# FACTORS ASSOCIATED WITH ELK (*CERVUS CANADENSIS*) DISTRIBUTIONS DURING RIFLE SEASON AND INDIVIDUAL RESPONSES TO HARVEST RISK IN A PRAIRIE ENVIRONMENT

by

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# ABSTRACT

Hunting pressure alters habitat selection of elk and understanding responses to pressure is important for effective population and habitat management. While elk responses to hunting are well-studied in forested and mountainous environments in the western U.S., little is known about elk habitat selection in more open prairie landscapes. Our objectives were to evaluate the effects of landscape and environmental factors on elk habitat selection during the rifle season, assess individual variability, and investigate relationships between selection and harvest risk for male and female elk in two populations: the Custer Forest and Missouri River Breaks in eastern Montana, USA. We also provided management recommendations for habitat characteristics that allowed elk to mitigate exposure to harvest risk (i.e., security habitat) based on where most elk use occurred. We used resource selection function modeling with a use-available design and added random effects to estimate selection patterns for individual elk. Resource selection coefficients indicated that elk generally selected areas with restricted hunter access, rugged terrain, and greater distances from motorized routes with a few notable differences for elk in the Missouri River Breaks. In particular, canopy cover was consistently associated with large increases in relative probability of use. Estimates of individual random coefficients indicated that while elk typically shared the same direction of selection for a given covariate, individuals varied in the strength of these relationships, likely due, in part, to varying exposure to risk. Individual elk increased selection for habitat features that provided security when faced with higher harvest risk (i.e., the proportion of used locations that fell on publicly accessible lands). Our results indicated canopy cover was a particularly important factor associated with elk selection during the rifle season in our prairie landscapes where available cover is relatively limited. The relative importance of other factors varied depending on study area and sex. Based on where most elk use occurred, we recommend managing for security and preferred security areas with canopy cover ≥28% and ≥37% in the Custer Forest and ≥3% and ≥5% in the Missouri River Breaks, respectively, during the rifle season in these areas and prairie landscapes with similar habitat attributes.

# INTRODUCTION

Understanding wildlife habitat selection patterns is crucial for developing effective habitat and population management strategies (Morrison et al. 2012). Factors such as varying environmental and habitat conditions (van Beest et al. 2012, Aikens et al. 2020a, b) and the presence of predators, including the resulting spatiotemporal variation in predation risk (Werner et al. 1983, Tolon et al. 2009), can drive habitat selection behavior. Trade-offs associated with habitat-use decisions influence growth, survival, and reproduction of individuals, and, therefore, impact individual fitness (Morris 1989, Rosenzweig 1991) as well as population growth rate, composition and size (Werner et al. 1983), thus highlighting the utility of information about habitat selection patterns in managing wildlife populations.

For hunted populations, harvest risk imposed by human hunters can also influence behavior and habitat selection, with responses to harvest risk documented in numerous species (Tolon et al. 2009, Basille et al. 2013, Bonnot et al. 2013, Stillfried et al. 2015, Stewart et al. 2022). In response to perceived risk, animals may alter daily habitat-use patterns (Bonnot et al. 2013), shift use towards areas protected from hunting (Tolon et al. 2009), increase avoidance of areas with higher risk (Stewart et al. 2022), or select other habitat features that reduce their vulnerability to hunters (i.e., security habitat) (Hillis et al. 1991). Additionally, the type and strength of an individual's behavioral response may be tied to the spatial distribution or structure of risk and the level of risk experienced by the individual (Tolon et al. 2009). In cases where targeted species effectively evade or are not accessible to hunters, managers may be unable to achieve harvest objectives and encounter difficulty controlling population size (Haggerty and

Travis 2006, Stewart et al. 2013). Thus, behavioral responses to human hunting can influence the success of harvest strategies and have important implications for population management.

As has been found in other hunted species, hunting pressure alters the behavior and habitat selection of elk (*Cervus canadensis*) (Proffitt et al. 2009, 2013, Sergeyev et al. 2020). Elk play important roles in predator-prey dynamics (Garrott et al. 2008), nutrient cycling and altering plant community structure (Hobbs 1996). In addition to their ecological significance, elk are an economically and socially important game species (McCool 1996, Donovan and Champ 2009) and are particularly valued for providing recreational hunting opportunities (Eliason 2008, Gude et al. 2012). During periods of hunting pressure, elk typically move farther from roads, where hunter activity is often concentrated, and increase use of dense vegetation and rough terrain to minimize perceived harvest risk (Unsworth et al. 1998, Skovlin et al. 2002, Lowrey et al. 2020).

In addition to natural habitat features that elk may select to mitigate perceived harvest risk, spatial patterns of hunting pressure can also influence selection (Cleveland et al. 2012). In areas characterized by a matrix of public-private landownership with varying levels of hunter access, elk may preferentially select refuge areas where hunting pressure is relatively low or nonexistent. These areas can include privately owned lands that restrict or prohibit hunter access (Burcham et al. 1999) and public lands with limited access or restrictive harvest regulations (Mikle et al. 2019). Redistributions of elk to areas with less hunting pressure have been tied to the onset of the fall hunting season in some populations (Vieira et al. 2003). Elk selection of lands with restrictive hunter access and ensuing growth in local elk population size can lead to reduced hunter success and satisfaction, intensified landowner conflict, and problematic elk distributions that create additional hurdles for elk population and habitat management (Burcham et al. 1999, Haggerty and Travis 2006).

Elk have been distributed primarily in forested and montane environments in the western United States throughout the last century and elk habitat selection and behavior in response to hunting pressure are well-understood in these environments (Skovlin et al. 2002). Consequently, conventional management strategies for providing security habitat (i.e. habitat features that reduce elk vulnerability to hunters) 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 previous studies. Such differences in available habitat likely carry implications for elk habitat selection during periods of hunting pressure 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). This lack of information makes managing for elk security in prairie regions difficult, especially when coupled with other management challenges.

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, individual selection patterns may vary in direction and strength depending on the level of harvest risk present in an individual's home range (DeVoe et al. 2019). However, more work is needed to understand if and how selection for security features changes across the gradient of harvest risk experienced by individual elk during the hunting season, 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 (Montana Department of Fish, Wildlife and Parks 2023) further emphasize the need for information about habitat selection in prairie environments. Specifically, the Missouri River Breaks and Custer Forest elk populations, in eastern Montana, USA, 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. Local management need as well as community and conservation partner interest exist in these areas in regard to elk population and habitat management.

To investigate elk-habitat relationships in the presence of hunting pressure, we evaluated resource selection during the rifle season for male and female elk in two populations occupying prairie landscapes with varying levels of harvest risk. We addressed three specific objectives with our analysis. Our first objective was to evaluate relationships between resource selection and landscape and environmental factors we hypothesized to be important in influencing population distributions during the rifle season for male and female elk. Second, 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. Lastly, we identified security area metrics derived from our top resource selection function models to provide recommendations for elk security habitat management in prairie landscapes.

## Study Area

We conducted this study in two areas of eastern Montana, the Missouri River Breaks approximately 150 km northeast of Lewistown and the Custer Forest 200 km east of Billings, Montana, USA. The study areas encompass the rifle hunting season ranges (approximately 21 Oct – 28 Nov) of the respective elk populations from 2021 through 2023. The Missouri River Breaks study area encompasses 4,301 $km^2$ and falls mainly in Montana hunting district (HD) 700 in addition to small portions of 410 and 701. 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 big sagebrush (*Artemisia tridentata*) and western wheatgrass (*Pascopyrum smithii*); and timbered drainages and coulees near the Missouri River, Fort Peck Reservoir and Musselshell River dominated by ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (*Juniperus scopulorum*). Plains cottonwood (*Populus deltoides*) and willow (*Salix* spp.) were common in riparian areas along major drainages. Elk were sympatric with white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). Predators occupying the area included coyote (*Canis latrans*), bobcat (*Lynx rufus*) and mountain lion (*Puma concolor*).

