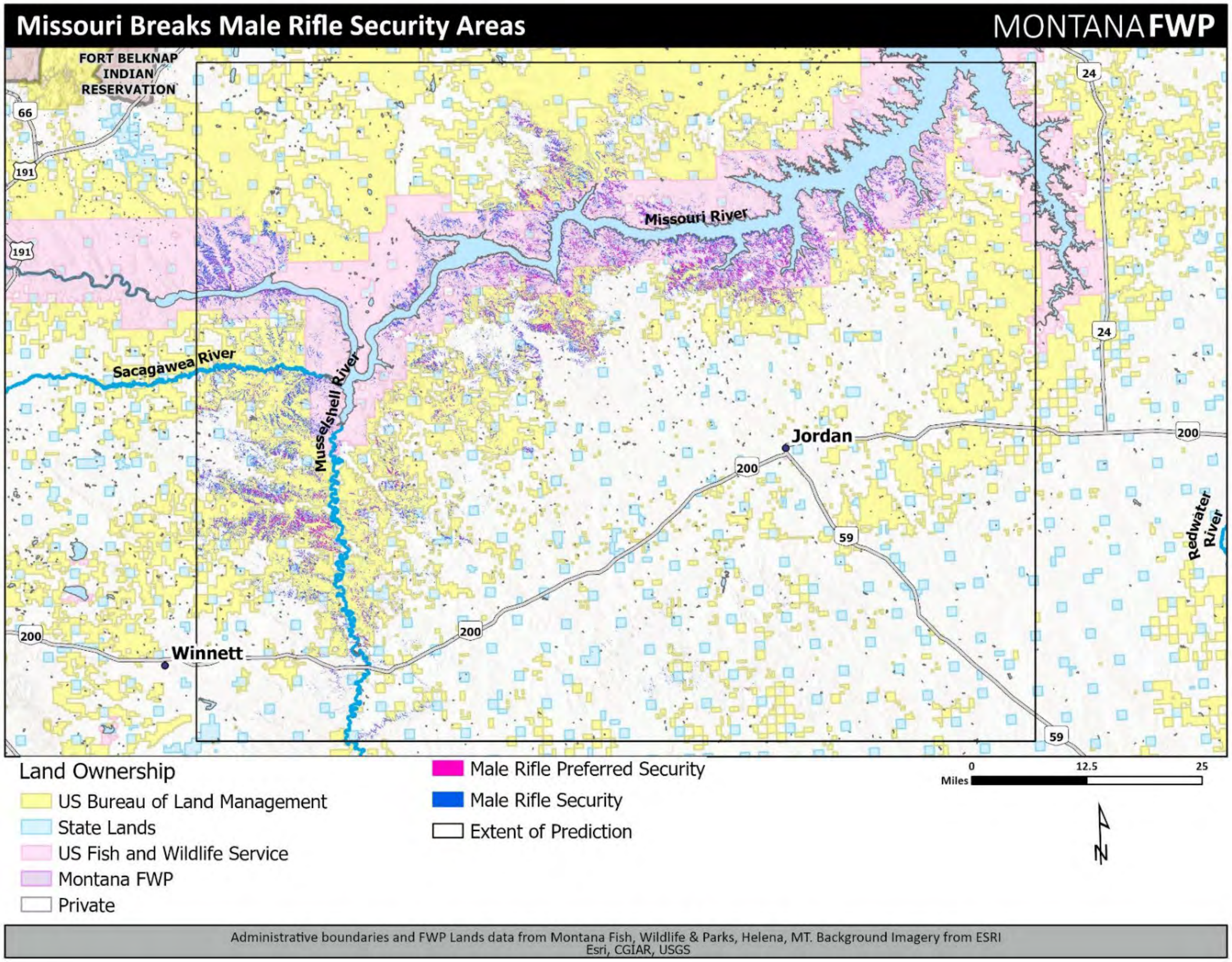

Figure 51. Map depicting security and preferred security areas, based on thresholds calculated from resource selection models, for male elk during the rifle season in the Missouri Breaks study area, eastern Montana, 2022-2024.

DISCUSSION

During archery and rifle season, elk in our prairie-breaks study areas typically selected for areas that restrict hunter access. Elk utilization of areas that limit hunter access is a common behavioral response to hunting pressure in Montana and throughout the western U.S. (Proffitt et al. 2013, Ranglack et al. 2017, Sergeyev et al. 2022) and has previously been documented in other parts of the Missouri Breaks (Proffitt et al. 2016). This behavioral pattern can present a challenge to wildlife managers aiming to provide sufficient opportunities to harvest elk on public lands, reduce landowner conflict stemming from elk use, and meet harvest objectives (Burcham et al. 1999, Haggerty and Travis 2006). In the Custer Forest study area, there is concern around problematic distributions, where elk congregate on private lands with limited hunting access, and our results suggest that elk use of restricted access lands intensifies during the rifle season. Currently, opportunities to harvest female elk are limited (via license quota) on the Custer National Forest and our results support continuing with this strategy to avoid further encouraging elk movement to private lands where they contribute to landowner conflicts and to maintain elk distributions in publicly accessible areas.

Elk responses to hunter access management in the Missouri Breaks were somewhat more nuanced. Female elk demonstrated preference for restricted access lands during both archery and rifle seasons, while male elk displayed a major shift in selection patterns – they preferred restricted access lands during archery season and switched to open access in rifle. The Missouri Breaks experience significantly higher hunting pressure during the archery season, with HD 700 offering 800 archery permits versus only 250 rifle permits. Observations indicate that much of the elevated archery pressure occurs on private lands as outfitted hunts and in Type 2 Block Management Areas, which may trigger elk movements from restricted to open access and prompt them to seek security habitat on the Charles M. Russell National Wildlife Refuge and surrounding BLM lands. Alternatively, this apparent shift could also be explained, in part, as elk movement toward wintering areas rather than as a response to hunting pressure.

Distance to motorized routes is typically an important factor for elk security and often a core consideration for managing elk habitat during the hunting season (Hillis et al. 1991, Unsworth et al. 1993, Lowrey et al. 2020). While Custer Forest elk exhibited expected responses to roads, we were largely unable to detect clear population-level responses to motorized routes in the Missouri Breaks. This area has relatively few public roads and most are primitive routes with dirt and gravel surfaces. Conditions on these primitive roads can change rapidly in wet weather, particularly during the rifle season as winter weather increases. Many roads can quickly become impassable and limit hunter access to more remote areas. Consequently, elk may not respond strongly to motorized routes if they are used infrequently by hunters. Given the remoteness of this area, another possibility is that our spatial data underlying the distance to motorized route covariate did not accurately depict existing roads, which would also make it difficult to detect consistent elk responses. Although we only captured a clear population-level response to roads for males during the archery season, our estimates of individual random coefficients provided evidence that individual elk had differing relationships with route distance. While most individuals demonstrated no selection for this covariate, a subset of male and female elk did show preference for increasing route distance. It's possible that elk respond to roads only in some parts of the Missouri Breaks, perhaps in areas where routes are reliably drivable or that experience higher hunter numbers.

Canopy cover played an outsized role in elk selection patterns across seasons, study areas, and sexes, which suggests it is a major factor for elk habitat and security in prairie-breaks environments. In our resource selection models, increasing canopy cover was consistently associated with the greatest increases in relative probability of use as compared to other covariates (Figures E2-E9). Though the effects of canopy cover on elk habitat use during hunting seasons and implications for security habitat definitions vary between studies, tree cover becomes more important in areas where it is less available (Christensen et al. 1993, Unsworth et al. 1993, Lowrey et al. 2020). Accordingly, even sparse or patchy canopy cover may be disproportionately important in providing security in our prairie regions. In the Missouri River Breaks, we estimated security and preferred security thresholds at quite low canopy cover values of just 2-6%. In the Custer Forest, these thresholds were more typical of forested systems at 21-43%. For comparison, other recent studies have recommended managing for canopy cover security thresholds at 23-60% for public lands in the Elkhorn Mountains, Montana (Lowrey et al. 2020) and ≥13% across southwest Montana (Ranglack et al. 2017). Given its role in our study areas, strategies to preserve existing canopy cover may be an important consideration for elk habitat management in prairies. For instance, large-scale severe or stand-replacing wildfires have the potential to eliminate secure patches of cover, and approaches to improve forest resilience to fire may hold value for preserving elk security in relatively open environments.

We also recommend managing for areas at least 412-1,011 m and 515-891 m from any motorized route for male and female elk, respectively, in the Custer Forest during the rifle season. These values are significantly lower than those reported by similar studies; Lowrey et al. (2020) stated that distances to motorized routes of 1,846-3,679 m characterized most elk use in the Elkhorn Mountains and Ranglack et al. (2017) recommended managing for areas ≥2,760 m from motorized routes. The difference may arise from our inclusion of both public and private motorized routes in our distance raster and from the fact that relatively high road densities exist on the Custer National Forest, such that greater distances aren’t common in the study area. Consequently, seasonal closures on the Custer National Forest would likely still provide elk security beyond the range of security thresholds presented here. In the absence of a strong elevational gradient in our eastern Montana study areas, identifying and protecting rifle season security areas in rugged terrain with values of at least 7-19 and 13-23 on the terrain ruggedness index (Riley et al. 1999) in the Custer Forest and Missouri Breaks, respectively, may further enhance elk security.

Individual elk varied significantly in their selection patterns, and corresponding with findings from other Montana elk populations (Proffitt et al. 2016, DeVoe et al. 2019), exhibited altered habitat relationships depending on harvest risk. Generally, individuals shared the same direction of selection for a given habitat feature but varied in the strength and magnitude of the relationship. Although some of the variability we observed may simply be the result of differences in local habitat availability, some also appears to be related to the level of harvest risk that individuals experienced, where elk with the strongest positive relationships with security habitat features were also exposed to the highest risk.

Interestingly, elk in the two study areas appear to rely most on different security features in their harvest risk responses. Across archery and rifle seasons and sexes, elk in the Custer Forest regularly responded to risk by increasing their selection strength with canopy cover, while in contrast, elk in the Missouri Breaks most often exhibited risk responses with terrain ruggedness (Tables 14 and 15). Therefore, relative to other factors, canopy cover and ruggedness seem to be key components of elk habitat during the hunting season and managers may want to specifically target these features when aiming to protect security habitat in the Custer Forest and Missouri Breaks, respectively. Additionally, for public lands that are characterized by elevated levels of hunting pressure, managers should consider employing more conservative versions of our security thresholds, which were calculated using models built with observations from elk experiencing a gradient of harvest risk. Maintaining or increasing security habitat on public lands may help offset the effects of higher hunter pressure, thereby increasing the amount of time elk spend on publicly accessible lands.

In this study, we identified key landscape and environmental factors affecting elk distributions during fall hunting seasons in prairie-breaks systems. We also provided recommendations for defining security areas in similar landscapes based on percent canopy cover, distance to motorized routes, and terrain ruggedness, which may be employed to help maintain or manipulate desirable elk distributions. As elk populations expand in Montana's eastern prairie regions and elk hunting in these areas continues to grow in popularity, this work will aid FWP and partners in making informed decisions regarding elk habitat and harvest management in the region.

Management Implications

Given the importance of canopy cover for elk security, it is vital that land managers continue to enhance forest health and resilience to wildfire. Past fires have significantly affected elk habitat in these prairie regions of eastern Montana. For example, in the Ashland Ranger District of the USFS, live, green timber cover declined from approximately 50% of the district to about 25% from the late 1990s to the late 2010s due to wildfire (Scott Studiner, USFS, personal communication). Similarly, a large-scale, severe fire (the Lodgepole Complex Fire, July 2017) eliminated large tracts of tree cover in the Missouri Breaks and substantially altered elk distributions in subsequent years. Accordingly, even small reductions in cover may negatively impact elk security in these districts, and reducing the risk of high severity wildfires would help managers maintain the existing cover that these elk populations currently use. Working with agency partners and private landowners on grazing system plans, invasive grass prevention and removal, and prescribed burns may be approaches managers could utilize to help minimize wildfire risk and severity. In these areas, federal agency partners, namely the BLM and USFWS in the Missouri Breaks and USFS in the Custer Forest, manage the majority of the elk security habitat, as well as grazing leases, on their respective lands. The Custer National Forest, in particular, conducts prescribed burns, forest thinning, and other efforts in order to minimize wildfire severity and increase tree survival in the event of a fire, and the BLM and DNRC also conduct similar efforts on their respective lands in the Custer Forest study area.

Road access is difficult for wildlife managers to influence in these areas. In the Missouri Breaks, the majority of road access is controlled by private landowners, and publicly accessible roads are variable in their drivability depending on weather conditions. Further, road closures on BLM and CMR lands are difficult to maintain and enforce due to work force reductions in those agencies and the inherent challenges of working in remote areas. However, wildlife managers may partner with agency land managers and like-minded private landowners to reduce road access to elk security areas during the hunting season when possible. Additionally, it has become increasingly popular to reach parts of the Missouri Breaks by boat from the shore of Fort Peck Reservoir, greatly increasing hunter access to elk security habitat on the CMR. Boat access on the reservoir may be difficult to control, but wildlife managers could consider possible regulations or restrictions if hunting pressure from the lake shore needs to be reduced. While multiple seasonal road closures are in effect on the Custer National Forest, many of these roads are still driven at varying levels of use. Efforts by FWP and USFS law enforcement have been undertaken to reduce this conflict. However, the relatively open landscapes make it difficult to effectively close roads to provide elk security. Managers may continue investing in solutions to enforce road closures to improve elk security areas and increase the amount of time elk spend on publicly accessible lands.

Male elk in the Missouri Breaks exhibited a notable shift from preferring restricted access lands in the archery season to open access lands in the rifle season. Anecdotal evidence suggests that there is relatively high hunter pressure during the archery season on restricted access areas, especially those with active outfitters, and many properties experience the majority of their hunting activity during the archery season. These properties also have exclusive access to private roads, an additional factor which may influence bull elk distributions. Thus, the change in elk preference between the access types is hypothesized to be driven by relatively high hunting pressure during the archery season that triggers elk movement from restricted access to more secure habitat on open access lands (i.e., more rugged terrain with higher canopy cover on the CMR and adjacent parcels). In this district, hunting pressure is largely determined by permit quotas, and wildlife managers should take these patterns into account when considering adjustments to either-sex quotas. Importantly, this area is considered a special management district for male elk with a stated goal to maintain equitable harvest between archery and rifle hunters (a goal that is currently being met), and quota adjustments may be useful to managers if changes to bull numbers or age class composition are desired. However, should quotas be adjusted in the future, managers will need to consider potential consequences for harvest success in both seasons. Modifications of archery quotas, in particular, could have indirect effects on rifle harvest success as the availability of bulls for hunter harvest will be determined by how, and to what extent, changes in hunting pressure alter bull distributions and the timing of elk movements between access types.

Harvest management in the Custer Forest study area has been relatively controlled for female elk on the highly accessible Custer National Forest, whereas cow license opportunity is liberal on private land and other public lands. These research results reveal that a segment of the elk population spends the majority of their time on the Custer National Forest, despite relatively strong hunter presence. Therefore, it may be prudent for FWP to continue to limit the amount of cow elk licenses valid on the Custer National Forest in order to avoid overharvesting that segment of the elk population.

ACKNOWLEDGEMENTS

Financial support for this project was provided by Federal Aid in Wildlife Restoration Grant W-179-R and Department of Interior Bureau of Land Management Cooperative Agreement #L20AC00497. Justin Gude at Montana FWP provided administration and implementation support for the project. We thank pilots Rick Swisher and Jonathan Larivee of Quicksilver Air Inc. for capture of study animals. We also thank contract pilots Monte Reeder and Rod Weeding for assisting in capture efforts with spotter planes. We thank Montana FWP staff Jesse DeVoe, Jenny Jones, Shane Petch, Cory Loecker, Alex Kunkel, Jay Kolbe, Brad Schmitz, and Brett Dorak for assisting with fieldwork, assisting with analyses, and providing valuable feedback throughout the project. We thank John Draper for assistance with analyses. We thank the Bureau of Land Managment, US Fish and Wildlife Service, US Forest Service, MT Department of Natural Resources and the many private landowners who allowed us access to their properties for this project. Title page photo credit: Cory Loecker.

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APPENDIX

Appendix A. Variable plots for each elk unit presented by administrative region

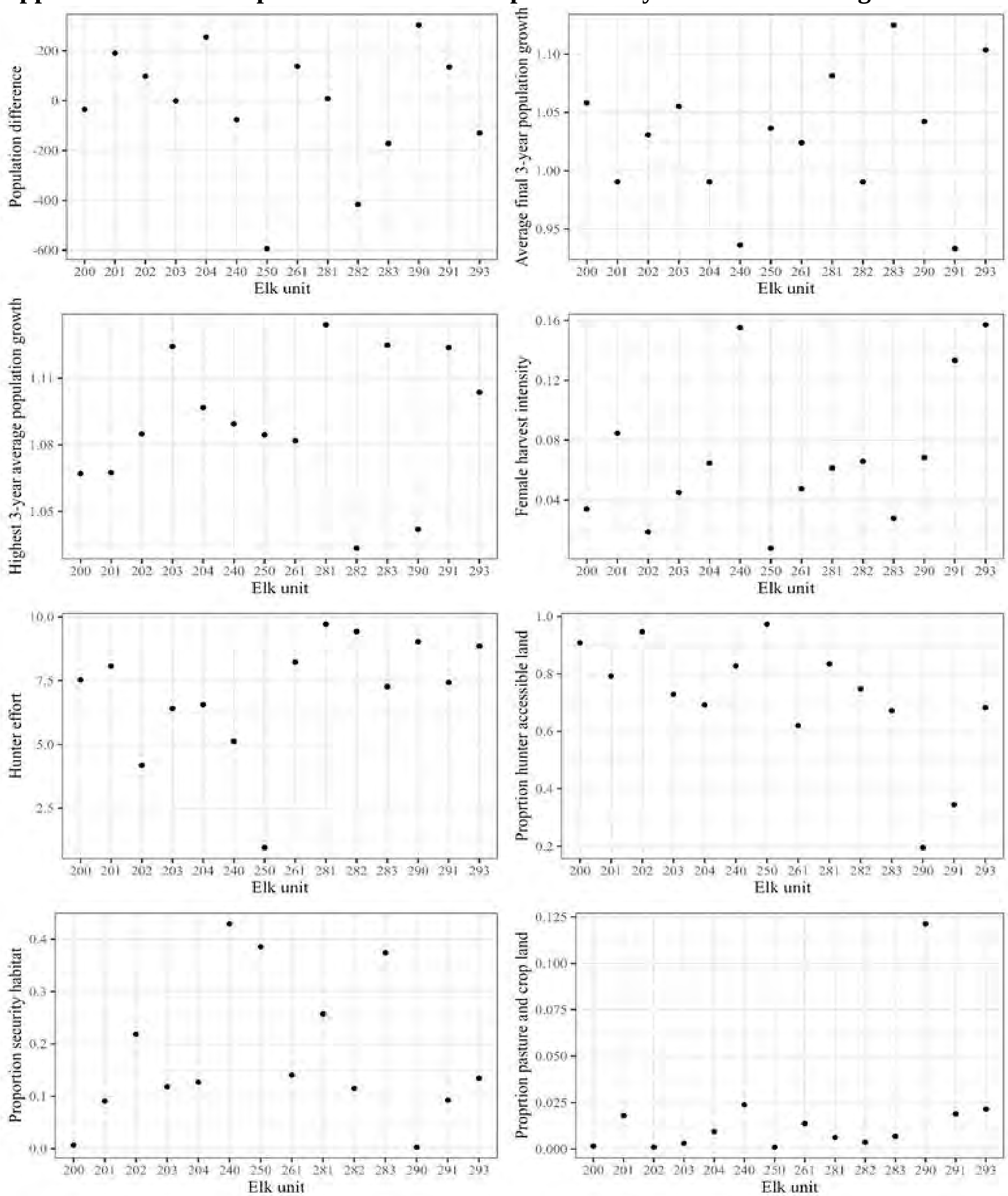

Figure A1. Values for variables used in regression modeling are presented for Region 2. Elk unit 210 includes hunting districts 210, 211, 212, and 216. Elk unit 282 includes hunting districts 282 and 285. Elk unit 290 includes hunting districts 290 and 298.

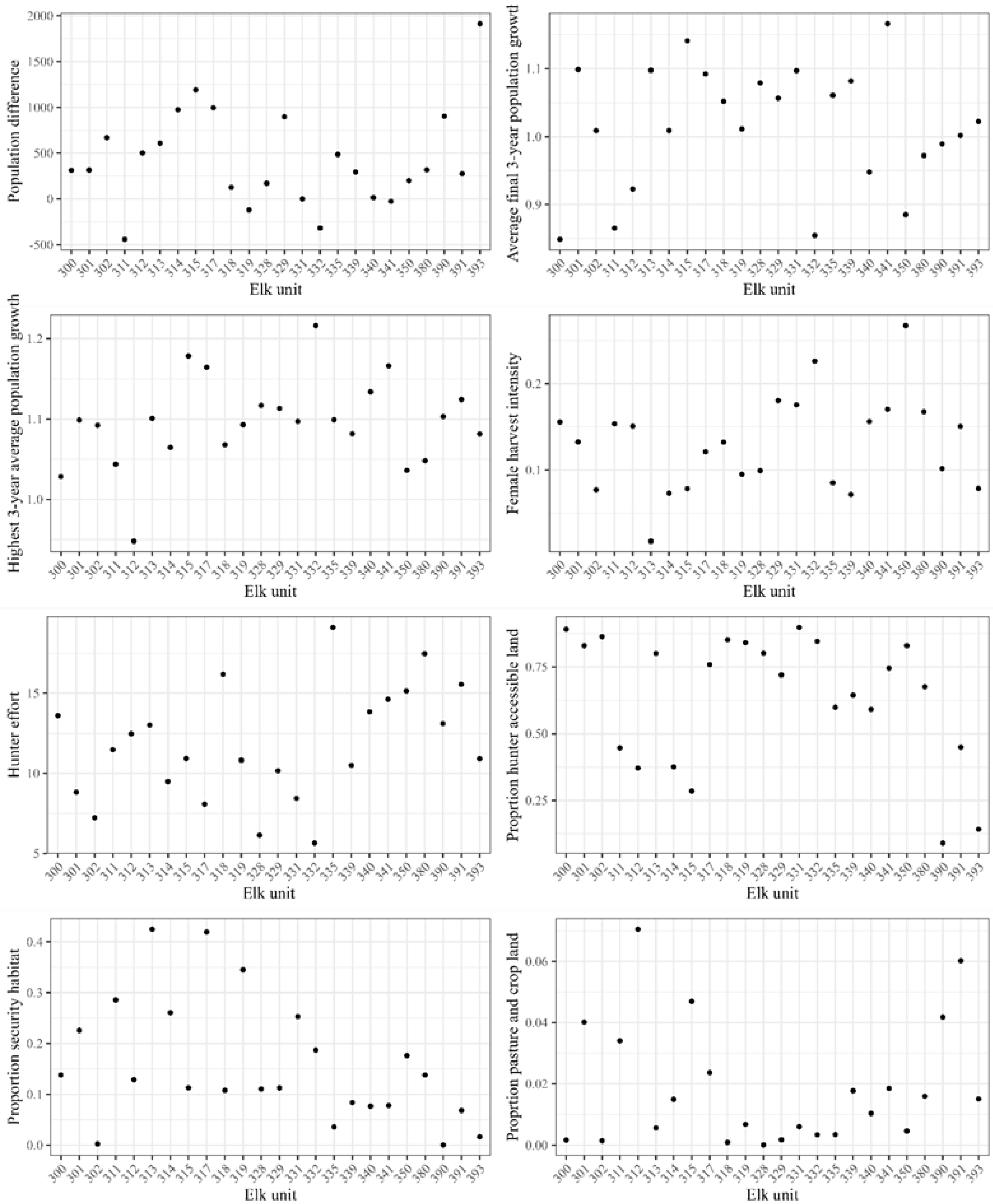

Figure A2. Values for variables used in regression modeling are presented for Region 3. Elk unit 301 includes hunting districts 301 and 309. Elk unit 320 includes hunting districts 320 and 333. Elk unit 322 includes hunting districts 322, 323, 324, 325, 326, 326, 327, and 330. Elk unit 339 includes hunting districts 339 and 343. Elk unit 350 includes hunting districts 350 and 370. Elk unit 360 includes hunting districts 360, 361, and 362.

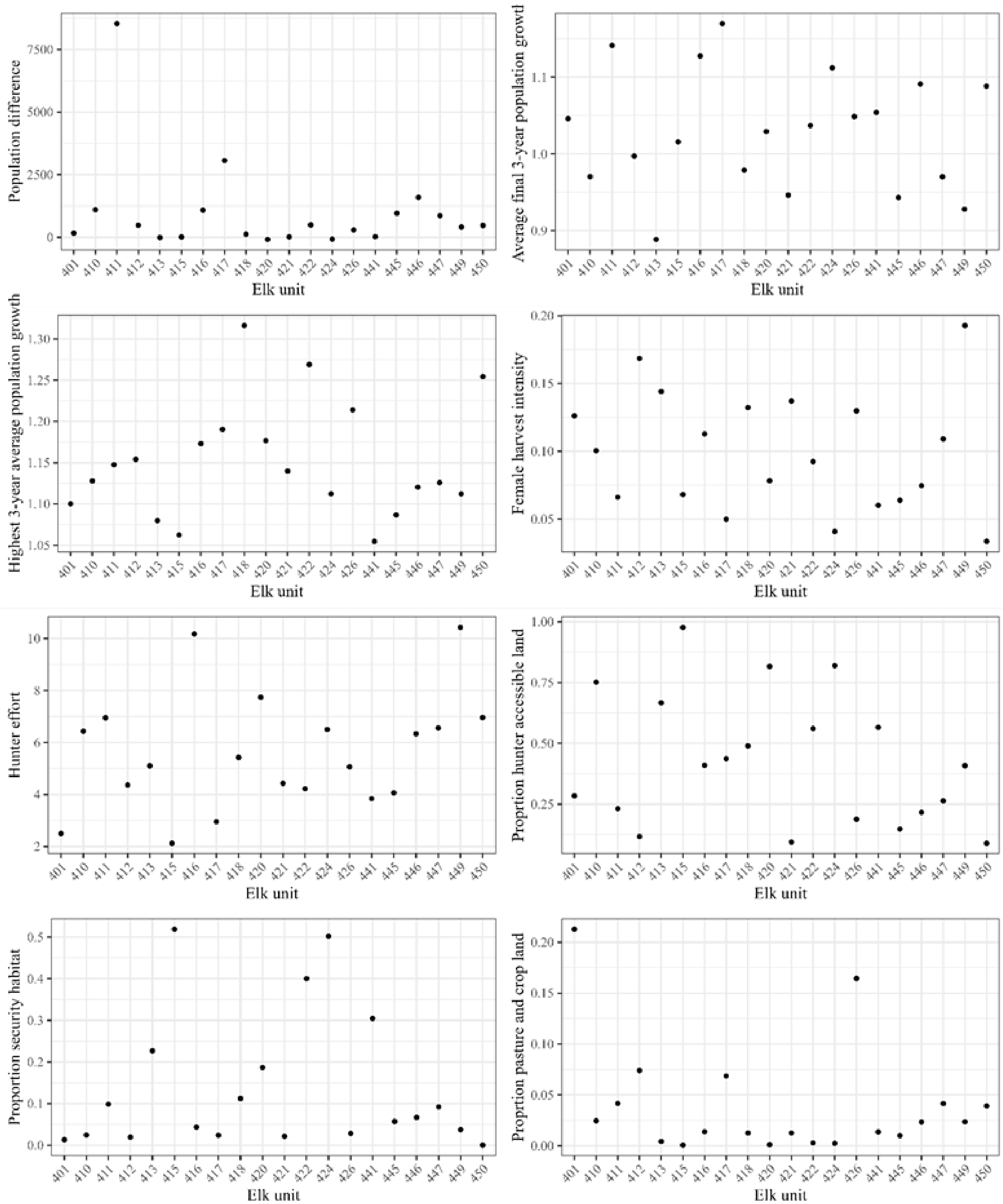

Figure A3. Values for variables used in regression modeling are presented for Region 4. Elk unit 411 includes hunting districts 411, 511, and 530. Elk unit 420 includes hunting districts 420 and 448. Elk unit 421 includes hunting districts 421 and 423. Elk unit 424 includes hunting districts 424, 425, and 442. Elk unit 445 includes hunting districts 445 and 455. Elk unit 449 includes hunting districts 449 and 452.