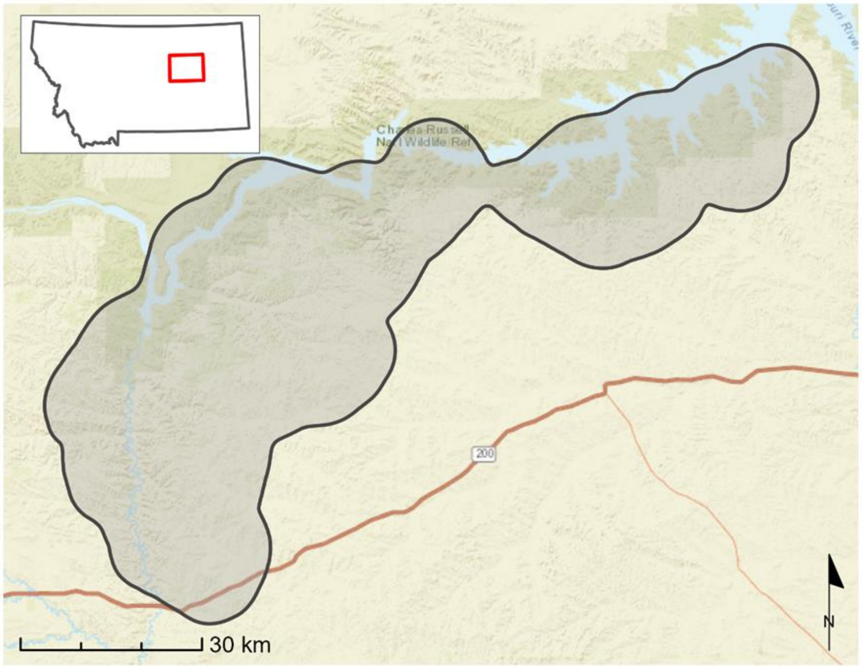

Figure 1. The Missouri River Breaks elk population rifle season range in northeastern Montana, USA, 2022-2023.

The Custer Forest elk range covers 4,081 km$^2$ and falls largely within HD 704, with a small portion in 705. The elk range was centered around lands managed by the U.S. Forest Service, Custer National Forest that comprised 30% of the area. About half of the area was private (55%), in addition to 5% and 10% managed by state entities and the Bureau of Land Management, respectively. Elevations were between 907 m and 1,569 m and topography ranged 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 contained privately-owned ranchlands; sagebrush steppe and mixed-grass prairies with by big sagebrush and western wheatgrass; and xeric forest communities dominated by ponderosa pine and Rocky Mountain juniper with understories comprised of grassland species and shrubs like western snowberry (*Symphoricarpos occidentalis*). Elk were sympatric with white-tailed deer and mule deer, and predators included coyote, bobcat, mountain lion, and American black bear (*Ursus americanus*).

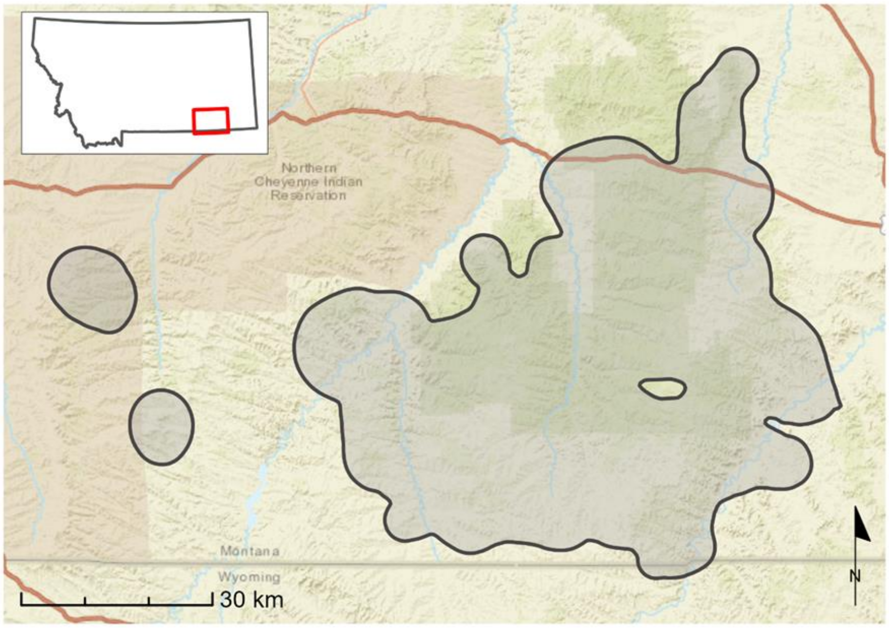

Figure 2. The Custer Forest elk population rifle season range in southeastern Montana, USA, 2021-2023.

Montana Fish, Wildlife & Parks (MFWP) conducts annual or biennial winter area surveys to monitor elk population trends. In the Missouri River Breaks, reliable and repeatable biennial elk surveys began in 2008, and counts have remained fairly steady around 1,200 to 1,300 elk since 2012. The most recent count in winter 2022 observed 1,379 elk. Elk in the Custer Forest are surveyed as part of a larger southeastern Montana elk management unit encompassing hunt districts 702 and 705 in addition to hunt district 704 where the core of the study area occurs. Aerial surveys for portions of the larger management unit were initiated between 2011 and 2016.

Elk counts remained steady around 2,000 animals from 2016 through 2020, before climbing to a high of 3,721 animals based on surveys conducted in the winters of 2022 and 2023. Archery hunting occurred in September and early October over a 6-week season followed by the rifle hunting season that began in late October and continued over 5 weeks into late November.

Most opportunities to hunt elk in the Custer Forest were allowed through limited drawings. Hunters with only a general elk license could harvest a spike bull or antlerless elk, though not on National Forest lands during rifle season. Hunters successful in drawing a permit (quota 225-280) or a license (quota 600) could harvest either-sex or antlerless elk, respectively, in HDs 702, 704 and 705 during archery or rifle season. Though quota and regulations varied between years, a number of archery-only permits (4,000 in 2021 and 1,000 in 2022-2023) were available to harvest either-sex elk in multiple HDs including 704. Beginning in 2022, a late season hunt (late-November to mid-February) was initiated that allowed harvest of antlerless elk on private lands only. In the Missouri River Breaks 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. During mid-December, a special season allowed hunters to harvest elk with a muzzleloader in both study areas. 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. In the two years of study in the Missouri River Breaks, 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.

# METHODS

## Data Collection

We captured 40 adult female and 20 adult male elk (>1.5 years old) in the Custer Forest population in late January and early February 2021. We captured an additional 4 female and 5 male elk in January 2022 and another 5 females and 4 males in January 2023, which yielded a total of 78 captured elk. We captured 40 adult female and 20 adult male elk in the Missouri Breaks population in January 2022, and supplemental capture efforts in January 2023 added 6 female and 10 male elk, which yielded a total of 76 captured elk. Animals were captured using either helicopter net-gunning or chemical immobilization, all in accordance with animal welfare protocols approved by Montana Fish, Wildlife and Parks. We outfitted captured elk with Iridium remote upload global positioning system (GPS) radio-collars (Lotek Wireless, model LiteTrack Iridium 420, New Market, Ontario, Canada) that were programmed to collect hourly locations, stay on for 3 years, and to transmit a mortality signal if stationary for >10 hours.

## Covariate Data

We assessed evidence for potential relationships between elk habitat selection and six covariates: canopy cover, distance to motorized routes, terrain ruggedness, forage availability, 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, and a local Bureau of Land Management (BLM) layer for BLM lands. 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 2023a) 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 forage availability 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 is 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.

## Resource Selection Modeling

To evaluate factors associated with elk habitat selection during the rifle season, 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.

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 rifle 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. This process resulted in up to 4 locations per elk per day.