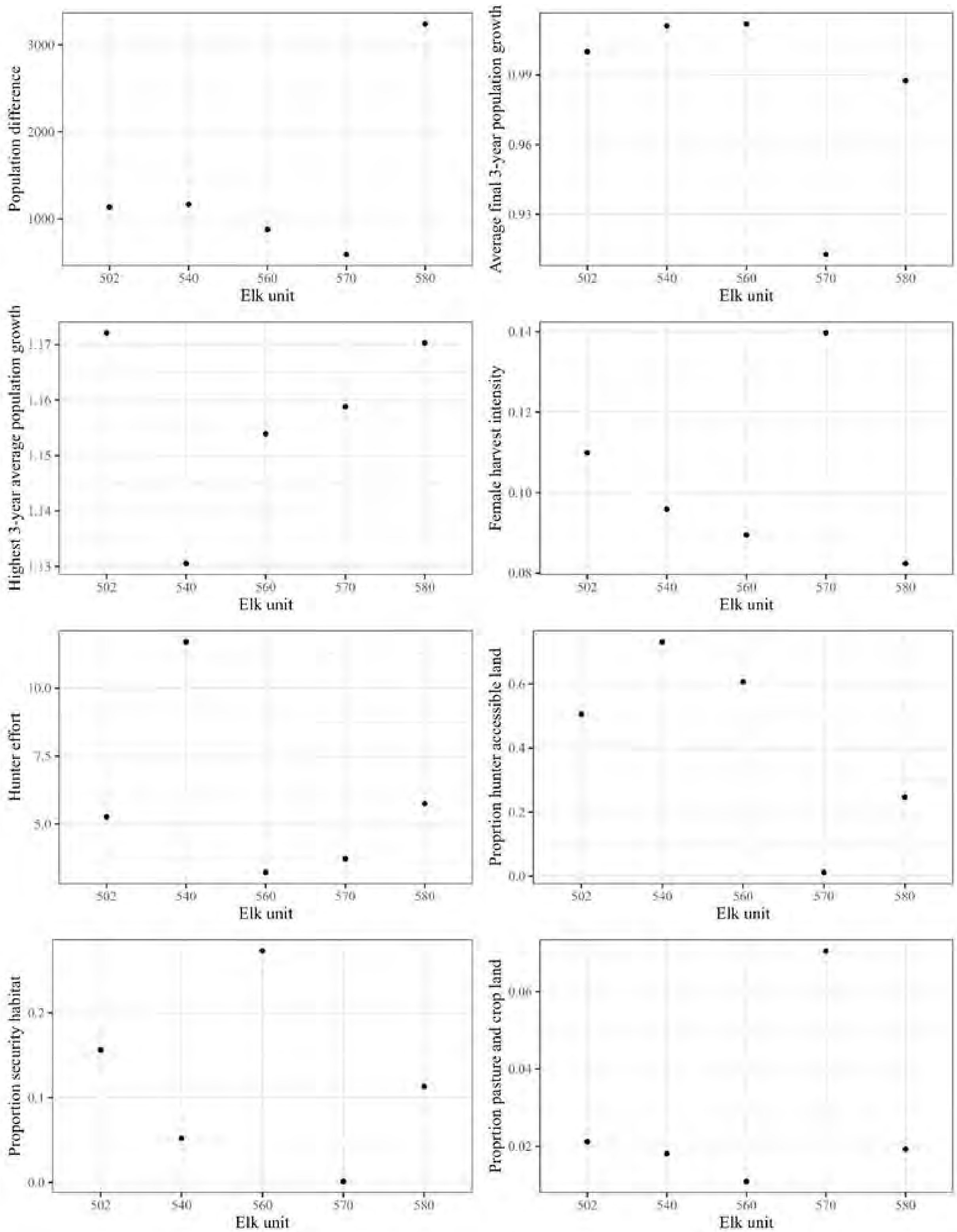

Figure A4. Values for variables used in regression modeling are presented for Region 5. Elk unit 502 includes hunting districts 502, 520, and 575.

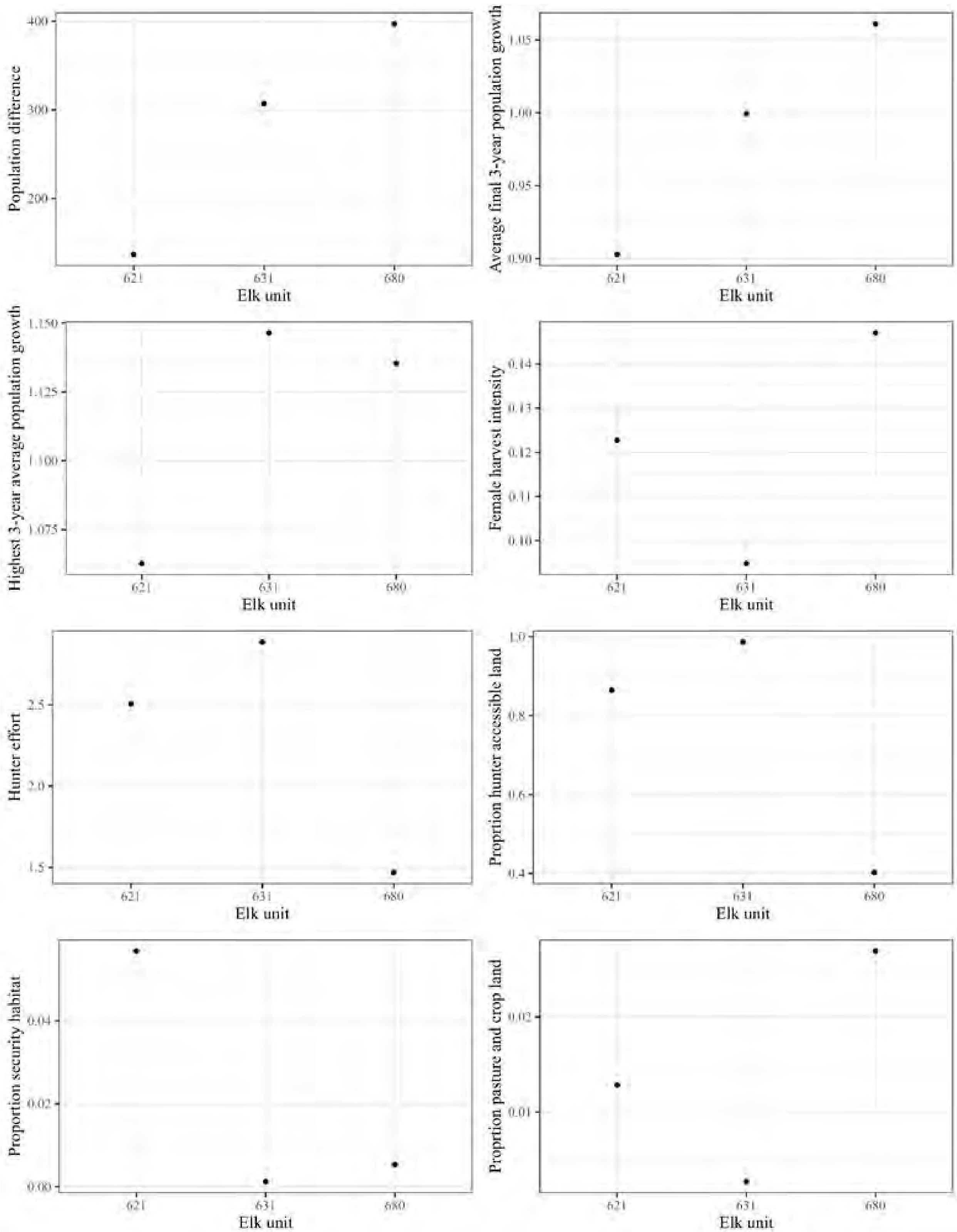

Figure A5. Values for variables used in regression modeling are presented for Region 6. Elk unit 621 includes hunting districts 621 and 622. Elk unit 631 includes hunting districts 631 and 632. Elk unit 680 includes hunting districts 680 and 690.

Appendix B. Detailed Devil's Kitchen habitat selection analysis model selection results

Table B1. Model selection results from the first step of model selection where linear and pseudothreshold (natural log) functional forms of continuous covariates were competed. Models explain female elk habitat selection during hunting season in the Devil's Kitchen study area in central Montana, USA.

Model	**AICc**	**ΔAICc**	**AICc Weight**
Terrain Ruggedness	592174	0	1
Terrain Ruggedness (log)	592922	748	0
Slope(log)	590740	0	1
Slope	592248	1508	0
SWE	592470	0	1
SWE (log)	592872	402	0

Table B2. Model selection results from the second step of model selection determining the most supported combination of landscape covariates explaining female elk habitat selection during hunting season in the Devil's Kitchen study area in central Montana, USA.

Aspect	Landcover	Ruggedness	Security	Slope	SWE	K	AICc	ΔAICc
0.128	+	-0.165	0.104	0.218	-0.077	10	586964.7	0
0.128	+	-0.164	NA	0.22	-0.077	9	587042.8	78.122
0.13	+	-0.163	0.105	0.219	NA	9	587386	421.376
0.13	+	-0.162	NA	0.221	NA	8	587465.2	500.534
0.108	NA	-0.159	-0.027	0.209	-0.08	7	587919.5	954.79
0.107	NA	-0.16	NA	0.206	-0.08	6	587925.7	961.04
NA	+	-0.177	0.105	0.2	-0.079	9	588131.8	1167.105
NA	+	-0.175	NA	0.202	-0.079	8	588210.1	1245.389
0.109	NA	-0.157	-0.032	0.21	NA	6	588380.4	1415.71
0.138	+	NA	0.087	0.195	-0.074	9	588388.1	1423.464
0.107	NA	-0.158	NA	0.207	NA	5	588389.8	1425.165
0.138	+	NA	NA	0.196	-0.074	8	588442.8	1478.083
NA	+	-0.175	0.105	0.202	NA	8	588582.5	1617.835
NA	+	-0.173	NA	0.204	NA	7	588661.5	1696.872
0.14	+	NA	0.088	0.197	NA	8	588776.1	1811.465
NA	NA	-0.167	0.023	0.201	-0.081	6	588809.3	1844.609
NA	NA	-0.167	NA	0.204	-0.081	5	588813.2	1848.569
0.14	+	NA	NA	0.198	NA	7	588831.4	1866.722
0.117	NA	NA	-0.054	0.182	-0.077	6	589261.4	2296.684
NA	NA	-0.165	0.018	0.202	NA	5	589285.5	2320.865
NA	NA	-0.165	NA	0.204	NA	4	589287.3	2322.635
0.113	NA	NA	NA	0.177	-0.077	5	589293.5	2328.805
0.117	NA	NA	-0.059	0.184	NA	5	589689	2724.372
0.114	NA	NA	NA	0.178	NA	4	589727.1	2762.382
NA	+	NA	0.087	0.174	-0.076	8	589758.6	2793.959
0.105	+	-0.129	0.135	NA	-0.08	9	589787.7	2823.042
NA	+	NA	NA	0.176	-0.076	7	589813	2848.374
0.105	+	-0.126	NA	NA	-0.08	8	589920.7	2956.031
NA	+	NA	0.087	0.176	NA	7	590173.4	3208.691
NA	+	NA	NA	0.178	NA	6	590228.1	3263.455
0.107	+	-0.126	0.136	NA	NA	8	590255.6	3290.969
NA	NA	NA	NA	0.172	-0.078	4	590298.4	3333.758
NA	NA	NA	-0.003	0.173	-0.078	5	590300.3	3335.661
0.106	+	-0.124	NA	NA	NA	7	590391	3426.338
NA	+	-0.14	0.134	NA	-0.082	8	590591.5	3626.866
0.115	+	NA	0.117	NA	-0.078	8	590718.7	3753.979
NA	+	-0.137	NA	NA	-0.082	7	590722.2	3757.534

NA	NA	NA	NA	0.173	NA	3	590739.7	3774.982
NA	NA	NA	-0.007	0.174	NA	4	590741	3776.356
0.097	NA	-0.115	0.095	NA	-0.082	6	590747.5	3782.793
0.115	+	NA	NA	NA	-0.078	7	590819.3	3854.609
0.103	NA	-0.108	NA	NA	-0.081	5	590853.9	3889.213
NA	+	-0.137	0.135	NA	NA	7	591081.9	4117.244
0.116	+	NA	0.119	NA	NA	7	591154.3	4189.664
NA	+	-0.135	NA	NA	NA	6	591214.6	4249.923
0.098	NA	-0.112	0.091	NA	NA	5	591239.2	4274.512
0.116	+	NA	NA	NA	NA	6	591256.9	4292.277
0.103	NA	-0.106	NA	NA	NA	4	591336.1	4371.472
NA	NA	-0.123	0.135	NA	-0.083	5	591462.3	4497.666
0.104	NA	NA	0.06	NA	-0.08	5	591513.7	4549.048
0.108	NA	NA	NA	NA	-0.079	4	591556.1	4591.435
NA	NA	-0.115	NA	NA	-0.082	4	591681.3	4716.651
NA	+	NA	0.115	NA	-0.079	7	591691.2	4726.528
NA	+	NA	NA	NA	-0.079	6	591787.9	4823.268
NA	NA	-0.121	0.131	NA	NA	4	591968.2	5003.498
0.105	NA	NA	0.057	NA	NA	4	591977.2	5012.507
0.108	NA	NA	NA	NA	NA	3	592014.4	5049.688
NA	+	NA	0.116	NA	NA	6	592146.7	5182.059
NA	NA	-0.113	NA	NA	NA	3	592174	5209.305
NA	+	NA	NA	NA	NA	5	592245	5280.36
NA	NA	NA	0.1	NA	-0.081	4	592347.2	5382.484
NA	NA	NA	NA	NA	-0.08	3	592469.6	5504.895
NA	NA	NA	0.096	NA	NA	3	592822.2	5857.575
NA	NA	NA	NA	NA	NA	2	592936	5971.298

Appendix C. Hunter harvest estimates from Devil's Kitchen hunting districts of interest

Table C1. Mean hunter harvest estimates across license years 2020-2022 in the three focal hunting districts (HDs) in the Devil's Kitchen study area. Harvest estimates were gathered during MTFWP's annual hunter harvest survey where a random sample of licensed hunters are called and asked about their effort and success while hunting.

	Early Shoulder		**Archery**		**General**		**Late Shoulder**	
HD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
445	15.2	10.2	36.3	11.8	209.3	22.9	41.6	7.9
446	3.0	3.3	55.6	20.9	261.7	42.4	40.2	3.4
455	0	0	10.2	2.5	114.8	26.7	0	0

Appendix D. Custer Forest and Missouri Breaks background and covariate development

Below are descriptions of covariate data sources, development steps and additional details.