To develop the sample of available locations, we pooled data from all years and both sexes and estimated population-specific rifle season ranges by randomly selecting 4 locations per individual per day and by then 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 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 forage availability. 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 ($AIC_c$, Burnham and Anderson 2002) to compare models and this process produced 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 investigated the functional relationship between individual selection for security attributes and exposure to harvest risk (see next section). Forage availability and snow water equivalent also remained in the model as fixed effects only to account for their effects while assuming that selection for these factors would be similar across individuals. We used these models, henceforth referred 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 a 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).

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 rifle season. 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.

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 elk use 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 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, respectively. 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.

# RESULTS

We retained radio-collar location data from 44 female and 22 male elk in the Custer Forest and 40 female and 14 male elk in the Missouri River Breaks for our analysis. After sub-setting to the rifle season, our data included 62,846 GPS locations from 120 elk spanning 217 animal years. There were 26 captured elk (15 in the Missouri Breaks and 11 in the Custer Forest) from which we collected no rifle season location data due to either collar malfunction or mortality. We excluded data from 13 elk (6 male and 7 female) from our analyses because we collected insufficient location data for them during the rifle season. Additionally, we censored data from a Custer Forest male after he dispersed far outside the study area. We recorded 17 mortalities (9 males, 8 females) in the Custer Forest and 22 (12 males, 10 females) in the Missouri River Breaks during the monitoring period between January 2021 and December 2023. The primary source of elk mortality was legal hunter harvest.

## Population-Level Resource Selection

In the Custer Forest, the global modeling approach revealed clear support ($\Delta AIC_c$ = 196.91) for a female resource selection model that included linear functional 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, which included random coefficients for canopy cover, terrain ruggedness and distance to motorized routes, 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 1 and Figure 3).

Table 1. Covariates and associated standardized coefficient estimates and 95% confidence intervals from the final resource selection model for female elk in the Custer Forest area of southeast 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 | 0.424 | (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) | - |

In the Missouri River Breaks, the top female resource selection model contained linear functional forms of canopy cover, distance to public motorized routes, terrain ruggedness and SWE, as well as a pseudothreshold functional form of herbaceous biomass. The next-best model had $\Delta AIC_c = 8.92$. Similar to results for Custer Forest females, the Missouri River Breaks final model for female elk indicated that preference increased as canopy cover, terrain ruggedness and herbaceous biomass increased, and declined as SWE increased. The distance to motorized routes coefficient estimate and associated confidence intervals from the final model ($\hat{\beta}$ = -0.007, 95% CI = -0.188, 0.175) indicated no clear relationship between female elk selection and route distance. Lastly, Missouri River Breaks females also preferred areas with restricted hunter access (Table 2 and Figure 4).

Table 2. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for female elk in the Missouri River Breaks area of northeastern Montana, 2022-2023.

| **Covariate** | **Functional form** | **Coefficient estimate** | **95% CI** | **Variance** |
|---|---|---|---|---|
| Access | Binary | 0.47 | (0.415, 0.525) | - |
| Canopy cover | Linear | 0.436 | (0.34, 0.532) | 0.090 |
| Distance to public motorized routes | Linear | -0.007 | (-0.188, 0.175) | 0.332 |
| SWE | Linear | -0.355 | (-0.381, -0.329) | - |
| Terrain ruggedness | Linear | 0.345 | (0.22, 0.47) | 0.150 |
| Herbaceous biomass | Psuedothreshold | 1.086 | (1.017, 1.155) | - |

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 3 and Figure 5).

Table 3. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for male elk in the Custer Forest area of southeastern 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) | - |

For male elk in the Missouri River Breaks, the top model from the candidate set included linear forms for canopy cover, distance to public routes, terrain ruggedness and herbaceous biomass, and a pseudothreshold form for SWE. The second-best supported model of the candidate set had a $\Delta AIC_c = 11.71$. The final model for the Missouri River Breaks male elk showed that males there had general similarities and some notable differences in their estimated selection patterns compared to the other groups of elk (Table 4 and Figure 6). In general, much like the other groups of elk, males in the Missouri River Breaks were more likely to select areas with greater values for canopy cover, distance to motorized routes, terrain ruggedness and herbaceous biomass and areas with lower SWE. In contrast to other groups, the hunter access estimate ($\hat{\beta}$ = -0.007, 95% CI = -0.131, 0.118) was close to zero and had a confidence interval that widely overlapped zero, which indicates that males in the Missouri River Breaks do not display selection among areas with different access levels at the population level. Like their female counterparts, male elk in the Missouri River Breaks also did not show clear preference or avoidance of distance to routes ($\hat{\beta}$ = 0.023, 95% CI = -0.428, 0.474). Finally, the estimate for terrain ruggedness was positive and had confidence intervals slightly overlapping zero ($\hat{\beta}$ = 0.305, 95% CI = -0.038, 0.648), which indicated that male elk probably selected higher values of terrain ruggedness. These findings are in contrast to those for both populations of female elk as well as the Custer Forest males, where the final models demonstrated clear preference for restricted access areas over open access and very strong negative or positive relationships between elk selection and every covariate (95% CI not overlapping zero), with the exception of distance to routes for Missouri River Breaks females.

Table 4. Covariates and associated standardized coefficient estimates, 95% confidence intervals, and random coefficient variance from the final resource selection model for male elk in the Missouri River Breaks area of northeastern Montana, 2022-2023.

| **Covariate** | **Functional form** | **Coefficient estimate** | **95% CI** | **Variance** |
|---|---|---|---|---|
| Access | Binary | -0.007 | (-0.131, 0.118) | - |
| Canopy cover | Linear | 0.802 | (0.659, 0.945) | 0.066 |
| Distance to public motorized routes | Linear | 0.023 | (-0.428, 0.474) | 0.717 |
| Terrain ruggedness | Linear | 0.305 | (-0.038, 0.648) | 0.410 |
| Herbaceous biomass | Linear | 0.501 | (0.436, 0.565) | - |
| SWE | Psuedothreshold | -0.111 | (-0.163, -0.058) | - |

In all cases, the inclusion of individual random effects in the final model improved model fit. The increased model complexity reduced $AIC_c$ by 1993.7 and 978.45 for Custer Forest females and males, respectively, and by 3743.31 and 1225.65 for females and males in the Missouri River Breaks. All final models demonstrated strong predictive performance, with the Spearman rank correlation coefficient from the k-folds cross validation averaging 0.73 for the Missouri River Breaks males and >0.99 for all other groups of elk across the five iterations.