Hunter access – This covariate distinguishes between lands accessible (open) to public hunters and lands that restricted access to public hunters, which may reflect differences in the intensity of hunting pressure. We considered publicly owned lands reachable via a public access point (e.g. public road) and private lands enrolled in the State of Montana's Block Management Program as a Type 1 Block Management Area (BMA), which do not require a reservation to hunt, to be open access. Conversely, restricted lands include privately-owned lands and public lands that lacked a known public access point. We also considered Type 2 Block Management Areas restricted access as these lands require a reservation to hunt, thereby limiting the number of hunters. We used a Montana Public Lands layer (Montana State Library) and the Protected Areas Database of the United States (U.S. Geological Survey 2022) to identify public lands in Montana and Wyoming, respectively. Montana Fish, Wildlife and Parks data was used to define Type 1 BMAs as well as areas within BMAs that prohibited hunting. We used our integrated motorized route layer, described below, to identify access points on public land, though we only included routes known to be open for public use in this step. We developed this covariate as binary open/restricted access at 30 m resolution.

Canopy cover – We used the Rangeland Analysis Platform (https://rangelands.app/) vegetation cover product (version 3.0, 30 m resolution) for annual percent tree cover for 2022 to represent canopy cover (Allred et al. 2021). Annual cover estimates are predictions produced by using a convolutional neural network model, the historical Landsat satellite record and 74,966 field plots collected by the BLM, NRCS, and NPS.

Distance to motorized route – We developed and tested two versions of the distance to motorized route covariate in this analysis, one including all roads and motorized routes regardless of public accessibility and a second including only routes known to be open to public use. To develop our underlying all motorized routes layer, we integrated data from several sources. The TIGER system for all roads (U.S. Census Bureau 2018) was used to define the majority of routes, including highways, county roads, two-tracks and four-wheel drive trails. We identified additional routes using U.S. Fish and Wildlife Service data for the Charles M. Russell National Wildlife Refuge and a local Bureau of Land Management layer. We also used a U.S. Forest Service Motor Vehicle Use layer to define additional roads and trails on the Custer National Forest, and to identify seasonally and permanently closed routes on Forest Service lands and remove them from the final dataset. In occasional cases where a route was disconnected from any other, we selected the clearest and most direct connecting route on aerial imagery and manually digitized it in ArcGIS Pro 3.2.2. Because of motorized boat access, we also included the shoreline of Fort Peck Lake (U.S. Geological Survey 2023a) as a road. To create a second layer with routes open to the public only, we removed all features identified as private routes or where public access was unknown. Finally, we created distance to route (m) rasters for each at a 30 m resolution in Program R using the terra package (Hijmans 2024).

Terrain ruggedness – We used the FedData package (Bocinsky 2023) in Program R to obtain a 30 m resolution digital elevation model (U.S. Geological Survey 2023b). We then used the terra package (Hijmans 2024) to estimate a terrain ruggedness index at 30 m resolution, calculated as the amount of elevation difference between a given pixel of the digital elevation model and its neighbors (Riley et al. 1999).

Snow water equivalent – To represent the effects of average snowpack conditions, we used the FedData package (Bocinsky 2023) in Program R to obtain 1 km resolution daily snow water equivalent data (Thornton et al. 2022). We then calculated average snow water equivalent (kg/m2) for each pixel across all days of the rifle season during 2019-2023 using the terra package (Hijmans 2024).

Herbaceous biomass – To represent average forage availability for elk during rifle season, we downloaded the Rangeland Analysis Platform (https://rangelands.app/) annual vegetation biomass product (version 3.0, 30 m resolution). Annual aboveground biomass estimates reflect only the new biomass accumulated in the current year and disregard biomass accumulated in past years. Aboveground net primary production was separated, and estimates were then calculated by converting carbon to biomass (Robinson et al. 2019, Jones et al. 2021). We calculated average aboveground herbaceous biomass (kg/ha) for each pixel across the years 2018-2022 using the terra package (Hijmans 2024).

Table D1. Covariates, functional forms and hypothesized direction of selection included in resource selection modeling for male and female elk in the Custer Forest and Missouri Breaks study areas, eastern Montana, USA, 2021-2024. The psuedothreshold form is achieved by applying a natural log transformation.

Covariate	**Functional form (hypothesis)**
Access	Categorical
Canopy cover	Linear (+), psuedothreshold (+)
Distance to motorized route All routes Public routes only	Linear (+), psuedothreshold (+)
Terrain ruggedness	Linear (+), psuedothreshold (+),
Snow water equivalent	Linear (-), psuedothreshold (-)
Herbaceous biomass	Linear (+), psuedothreshold (+)

Appendix E. Detailed Custer Forest and Missouri Breaks habitat selection results

Table E1. Proportions of used and available locations occurring on open access lands for male and female elk during rifle season in the Custer Forest (2021-2023) and the Missouri River Breaks (2022-2023, from an initial analysis (Krieger 2024) using the first two years of data only) study areas of central Montana.

Sex	**Proportion open access**	
	Available	**Used**
	Custer Forest	
Female	0.46	0.45
Male	0.45	0.38
	Missouri River Breaks	
Female	0.64	0.55
Male	0.65	0.68

Table E2. Mean, standard error, minimum and maximum values for all continuous covariates for male and female elk during rifle season in the Custer Forest study area, central Montana, 2021-2023.

	Used				**Available**			
Covariate	**Mean**	**Std. error**	**Min.**	**Max.**	**Mean**	**Std. error**	**Min.**	**Max.**
				Females				
Canopy cover (%)	22.82	0.18	0	97.52	10.28	0.07	0	100
Distance to any motorized route (m)	583.14	3.26	0	2710.65	441.96	1.62	0	2686.8
Distance to public motorized routes (m)	663.05	3.88	0	3632.35	517.75	2.04	0	3731.72
SWE (kg/m2)	2.66	0	0.82	7.6	2.77	0	0.81	7.6
Terrain ruggedness index	13.24	0.06	0.01	48.22	10.89	0.03	0	67.64
Herbaceous biomass (kg/ha)	904.05	2.98	12.82	2558.57	1060	1.49	1.39	2529.2
				Males				
Canopy cover (%)	28.01	0.34	0	81.63	10.17	0.1	0	100
Distance to any motorized route (m)	620.63	6.11	0	1958.98	440.86	2.3	0	2640.17
Distance to public motorized routes (m)	644.05	6.49	0	2305.32	514.71	2.86	0	3637.93

SWE (kg/m2)	2.82	0.01	0.88	4.39	2.78	0.01	0.81	7.6
Terrain ruggedness index	13.38	0.1	0.16	37.39	10.95	0.05	0.01	55.11
Herbaceous biomass (kg/ha)	867.67	5.89	51.83	2350.11	1065.4 3	2.13	2.87	2570.69

Table E3. Mean, standard error, minimum and maximum values for all continuous covariates for male and female elk during the rifle season in the Missouri Breaks study area, central Montana, 2022-2023 (from an initial analysis (Krieger 2024) including the first two years of data only).

	Used				**Available**			
Covariate	**Mean**	**Std. error**	**Min.**	**Max.**	**Mean**	**Std. error**	**Min.**	**Max.**
				Females				
Canopy cover (%)	6.55	0.1	0	52.91	3.36	0.03	0	63.9
Distance to any motorized route (m)	581.23	4.56	0	3349.4	566.72	2.36	0	3540
Distance to public motorized routes (m)	1147.48	11.41	0	5869.66	946.19	4.37	0	5931.51
SWE (kg/m2)	2.75	0.01	0.61	5.87	2.98	0	0.61	5.97
Terrain ruggedness index	13.26	0.08	0	48.1	12.16	0.04	0	75.85
Herbaceous biomass (kg/ha)	912.09	2.54	11.03	2401.62	858.44	1.2	0	2318.86
				Males				
Canopy cover (%)	10.58	0.23	0	72.18	3.36	0.05	0	60.16
Distance to any motorized route (m)	598.11	9.48	0	2821.44	563.42	3.95	0	3600.5
Distance to public motorized routes (m)	1253.07	27.14	0	5405.66	935.72	7.26	0	5824.95
SWE (kg/m2)	3.05	0.02	0.61	5.8	2.99	0.01	0.61	5.97
Terrain ruggedness index	14.96	0.2	0	42.75	12.24	0.07	0	68.69
Herbaceous biomass (kg/ha)	873.67	6.56	240.8 5	2364.93	858.95	2.03	0	2232.69

Table E4. Covariates and associated standardized coefficient estimates and 95% confidence intervals from the final resource selection model for female elk during archery season in the Custer Forest study area, central Montana, 2021-2023. Variance estimates represent the variance in random coefficients. The reference category for the access variable is open access.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.006	(-0.032, 0.044)	-
Canopy cover	Linear	0.944	(0.837, 1.050)	0.122
Distance to any motorized route	Psuedothreshold	0.442	(0.293, 0.592)	0.238
Terrain ruggedness	Psuedothreshold	0.342	(0.235, 0.449)	0.123
Herbaceous biomass	Psuedothreshold	0.467	(0.438, 0.496)	-

Table E5. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for male elk during archery season in the Custer Forest study area, central Montana, 2021-2023.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.983	(0.910, 1.056)	-
Canopy cover	Linear	0.896	(0.762, 1.031)	0.105
Distance to any motorized route	Psuedothreshold	0.651	(0.351, 0.950)	0.546
Terrain ruggedness	Psuedothreshold	0.226	(0.075, 0.377)	0.136
Herbaceous biomass	Psuedothreshold	0.501	(0.452, 0.550)	-

Table E6. Covariates and associated standardized coefficient estimates and 95% confidence intervals from the final resource selection model for female elk during archery season in the Missouri Breaks study area, central Montana, 2022-2024.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.318	(0.273, 0.363)	-
Canopy cover	Linear	0.908	(0.815, 1.001)	0.113
Distance to public motorized routes	Linear	-0.037	(-0.222, 0.148)	0.460
Terrain ruggedness	Linear	0.408	(0.209, 0.607)	0.538
Herbaceous biomass	Linear	0.517	(0.493, 0.541)	-

Table E7. Covariates and associated standardized coefficient estimates and 95% confidence intervals from the final resource selection model for male elk during archery season in the Missouri Breaks study area, central Montana, 2022-2024.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.380	(0.299, 0.460)	-
Canopy cover	Linear	0.840	(0.736, 0.944)	0.074
Distance to any motorized route	Psuedothreshold	0.928	(0.603, 1.254)	0.742
Terrain ruggedness	Linear	0.292	(-0.033, 0.616)	0.775
Herbaceous biomass	Linear	0.538	(0.497, 0.580)	-

Table E8. Covariates and associated standardized coefficient estimates and 95% confidence intervals from the final resource selection model for female elk during rifle season in the Custer Forest study area, central Montana, 2021-2023.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.424	(0.381, 0.468)	-
Canopy cover	Linear	0.976	(0.871, 1.081)	0.115
Distance to any motorized route	Linear	0.272	(0.181, 0.364)	0.090
SWE	Linear	-0.469	(-0.493, -0.445)	-
Terrain ruggedness	Psuedothreshold	0.341	(0.253, 0.429)	0.078
Herbaceous biomass	Psuedothreshold	0.483	(0.451, 0.516)	-

Table E9. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for male elk during rifle season in the Custer Forest study area, central Montana, 2021-2023.

Covariate	Functional form	Coefficient estimate	95% CI	Variance
Access	Binary	0.747	(0.662, 0.832)	-
Canopy cover	Linear	1.238	(1.05, 1.425)	0.180
SWE	Linear	-0.422	(-0.466, -0.377)	-
Distance to any motorized route	Psuedothreshold	1.465	(0.819, 2.11)	2.294
Terrain ruggedness	Psuedothreshold	0.427	(0.243, 0.612)	0.171
Herbaceous biomass	Psuedothreshold	0.603	(0.543, 0.663)	-

Table E10. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for female elk during rifle season in the Missouri Breaks study area, central Montana, 2022-2024.

Covariate	**Functional form**	**Coefficient estimate**	**95% CI**	**Variance**
Access	Binary	0.343	(0.296, 0.39)	-
Canopy cover	Linear	0.520	(0.434, 0.607)	0.089
Distance to public motorized routes	Linear	-0.030	(-0.235, 0.175)	0.520
SWE	Linear	-0.340	(-0.362, -0.318)	-
Terrain ruggedness	Linear	0.308	(0.201, 0.414)	0.135
Herbaceous biomass	Linear	0.449	(0.423, 0.475)	-

Table E11. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for male elk during rifle season in the Missouri Breaks study area, central Montana, 2022-2024.

Covariate	**Functional form**	**Coefficient estimate**	**95% CI**	**Variance**
Access	Binary	-0.180	(-0.288, -0.072)	-
Canopy cover	Linear	0.824	(0.697, 0.95)	0.07078
Distance to public motorized routes	Linear	0.065	(-0.337, 0.467)	0.77329
SWE	Linear	0.067	(0.02, 0.115)	-
Terrain ruggedness	Linear	0.319	(0.057, 0.581)	0.32206
Herbaceous biomass	Linear	0.412	(0.355, 0.469)	-

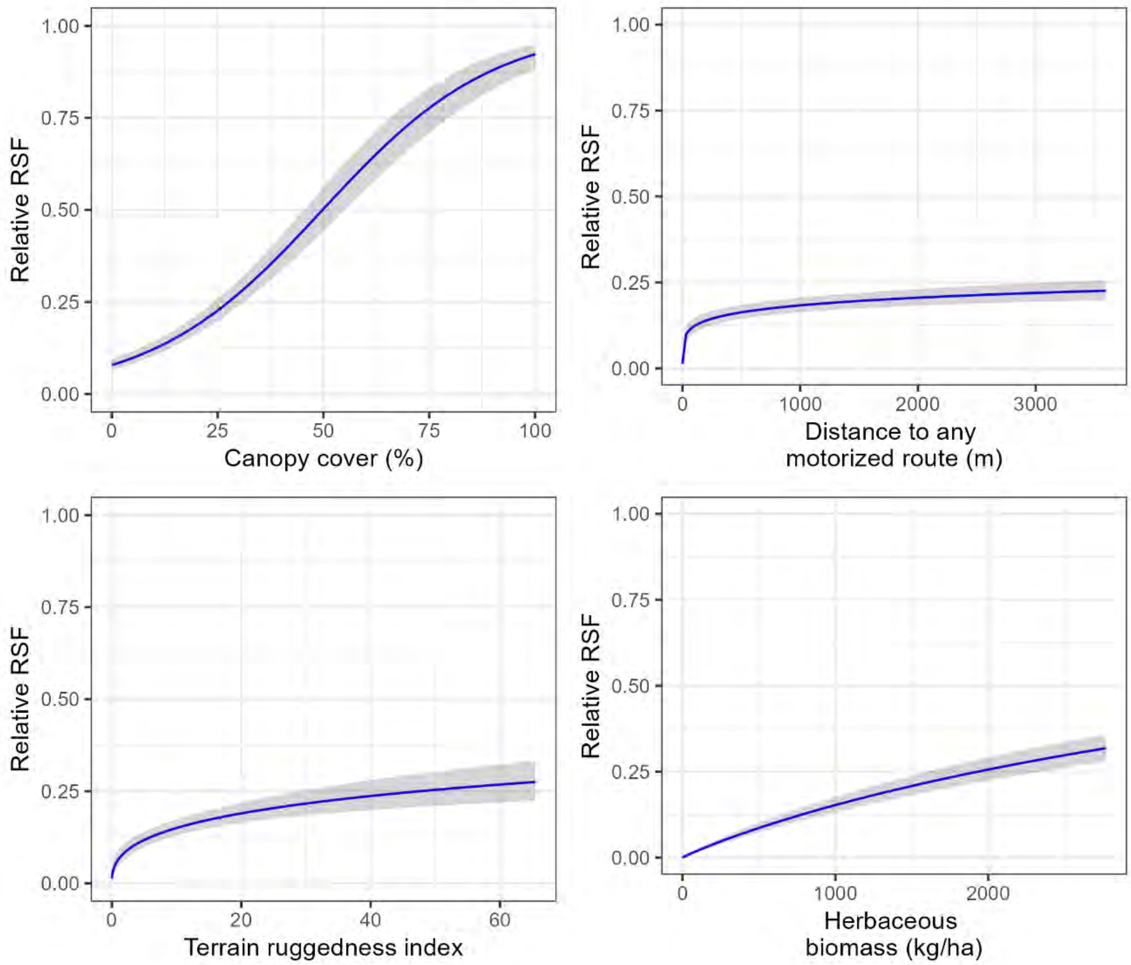

Figure E1. Predicted relative resource selection functions for female elk during the archery season in the Custer Forest study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