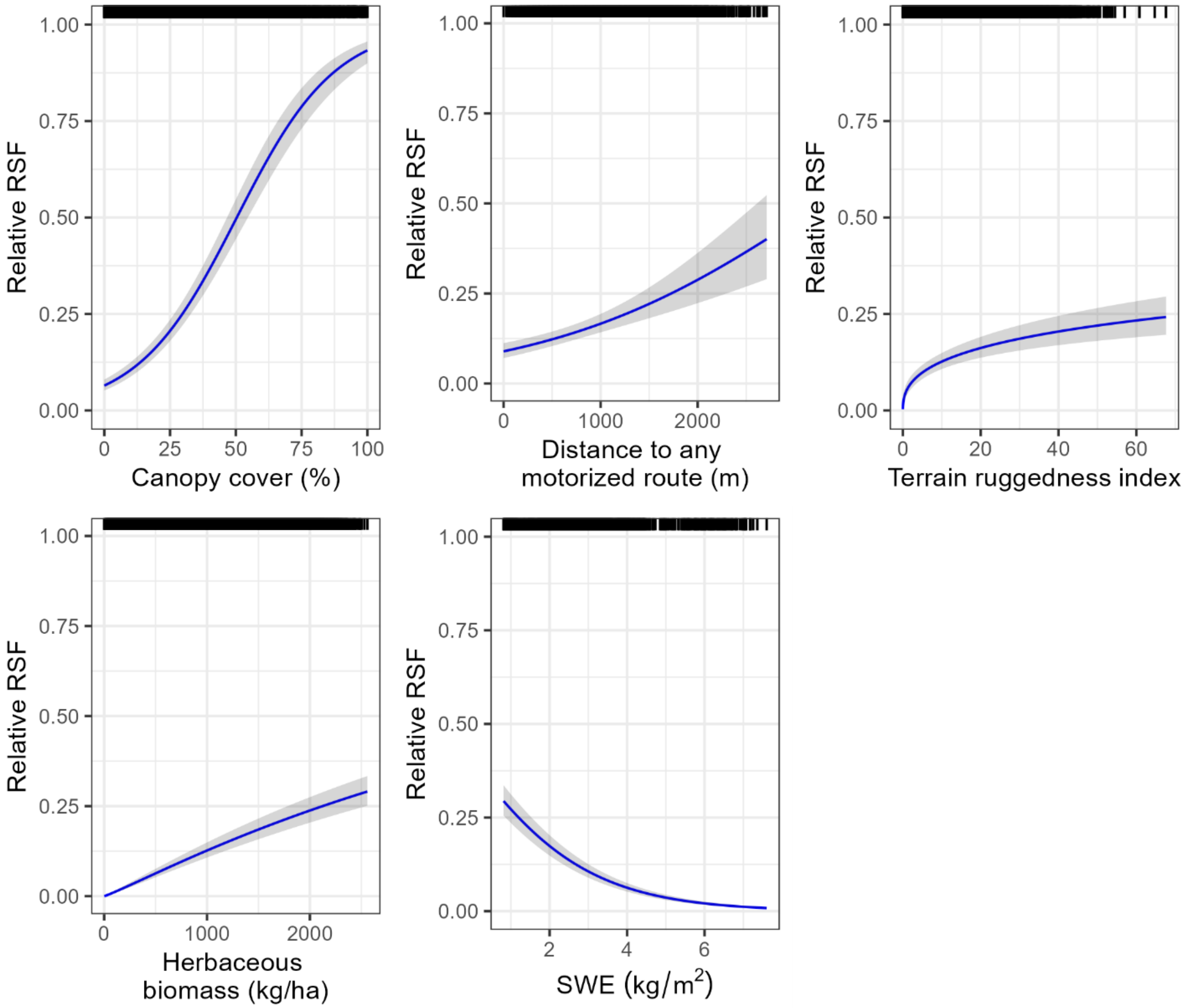

Figure 3. Predicted relative resource selection functions for female elk in the Custer Forest area of southeastern Montana, 2021-2023, using population-level fixed effects estimates from the final resource selection model.

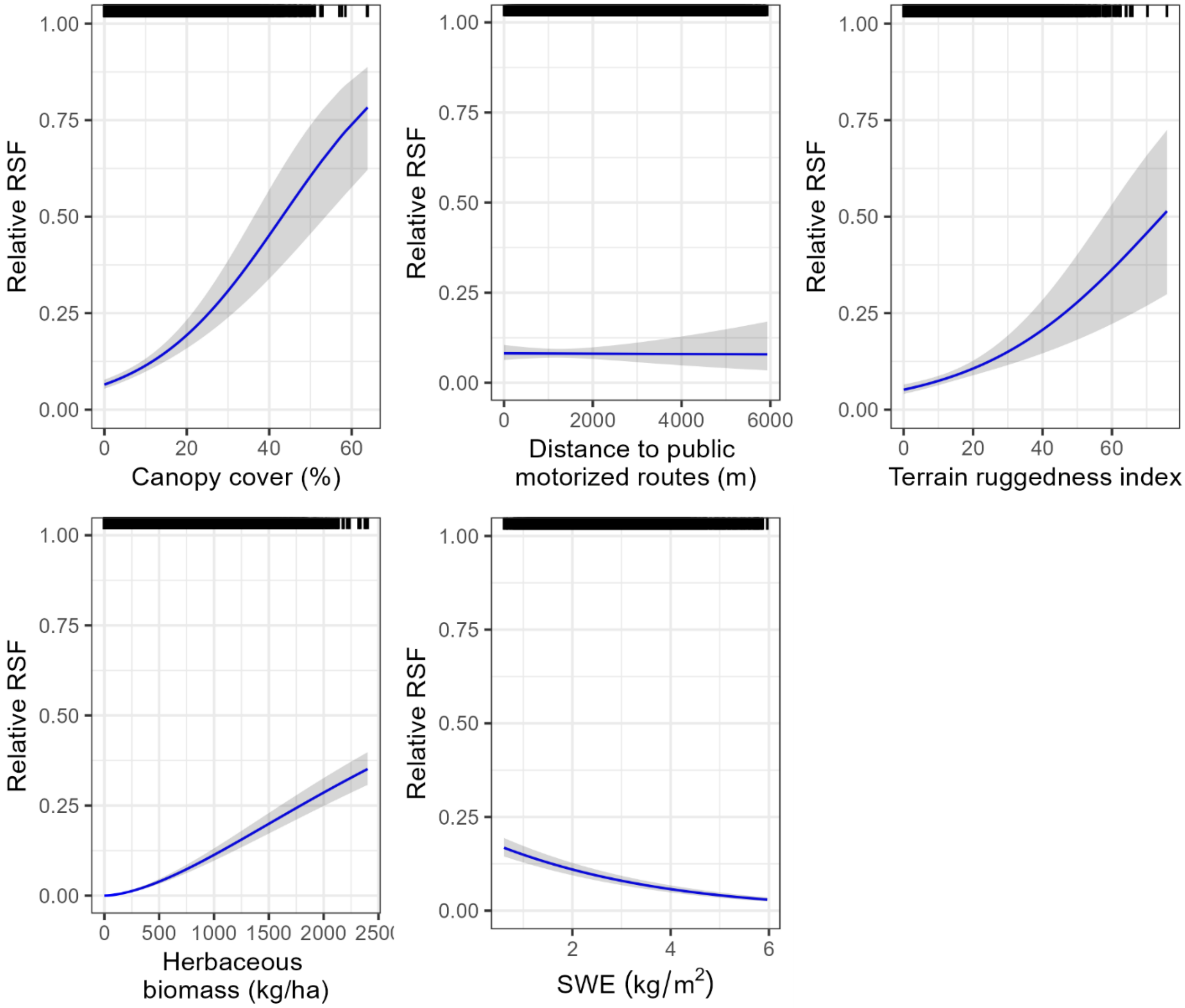

Figure 4. Predicted relative resource selection functions for female elk in the Missouri River Breaks area of northeastern Montana, 2022-2023, using population-level fixed effects estimates from the final resource selection model.

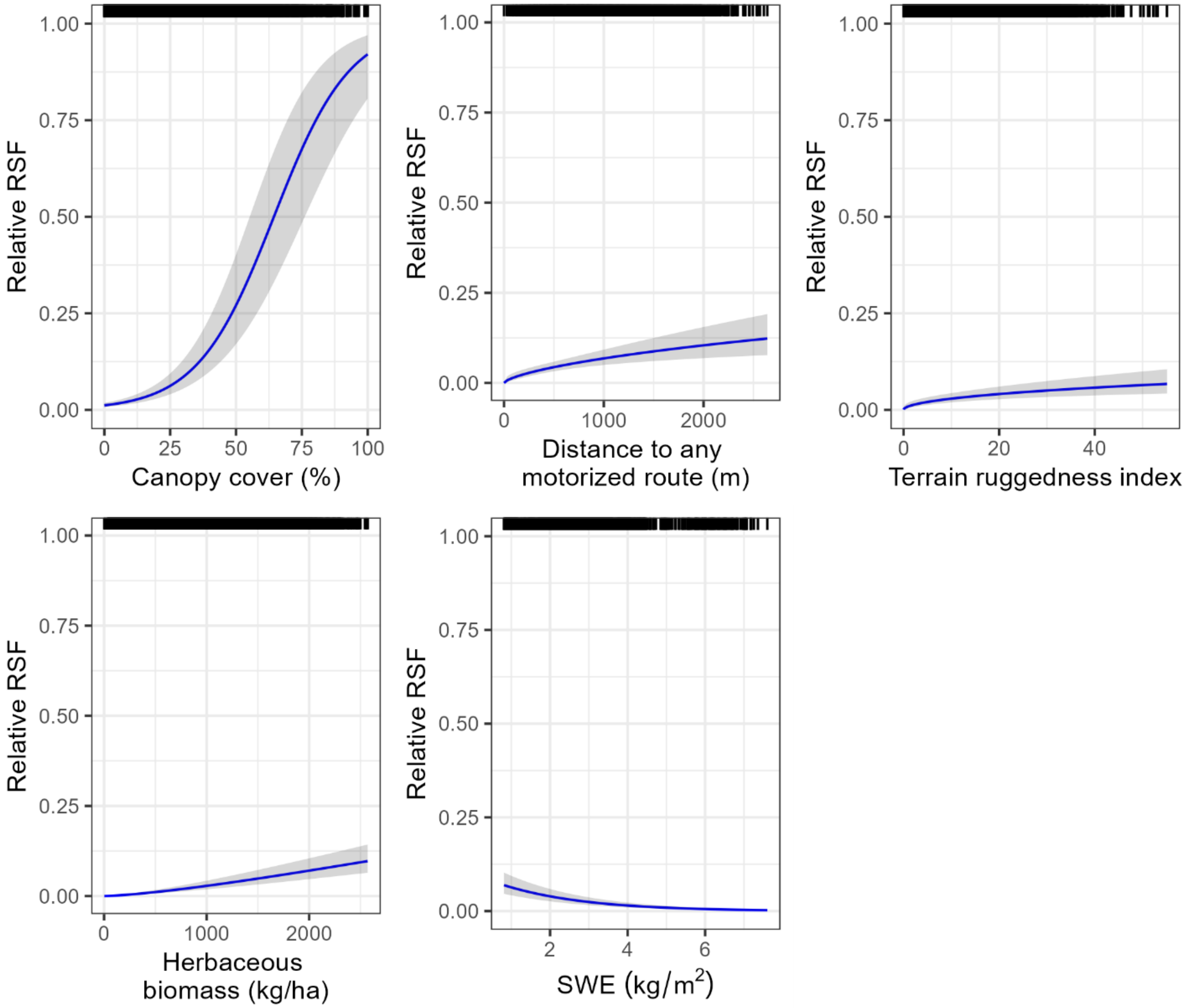

Figure 5. Predicted relative resource selection functions for male elk in the Custer Forest area of southeastern Montana, 2021-2023, using population-level fixed effects estimates from the final resource selection model.

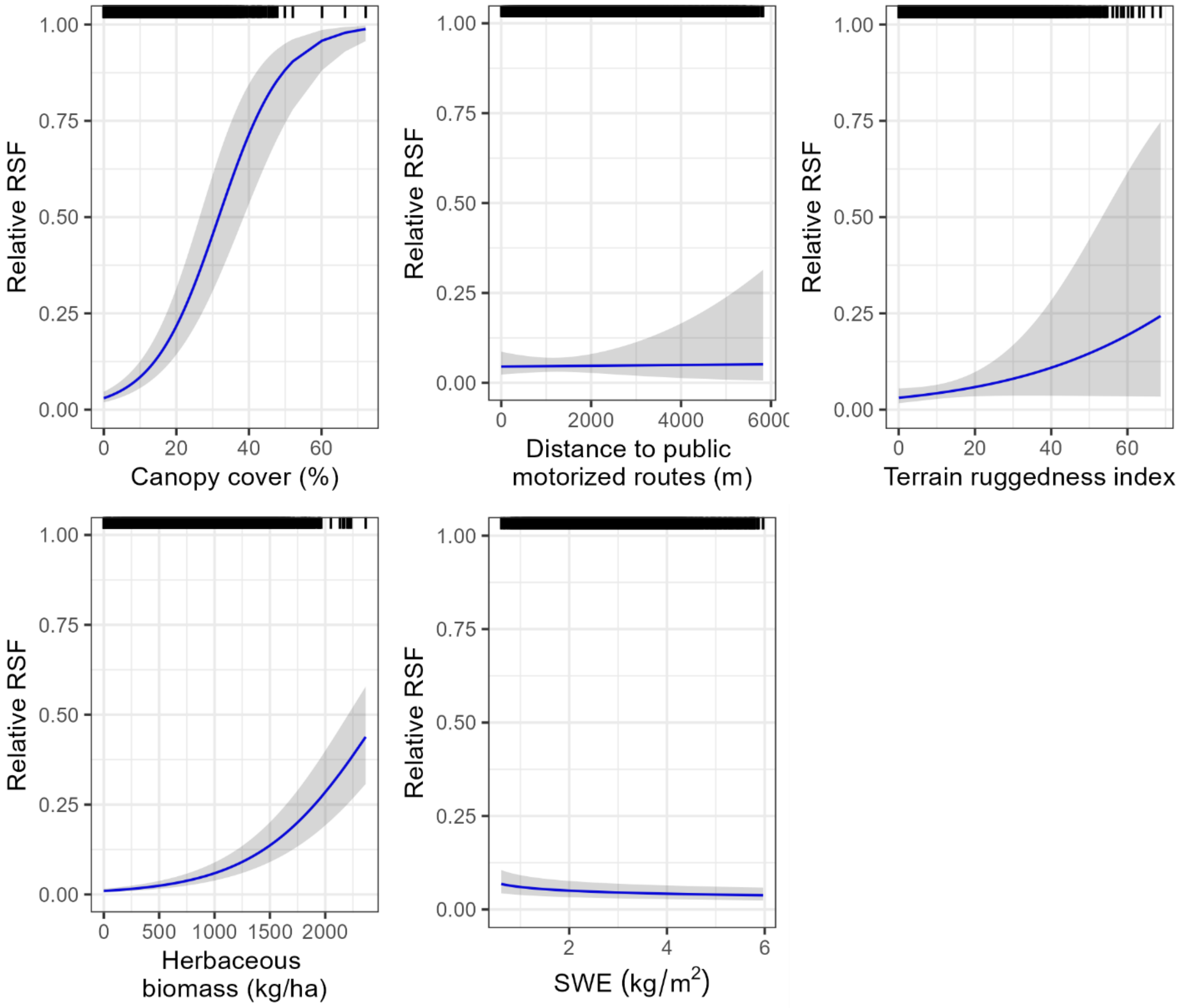

Figure 6. Predicted relative resource selection functions for male elk in the Missouri River Breaks area of northeastern Montana, 2022-2023, using population-level fixed effects estimates from the final resource selection model.

## Individual Variation and Functional Responses to Risk

Across all groups of elk, 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 (Appendix C, Figures C1-C4).

We found evidence that functional responses to harvest risk differed by population and sex. For Custer Forest females, there was strong evidence that selection strength for canopy cover ($\hat{\beta}$ = 0.534, 95% CI = 0.277, 0.791) and distance to motorized routes ($\hat{\beta}$ = 0.39, 95% CI = 0.15, 0.63) increased with increasing harvest risk, and no evidence of changing selection for terrain ruggedness ($\hat{\beta}$ = 0.044, 95% CI = -0.2, 0.287) (Figure 7). For male elk, harvest risk was associated with increased selection strength for more rugged terrain ($\hat{\beta}$ = 0.553, 95% CI = 0.057, 1.049) and canopy cover ($\hat{\beta}$ = 0.412, 95% CI = -0.147, 0.971), although evidence was limited for the latter, and there was little evidence of such a relationship with distance to routes ($\hat{\beta}$ = 0.679, 95% CI = -1.426, 2.784) (Figure 7).