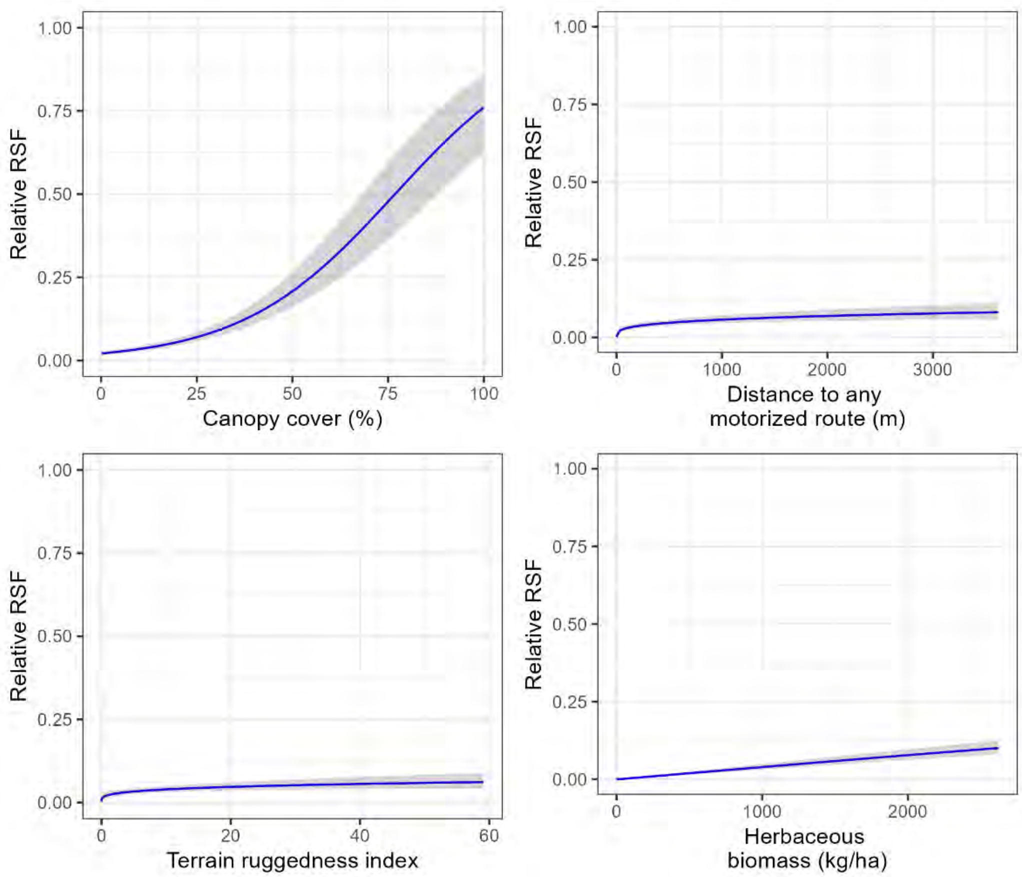

Figure E2. Predicted relative resource selection functions for male elk during the archery season in the Custer Forest study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

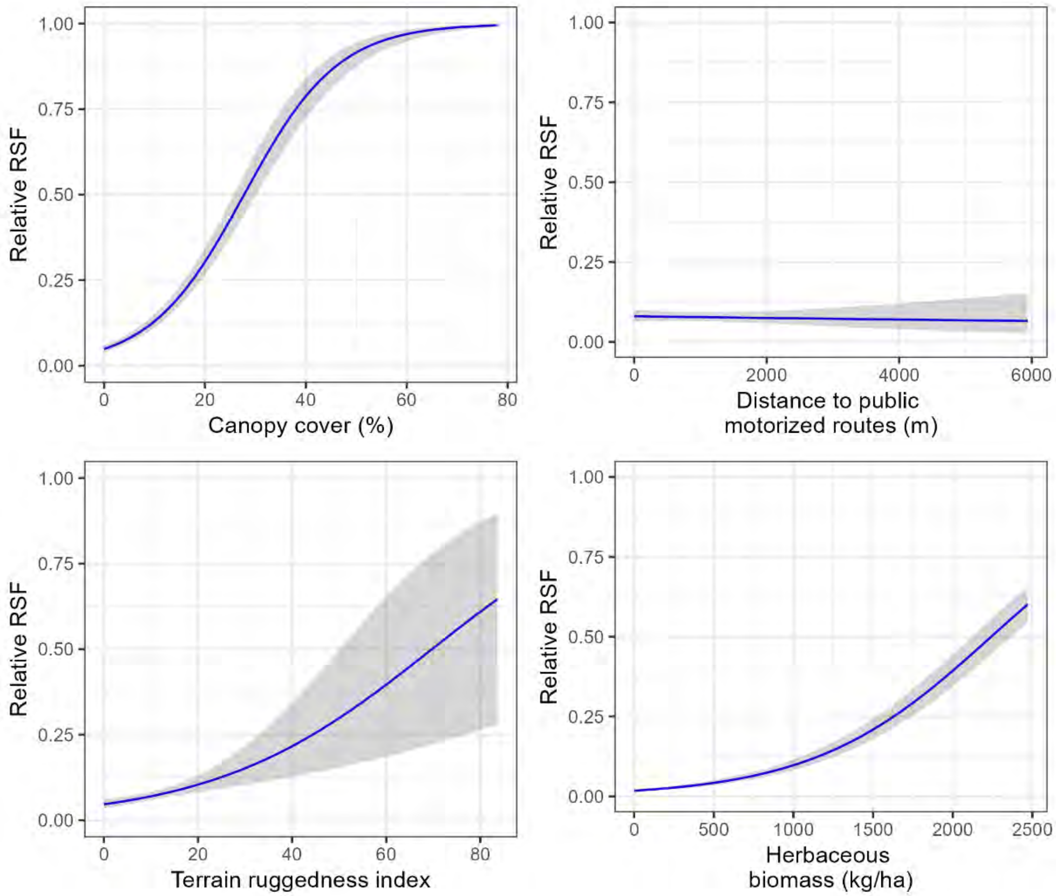

Figure E3. Predicted relative resource selection functions for female elk during the archery season in the Missouri Breaks study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

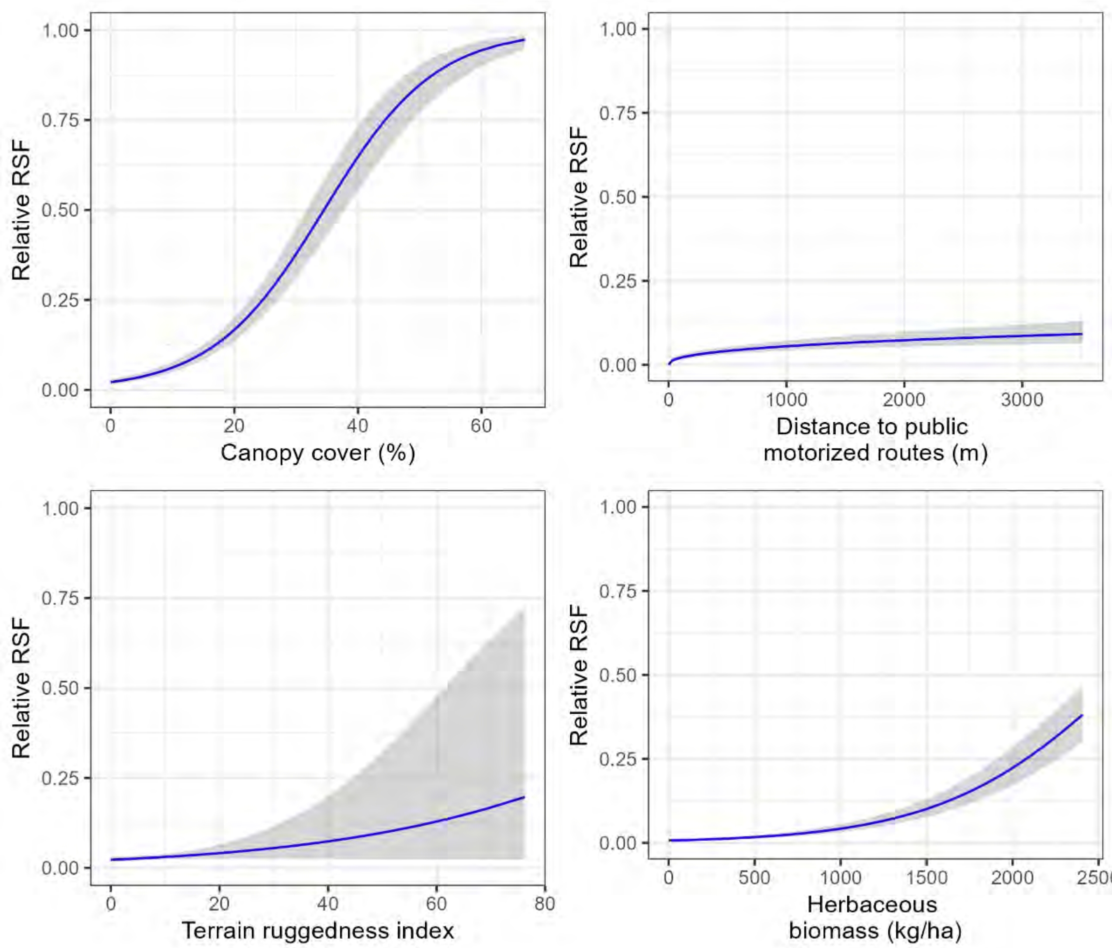

Figure E4. Predicted relative resource selection functions for male elk during the archery season in the Missouri Breaks study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

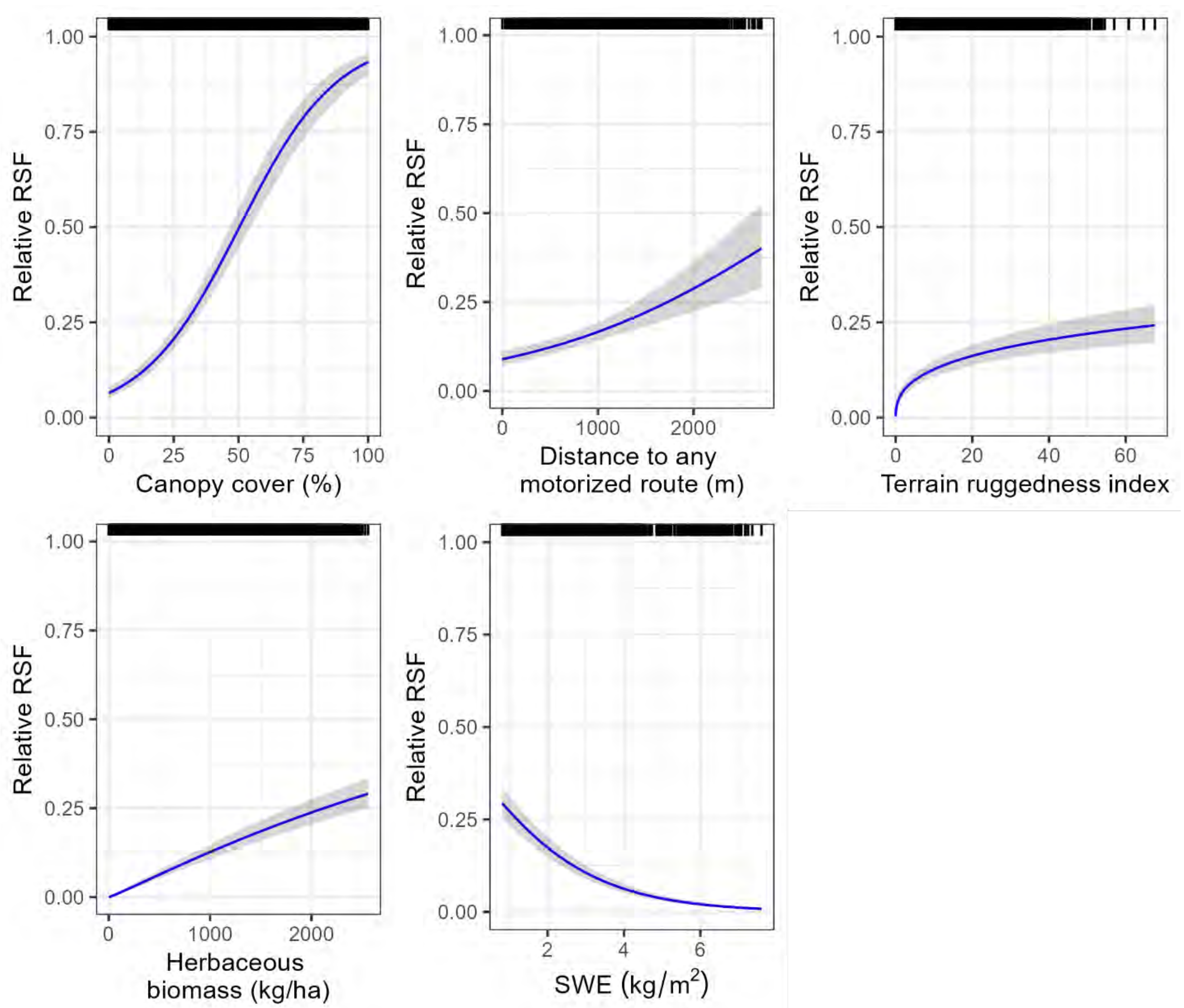

Figure E5. Predicted relative resource selection functions for female elk during the rifle season in the Custer Forest study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

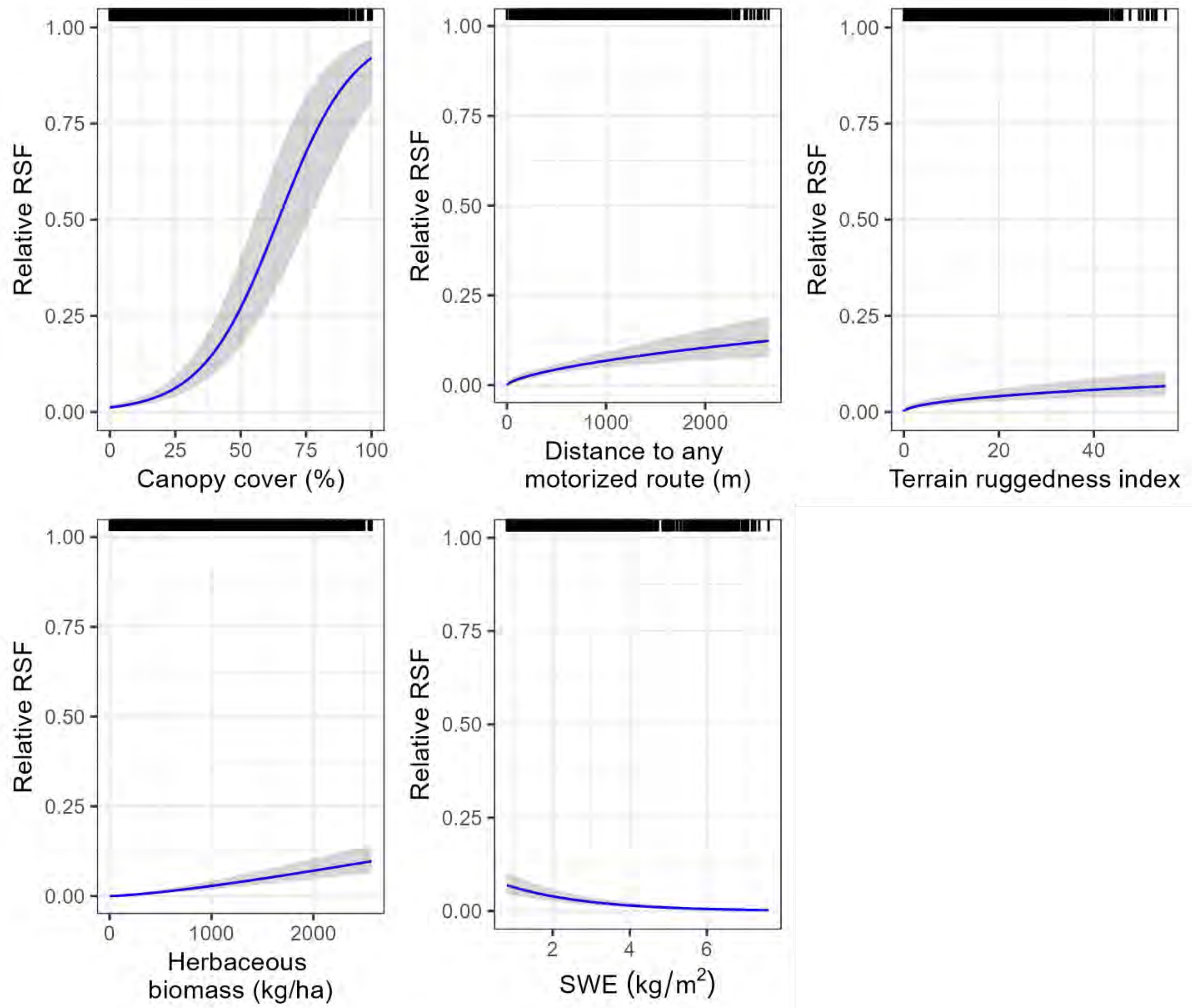

Figure E6. Predicted relative resource selection functions for male elk during the rifle season in the Custer Forest study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

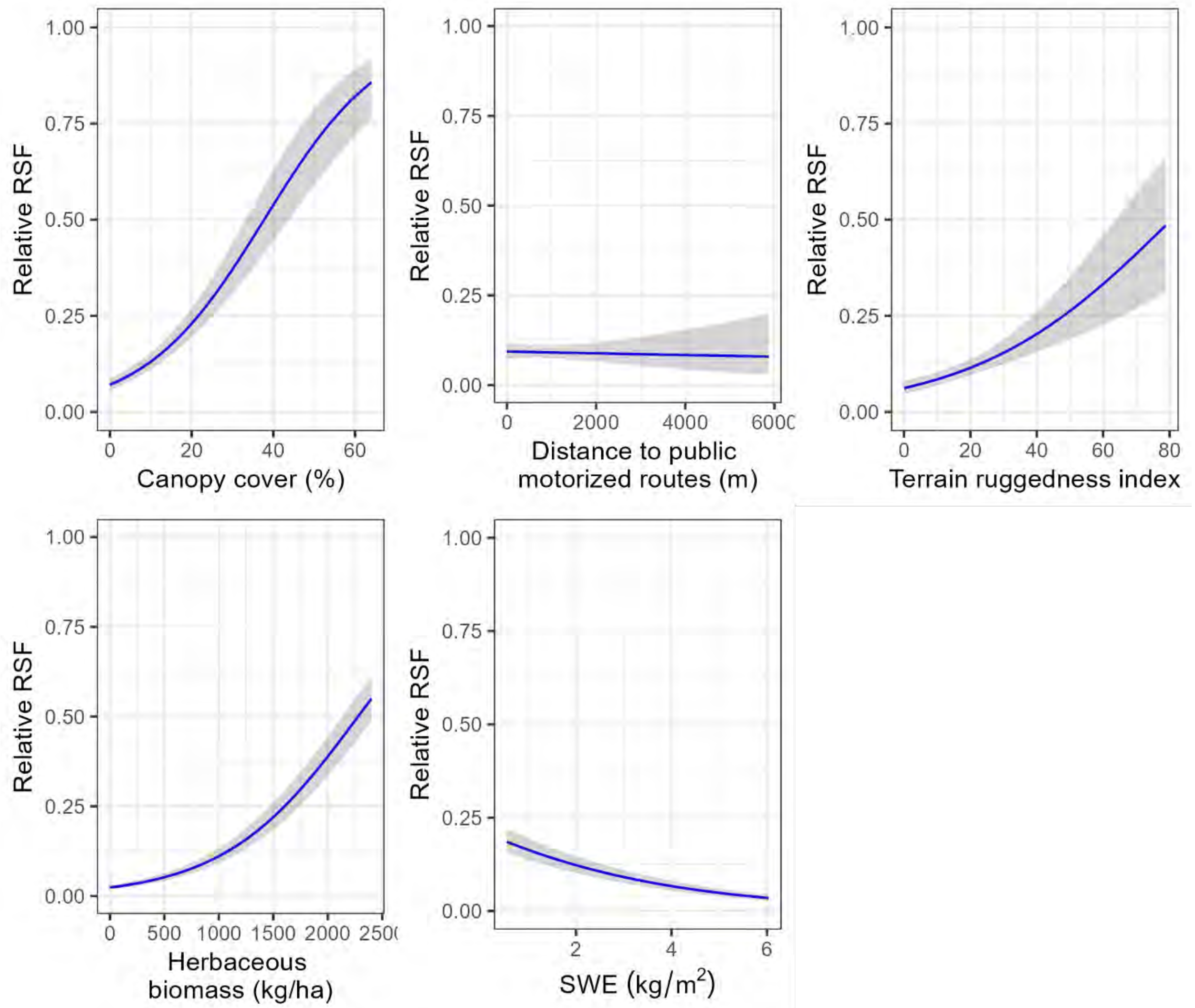

Figure E7. Predicted relative resource selection functions for female elk during the rifle season in the Missouri Breaks study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

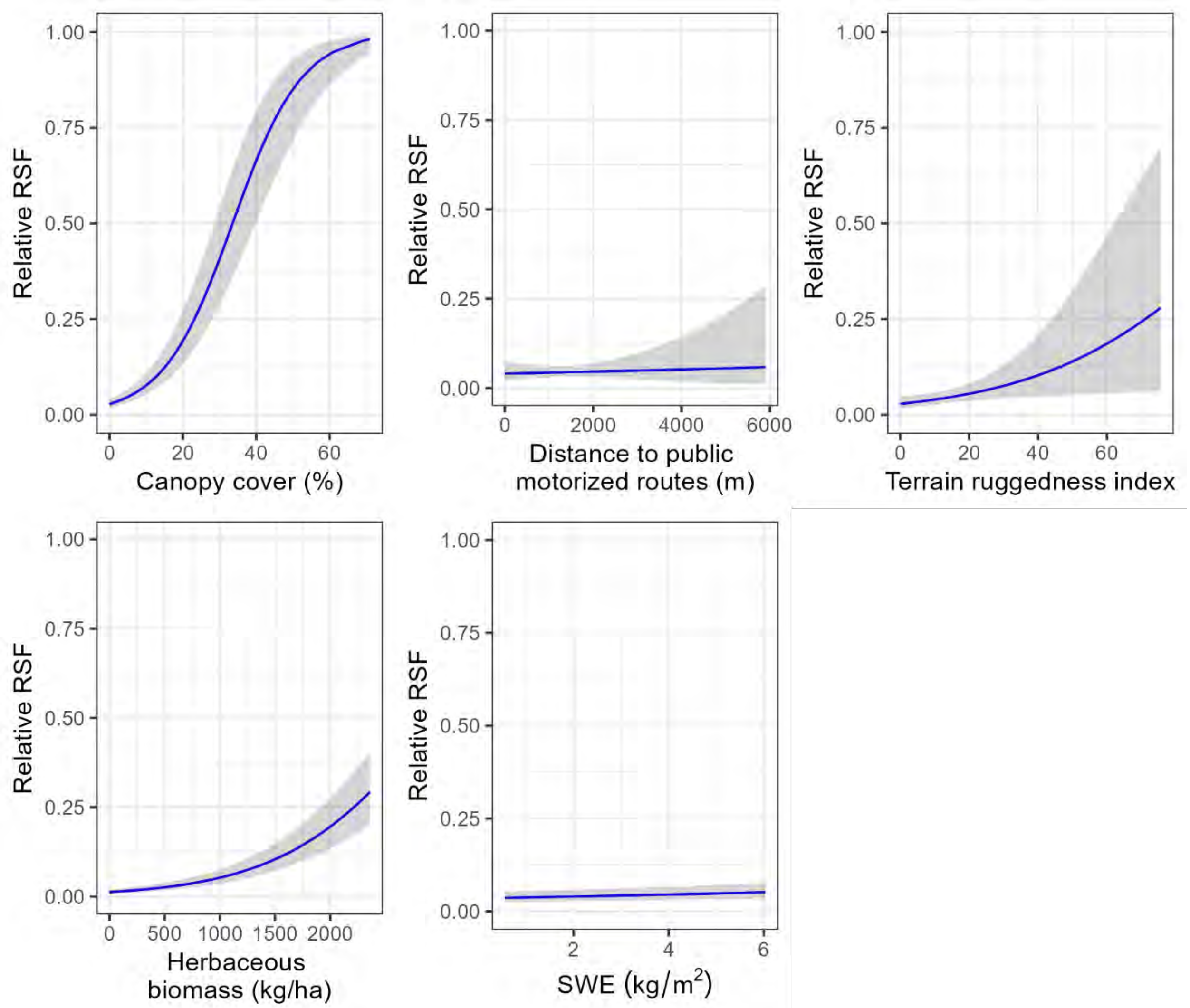

Figure E8. Predicted relative resource selection functions for male elk during the rifle season in the Missouri Breaks study area, central Montana, 2022-2024, using population-level fixed effects estimates from the final resource selection model.

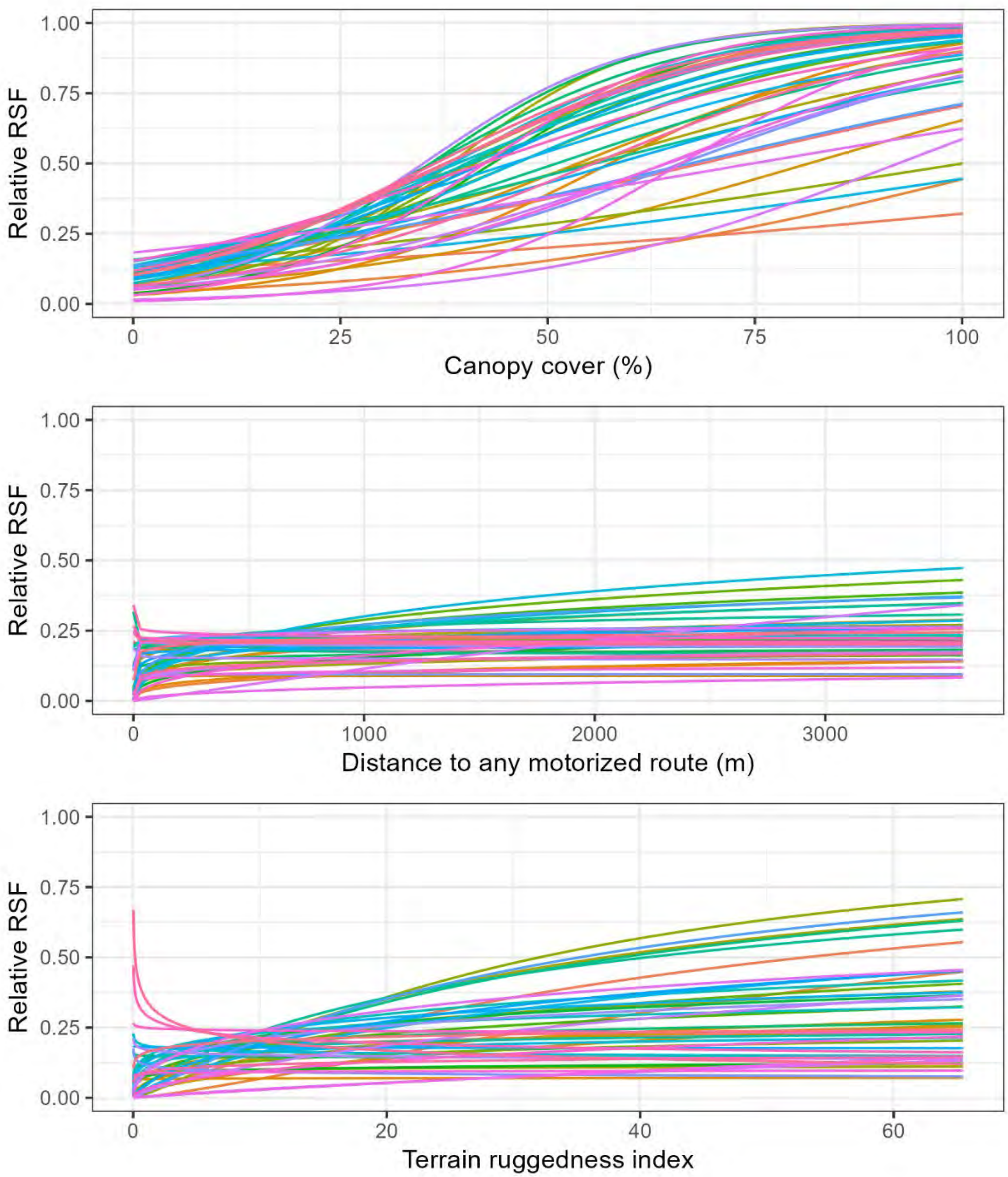

Figure E9. Predicted relative resource selection functions for individual female elk during the archery season in the Custer Forest study area, central Montana, 2021-2023, using individual-level random effects from the final resource selection model.