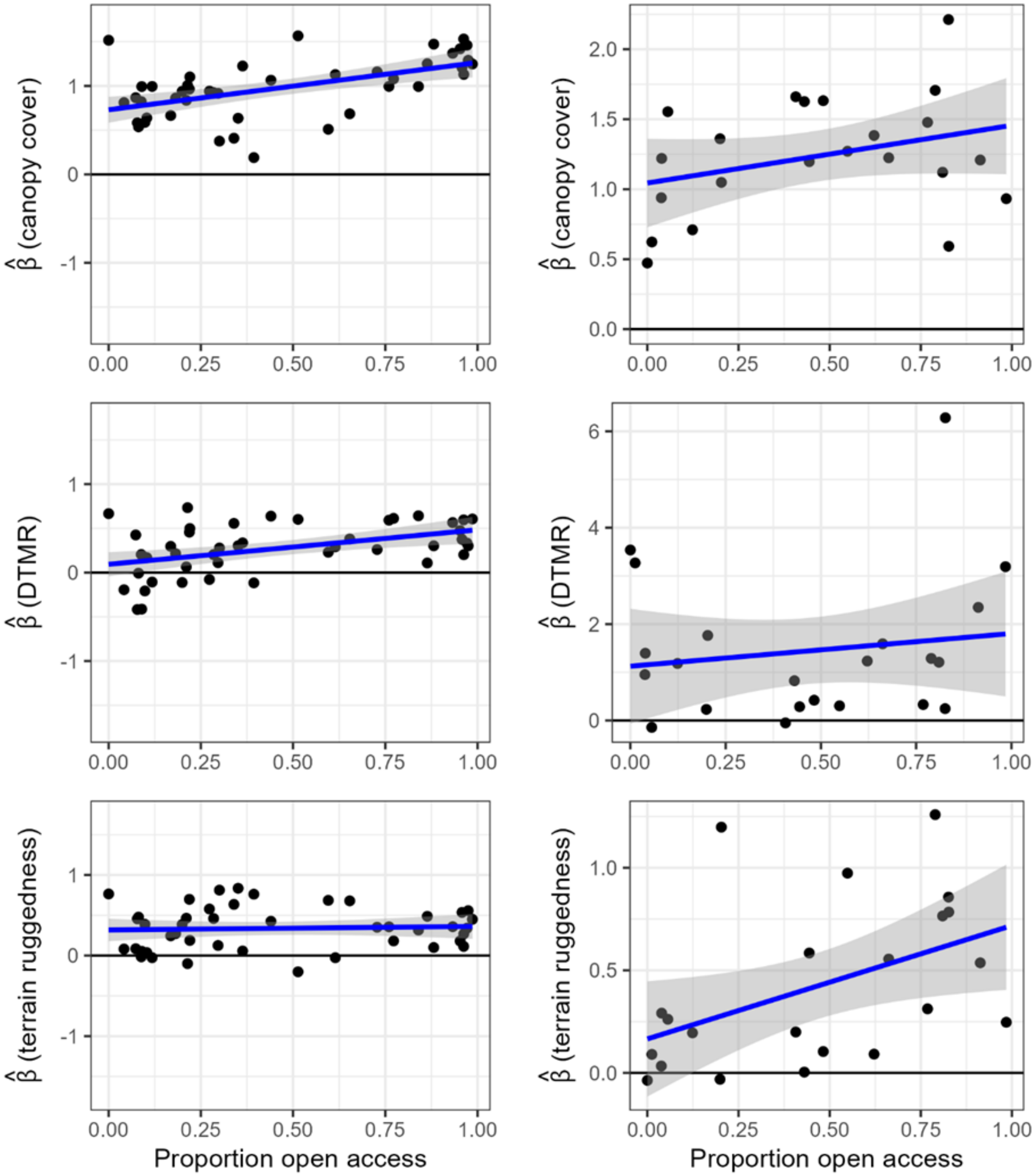

Figure 7. Functional responses between harvest risk (i.e., proportion open access) and resource selection for females (left) and males (right) in the Custer Forest area.

In the Missouri River Breaks (Figure 8), we found strong evidence of relationships between female elk selection and risk with canopy cover ($\hat{\beta}$ = 0.528, 95% CI = 0.157, 0.898) and terrain ruggedness ($\hat{\beta}$ = 1.184, 95% CI = 0.82, 1.549), and fairly weak support for this relationship with distance to routes ($\hat{\beta}$ = 0.518, 95% CI = -0.264, 1.301). For male elk, 95% confidence intervals that widely overlapped zero indicated no evidence for risk-related functional responses with any tested habitat feature.

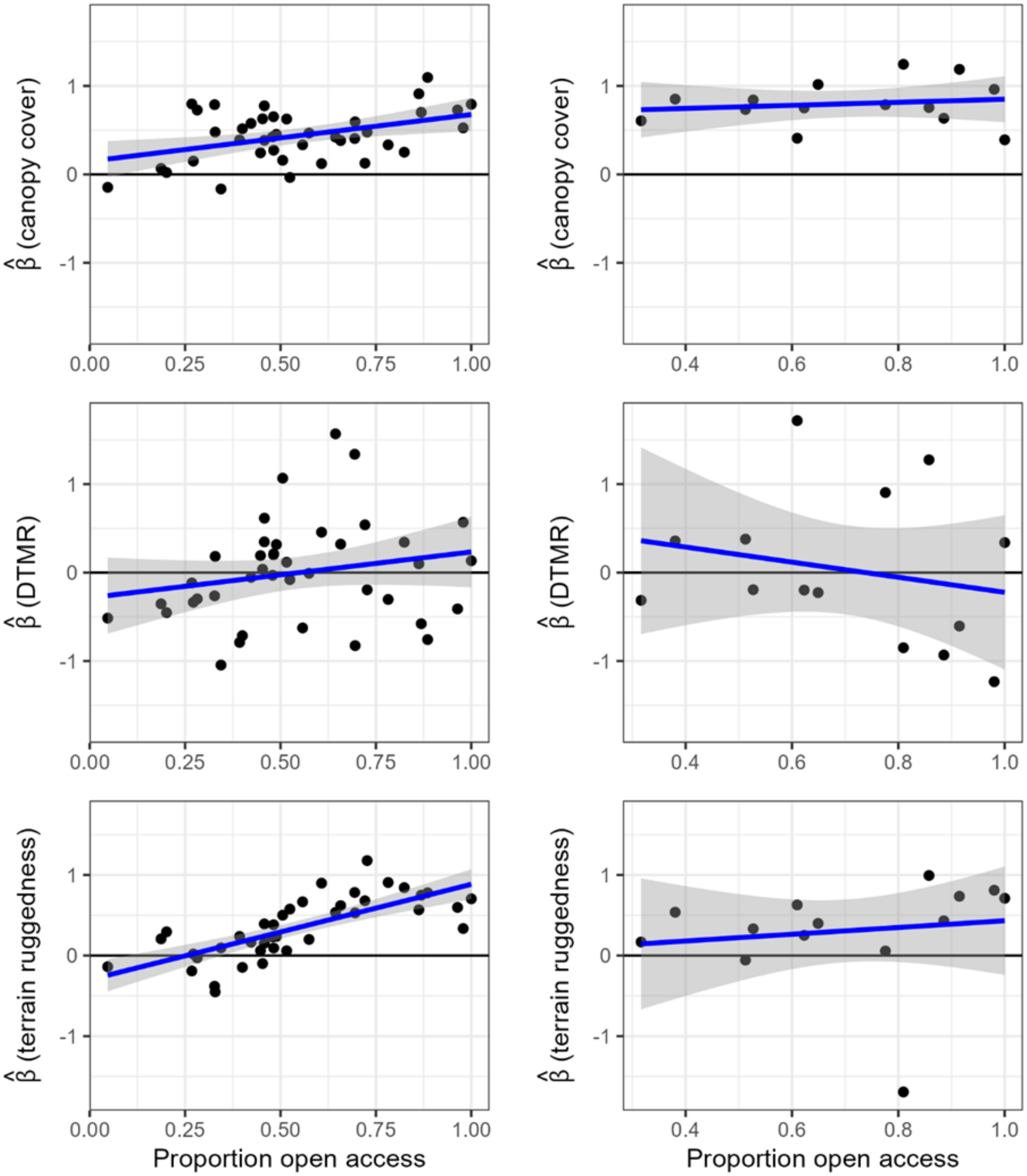

Figure 8. Functional responses between harvest risk (i.e., proportion open access) and resource selection for females (left) and males (right) in the Missouri River Breaks area.

## Security Area Thresholds

Security and preferred security thresholds differed substantially between the populations but were similar regardless of sex. 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 public motorized routes, and ruggedness values ≥7.00 and ≥19.21. 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 public motorized routes, and ≥7.33 and ≥18.44 on the ruggedness index. In the Missouri River Breaks, female elk selected security and preferred security areas with notably low canopy cover values at ≥2.74 and ≥5.09% and with ruggedness values ≥13.94 and ≥22.90. Similarly, male elk in the Missouri River Breaks selected security and preferred security areas with canopy cover ≥3.84 and ≥6.53% and values ≥13.48 and ≥22.72 on the ruggedness index. In the Missouri River Breaks, the 95% confidence intervals for the estimated distance to motorized routes coefficient widely overlapped zero for both sexes, suggesting this covariate was not strongly associated with selection during the rifle season.

# DISCUSSION

Our results indicated that elk selected for areas that had restricted hunter access, were farther from roads, had higher canopy cover, and had more rugged terrain during the rifle hunting season in our prairie study areas, albeit with some notable exceptions in the Missouri River Breaks. Elk utilization of areas with limited 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 been documented in other parts of the Missouri River 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, which is crucial for controlling population size (Burcham et al. 1999, Haggerty and Travis 2006). Altering the spatial distribution of hunting pressure by working with stakeholders to improve hunter access may be one tool available to manipulate elk habitat use and achieve more desirable distributions across a matrix of public and private lands (Sergeyev et al. 2022). Another management strategy for manipulating elk distributions may be to protect or increase elk security habitat on public lands to encourage elk to spend more time in these areas, though doing so requires location-appropriate definitions of security habitat that account for local habitat conditions and availability.

Interestingly, male elk in our Missouri River Breaks study area did not show selective preference among areas of differing hunter access, and in fact, limited evidence suggests that they may slightly prefer areas that were accessible to hunters. It is possible that this pattern was driven by relatively high hunting pressure on private lands in concert with adequate security habitat available on public lands, or alternatively, that hunting pressure is relatively low on public lands. In this area of the Missouri River Breaks, much of the public land is difficult to access and recent changes in hunting access management on private lands could drive unexpected changes in elk behavior and movement. Further, we did not detect relationships between male elk selection and the proportion of an individual's GPS locations falling on accessible lands, a result that could be caused by relatively equal harvest risk across the two access types. In contrast, female elk in the Missouri Breaks did exhibit preference for restricted access lands, suggesting that the gradient of harvest risk across open and restricted access lands may differ for male and female elk in this landscape. However, there are two aspects of our study design that could also contribute to this finding. First, we classified Type II BMAs as restricted access as they require reservations to hunt and are therefore usually more restrictive than Type I BMAs that allow hunters to administer their own access. In the Missouri River Breaks area, however, observations suggest that Type II BMAs don't severely limit hunter numbers and may have hunting pressure that is more similar to that on publicly accessible areas. Second, GPS collar malfunctions and elk mortalities, primarily from hunter harvest, resulted in a smaller number of individuals included in our analysis ($n = 14$), which may have limited our ability to capture strong population-level selection patterns. Despite these potential limitations, overall, our findings suggest that in mixed public-private landscapes with a variety of hunting access management strategies, a lack of a strong gradient of harvest risk across open and restricted access lands could produce limited elk responses to hunter access, contrary to patterns observed in other recent studies of elk habitat use during hunting seasons (Proffitt et al. 2013, 2016, Ranglack et al. 2017, Sergeyev et al. 2022).

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). However, we were unable to detect clear population-level responses to motorized routes for male and female elk in the Missouri River Breaks. This area has relatively few public roads and most are primitive routes with dirt and gravel surfaces. On these primitive roads, conditions can change rapidly in wet weather, with many roads quickly becoming impassable and limiting hunter access to some areas. Consequently, elk may not respond strongly to motorized routes if they are used infrequently by hunters. Given the remoteness of this area, yet another possibility is that our spatial data underlying the distance to motorized route covariate did not capture existing roads with complete accuracy, which would also make it difficult to detect consistent elk responses. Although we did not capture a clear population-level response to roads, 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. In contrast, we documented more consistent population-level responses to motorized routes in the Custer Forest area as predicted. Our findings suggest that elk responses to roads may need to be considered in context with surrounding landscape, and that elk may not respond consistently to route distance in areas like the Missouri Breaks that have few reliable roads to begin with and that are subject to changing conditions.

Elk in our study areas also selected for areas with greater canopy cover and more rugged terrain, presumably to mitigate exposure to harvest risk. Increasing canopy cover was associated with the greatest increases in relative probability of use as compared to other covariates. The effects of canopy cover on elk habitat use during hunting and implications for security habitat definitions vary between studies, though 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 3-5%. In the Custer Forest, these thresholds were more typical of forested systems at 27-36%. Our estimated security thresholds were very similar for male and female elk, so these values are appropriate for both sexes. 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). 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. 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 be due to the fact that we included both public and private motorized routes in our distance raster and that relatively high road densities exist on the Custer National Forest, such that greater distances from roads aren’t common in the study area. Consequently, seasonal closures on the Custer National Forest likely would 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, locating security areas in rugged terrain with values of 7-18 and 13-22 on the terrain ruggedness index (Riley et al. 1999) in the Custer Forest and Missouri Breaks, respectively, may further enhance elk security.

We found evidence of significant variability among individuals in selection patterns, and the inclusion of random coefficients improved model fit in all cases. Generally, individual elk shared the same direction of selection for a given habitat feature but varied in the strength and magnitude of the relationship. For example, every individual preferentially used higher canopy cover, but the relationship was stronger for some individuals than others. This pattern differed slightly for distances to motorized routes and terrain ruggedness, where individual selection patterns ranged from no apparent selection for the covariate to strong positive relationships. Although some of this variability 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 individuals with strongest positive relationships with security habitat features are also exposed to the highest levels of risk. Our investigation of risk-related responses in habitat selection provided evidence that elk increased their use of habitat features that provide security when faced with higher levels of harvest risk, which corresponds with findings for other Montana elk populations (Proffitt et al. 2016, DeVoe et al. 2019). Given these risk-related responses, managers should consider employing more conservative versions of our security thresholds, which were calculated based on models built with observations from elk experiencing a gradient of harvest risk, for public lands that are characterized by elevated levels of hunting pressure.

We also found that elk preferred greater herbaceous biomass and avoided areas with more snow accumulation. Nutrition during the late summer and fall is crucial to the growth of juveniles and yearlings, fat accretion in adults, pregnancy rates and overwinter survival, all of which influence elk population dynamics (Cook et al. 2004, 2013). We found that both male and female elk selected for herbaceous biomass, indicating that forage availability and quality remains an important driver of elk habitat use even into the late fall in our prairie study areas. Similarly, Mackie (1970) observed that occasional vegetative green-up during the fall influenced ungulate space use in the Missouri River Breaks, and it's possible that the selection for herbaceous biomass we observed is also partially driven by late season green-up in eastern Montana. We detected these relationships even though our covariates were based on data averaged over several years and included years preceding the study period, suggesting that spatial patterns of snow fall and vegetative production are at least somewhat spatially consistent through time even though the landscape is considered relatively homogenous (Proffitt et al. 2016). Therefore, managers may want to consider the potential effects of forage availability and snow accumulation on elk distributions during the hunting season.

As elk distributions expand in Montana's eastern prairie regions, understanding elk-habitat relationships in these areas will continue to be important for effective population and habitat management. Archery and rifle elk hunting are increasingly popular in HDs 700 and 704 where our study took place. Increases in hunter numbers, changes in access on private lands, as well as overall shifts in the distribution of hunting pressure may lead to changes in elk behavior and movement that will be important to document to continue to provide satisfactory hunter opportunity, meet harvest objectives and manage elk population size and distributions.