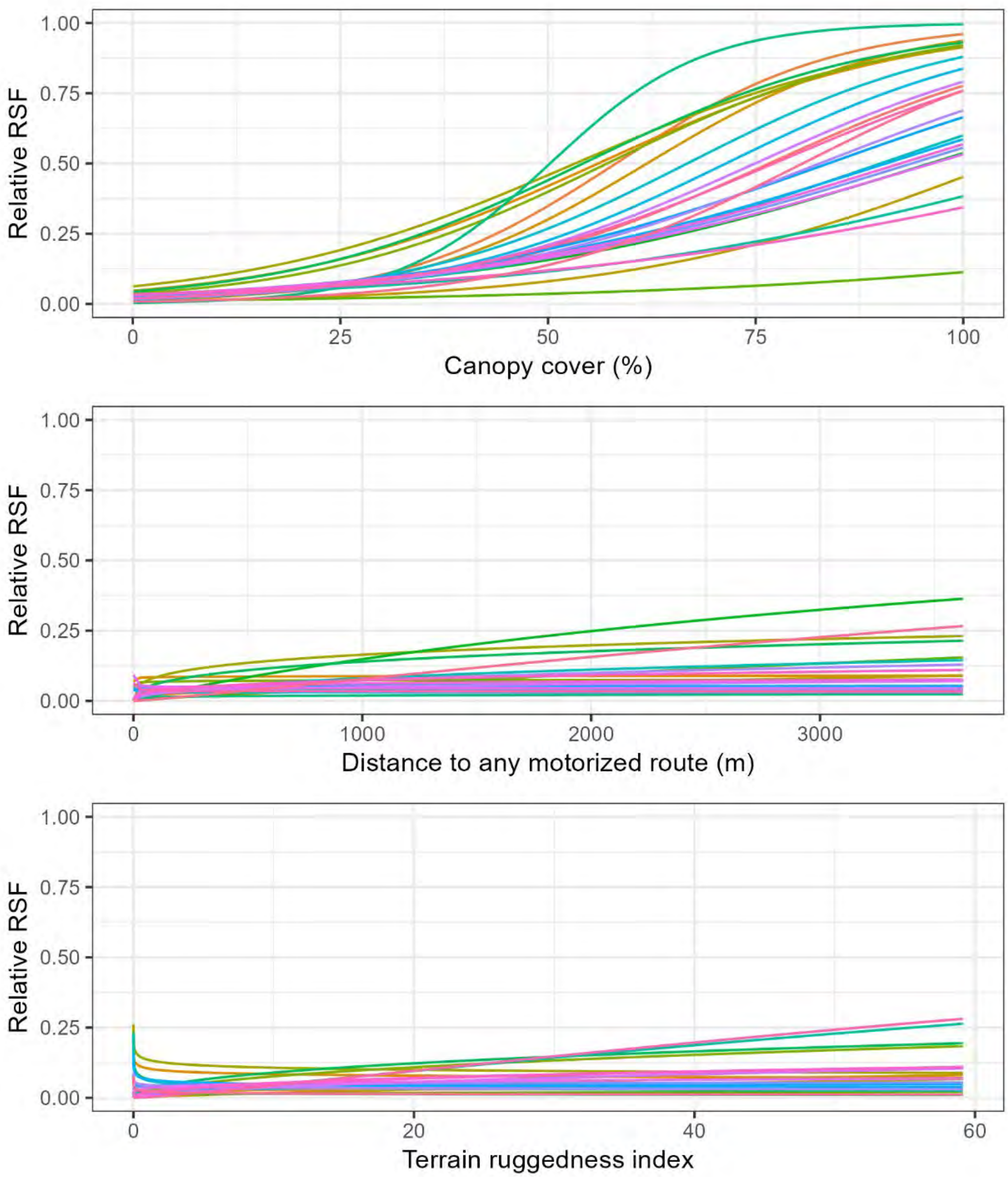

Figure E10. Predicted relative resource selection functions for individual male elk during the archery season in the Custer Forest study area, central Montana, 2021-2023, using individual-level random effects from the final resource selection model.

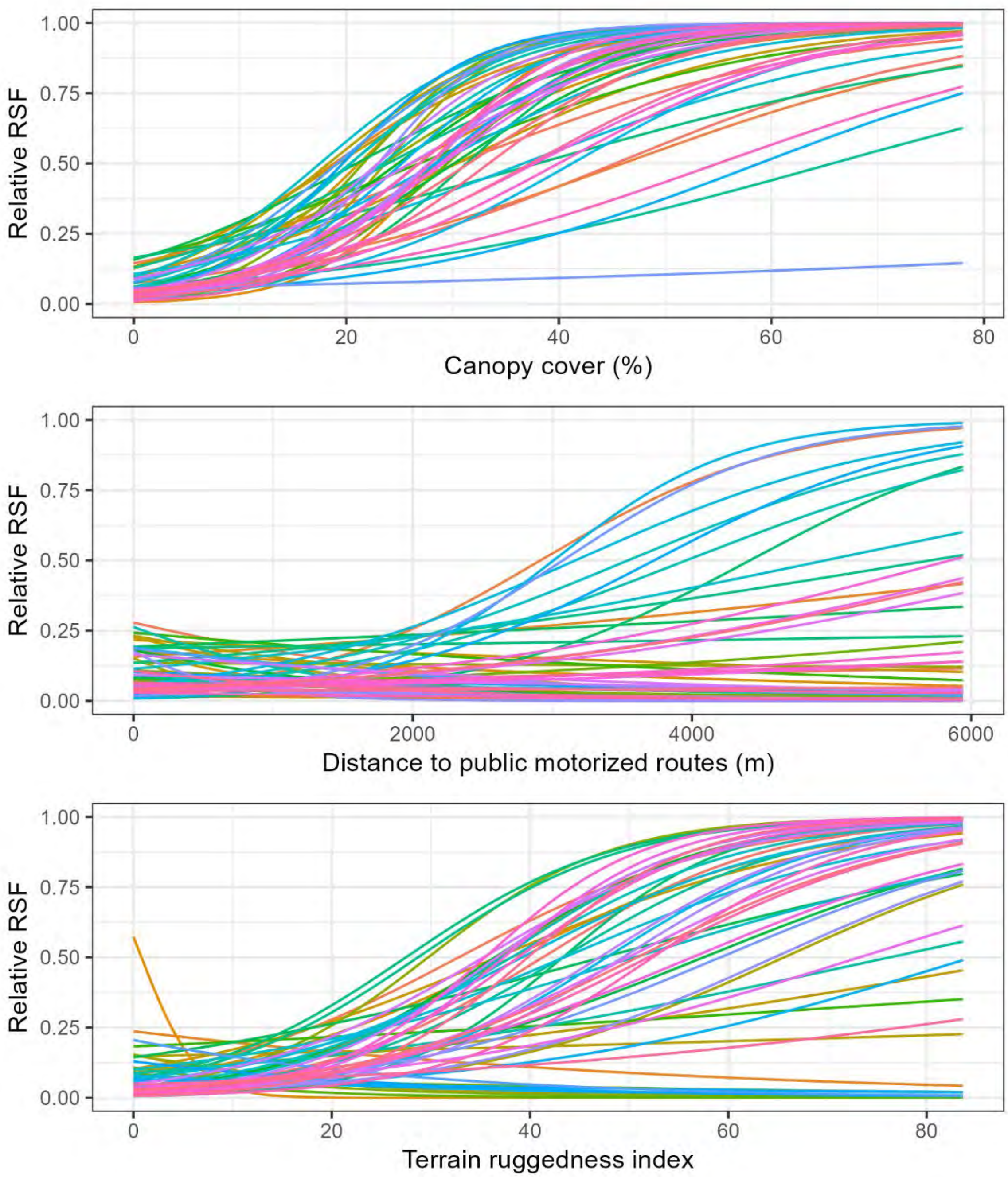

Figure E11. Predicted relative resource selection functions for individual female elk during the archery season in the Missouri Breaks study area, central Montana, 2022-2024, using individual-level random effects from the final resource selection model.

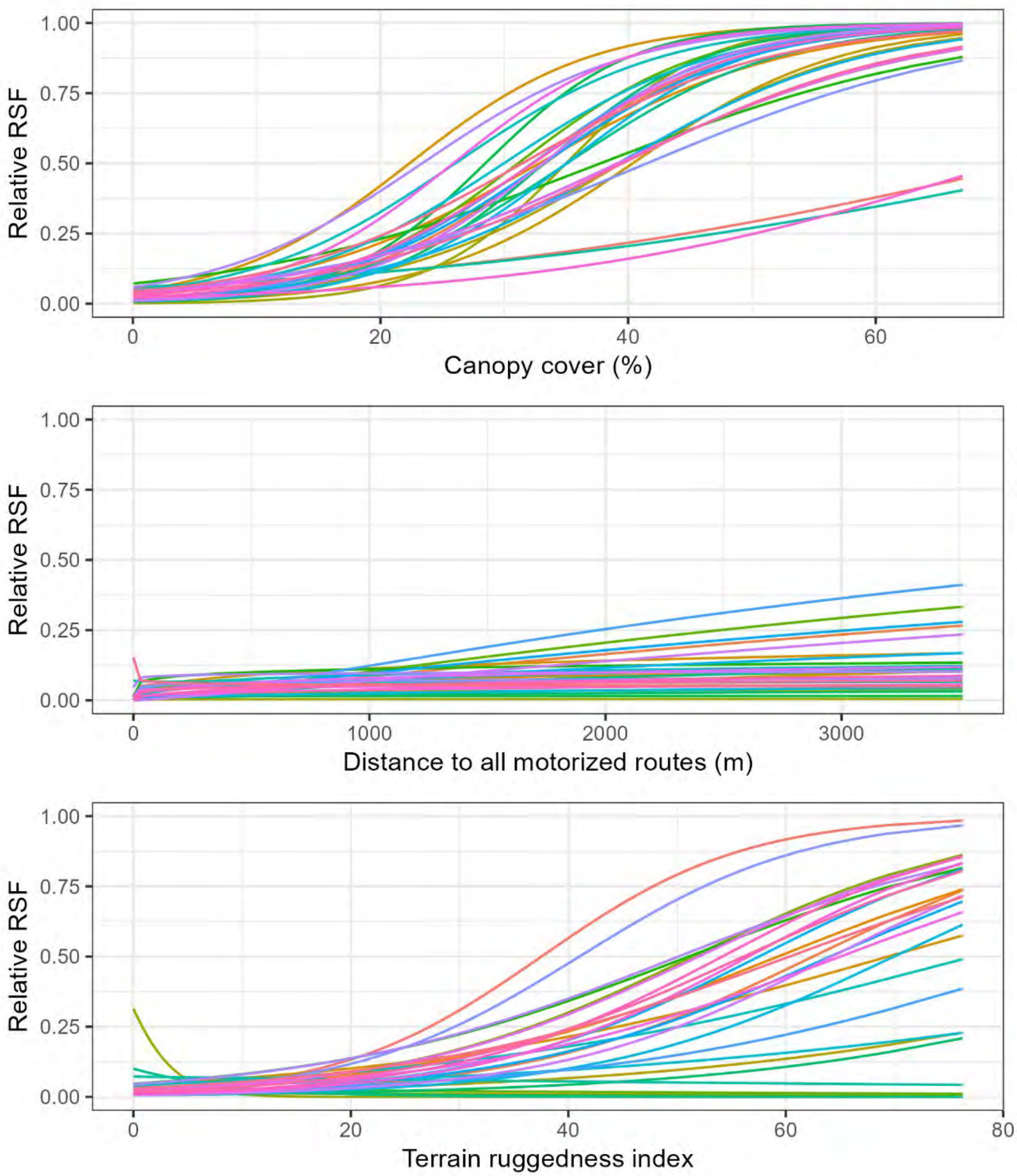

Figure E12. Predicted relative resource selection functions for individual male elk during the archery season in the Missouri Breaks study area, central Montana, 2022-2024, using individual-level random effects from the final resource selection model.

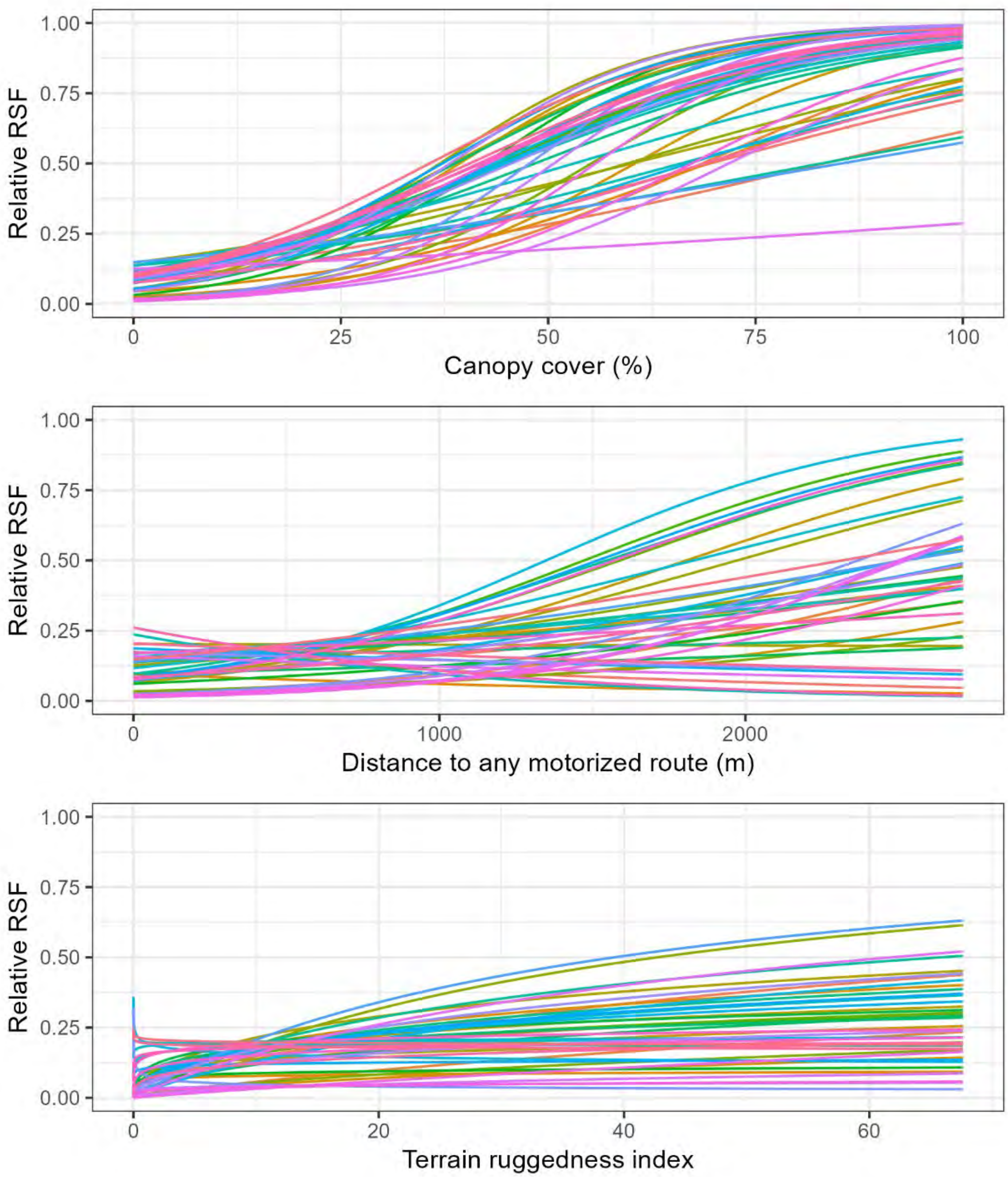

Figure E13. Predicted relative resource selection functions for individual female elk during the rifle season in the Custer Forest study area, central Montana, 2021-2023, using individual-level random effects from the final resource selection model.

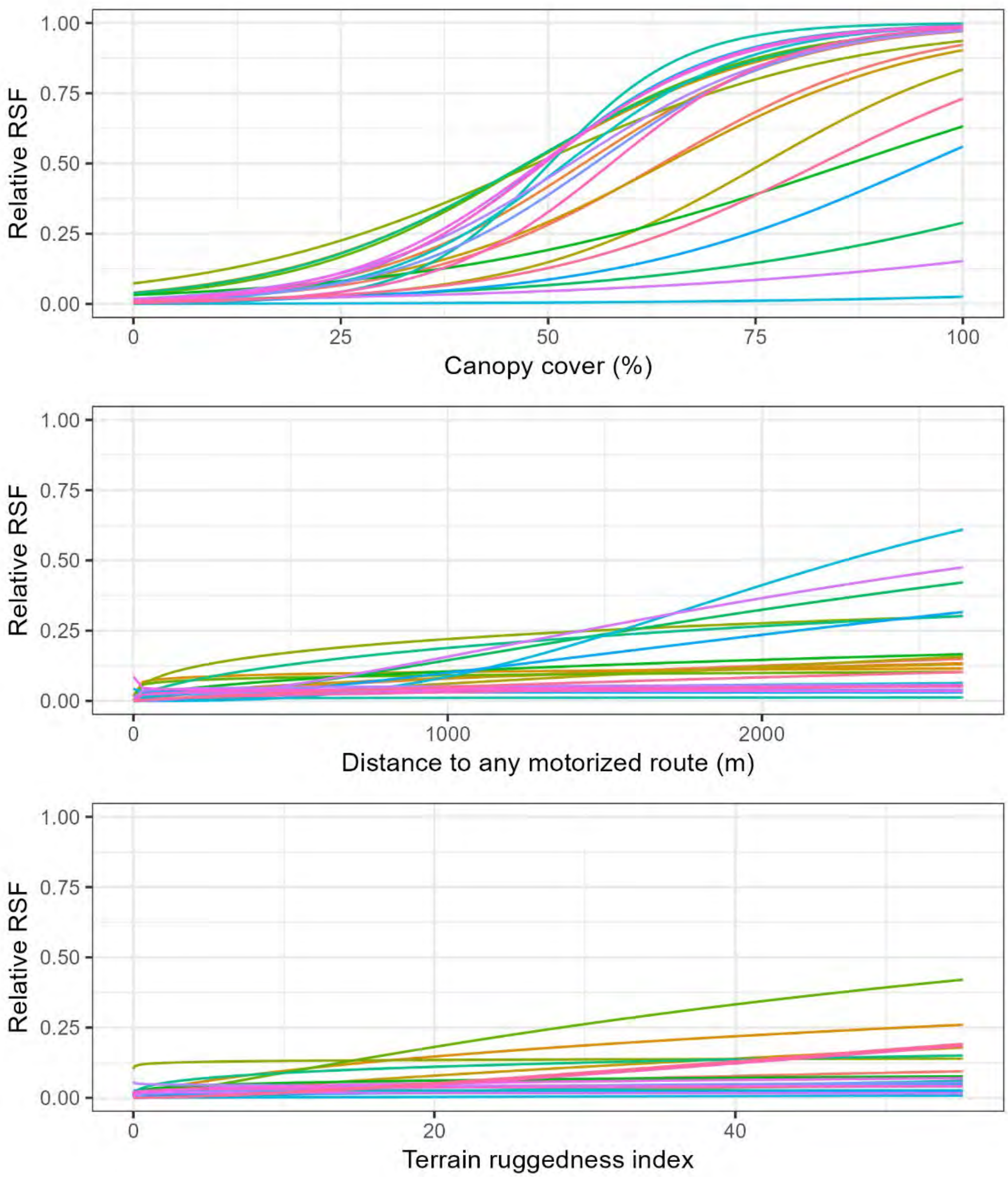

Figure E14. Predicted relative resource selection functions for individual male elk during the rifle season in the Custer Forest study area, central Montana, 2021-2023, using individual-level random effects from the final resource selection model.

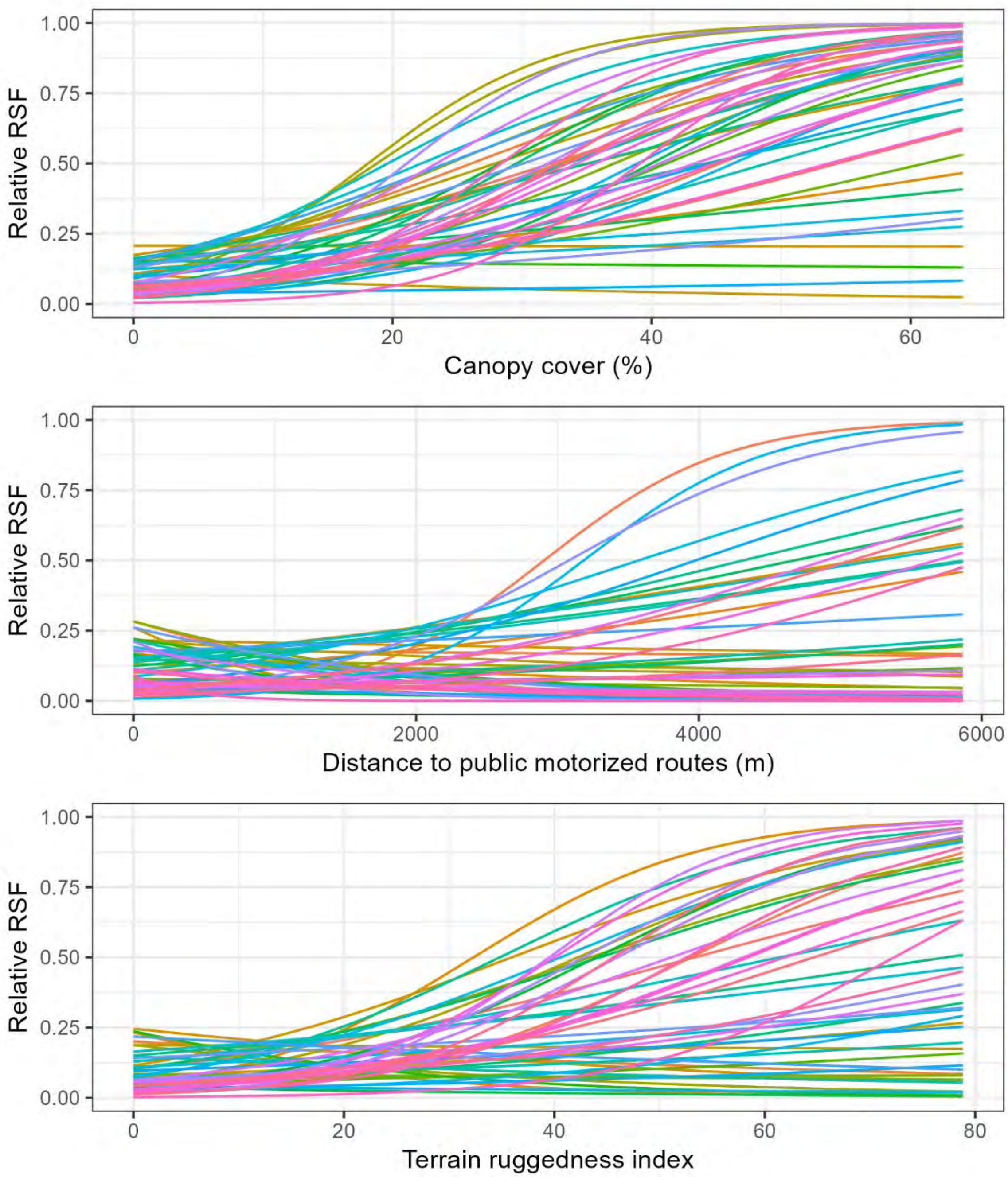

Figure E15. Predicted relative resource selection functions for individual female elk during the rifle season in the Missouri Breaks study area, central Montana, 2022-2024, using individual-level random effects from the final resource selection model.

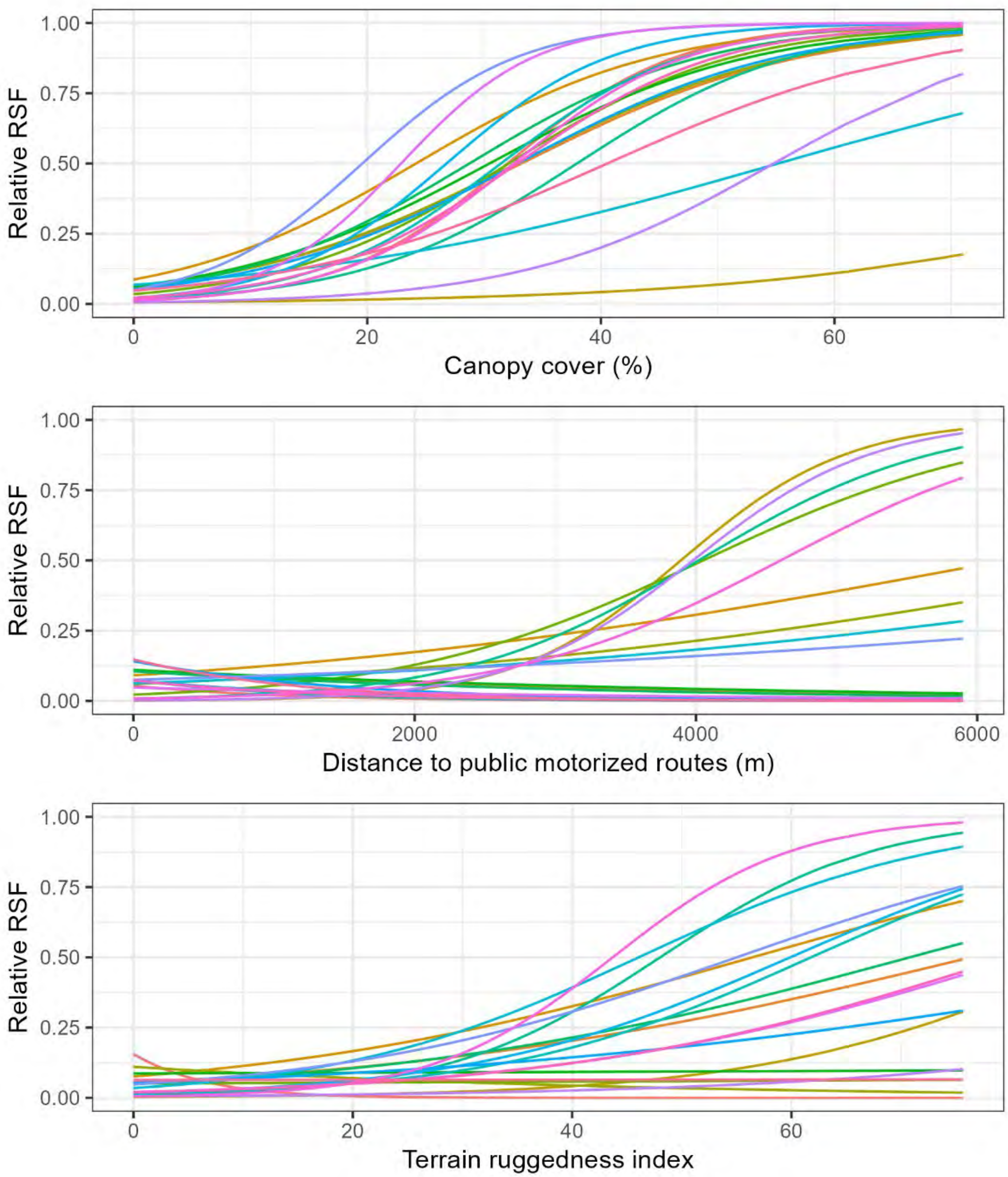

Figure E16. Predicted relative resource selection functions for individual male elk during the rifle season in the Missouri Breaks study area, central Montana, 2022-2024, using individual-level random effects from the final resource selection model.