# CONCLUSIONS

Elk GPS location data, remotely sensed habitat data, and resource selection function analyses revealed that, in general, elk in our prairie study areas preferentially used canopy cover and restricted hunter access during the rifle season. In addition, rugged terrain and distance from motorized routes may also increase elk security. However, there were a few key differences in our results depending on study area and sex, revealing that responses to route distance may be weaker in landscapes with few reliable roads and that gradients of harvest risk across open and restricted access lands may not always be strong enough to produce elk responses to hunter access. We also found evidence of functional responses between harvest risk and elk resource selection for habitat features that provide security. Elk exposed to higher levels of harvest risk, which is often greatest on lands that do not limit hunter access, tended to exhibit stronger preference for security habitat features including canopy cover, distance from motorized routes and rugged terrain. Although the strength of relationships between risk and elk habitat selection varied based on study area and sex and depended on the covariate, utilizing more conservative security threshold definitions for elk habitat on public lands during the rifle season may be an important management consideration. Our study focused on the rifle season and provided information pertaining to elk habitat selection during the late fall, but we still have limited knowledge of seasonal habitat use and movement patterns of elk during other parts of the year in prairie landscapes. Therefore, practical avenues for future research may include evaluating habitat selection during archery and late season hunts and during other important seasons to further enhance elk habitat management in prairie environments.

# APPENDICES

# APPENDIX A

## BACKGROUND AND COVARIATE DEVELOPMENT

Table A1. Start and end dates for the rifle season for each year of study based on Montana Fish, Wildlife and Parks harvest regulations.

| Year | Start | End |
|---|---|---|
| 2021 | 10/23/2021 | 11/28/2021 |
| 2022 | 10/22/2022 | 11/27/2022 |
| 2023 | 10/21/2023 | 11/26/2023 |

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).

**Forage availability** – 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 A2. Covariates, functional forms and hypothesized direction of selection included in rifle season resource selection modeling for male and female elk in the Custer Forest and Missouri Breaks populations, eastern Montana, USA, 2021-2023. 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<br>All routes<br>Public routes only | Linear (+), psuedothreshold (+) |
| Terrain ruggedness | Linear (+), psuedothreshold (+), |
| Snow water equivalent | Linear (-), psuedothreshold (-) |
| Forage availability | Linear (+), psuedothreshold (+) |

# APPENDIX B

## GPS LOCATION AND USED-AVAILABLE DATA SUMMARIES

Table B1. Summaries of GPS location data for male and female elk in the Custer Forest and Missouri River Breaks areas in southeastern and northeastern Montana, respectively, 2021-2023.

| **Sex** | **Animal count** | **Animal-year count** | **Total GPS locations** | **Avg. GPS locations per animal per rifle season** |
|---|---|---|---|---|
| **Custer Forest** | | | | |
| Female | 44 | 106 | 30,251 | 285.39 |
| Male | 22 | 28 | 7,624 | 272.29 |
| **Missouri River Breaks** | | | | |
| Female | 40 | 68 | 20,616 | 303.18 |
| Male | 14 | 15 | 4,355 | 290.33 |
| **Total** | | | | |
| | 120 | 217 | 62,846 | 287.80 |

Table B2. Proportions of used and available locations occurring on open access lands for male and female elk in the Custer Forest and Missouri River Breaks areas.

| **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 B3. Mean, standard error, minimum and maximum values for all continuous covariates for male and female elk in the Custer Forest population.

| | 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 | 1065.43 | 2.13 | 2.87 | 2570.69 |

Table B4. Mean, standard error, minimum and maximum values for all continuous covariates for male and female elk in the Missouri River Breaks population.

| | **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 | 240.85 | 2364.93 | 858.95 | 2.03 | 0 | 2232.69 |

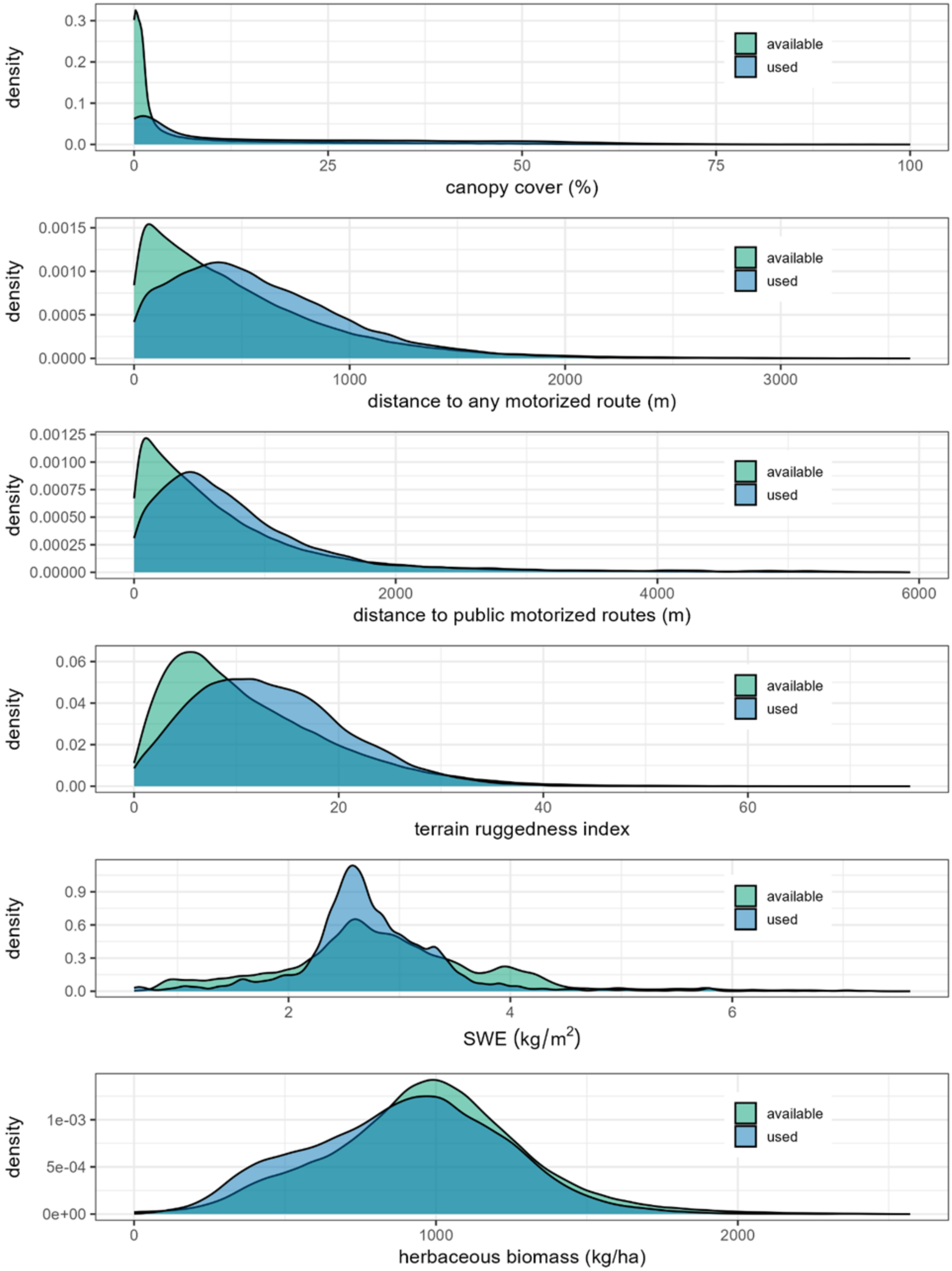

Figure B1. Density plots of all continuous covariates for used-available data pooled across sexes and the Custer Forest and Missouri River Breaks areas.

# APPENDIX C

## ADDITIONAL RESOURCE SELECTION MODELING RESULTS

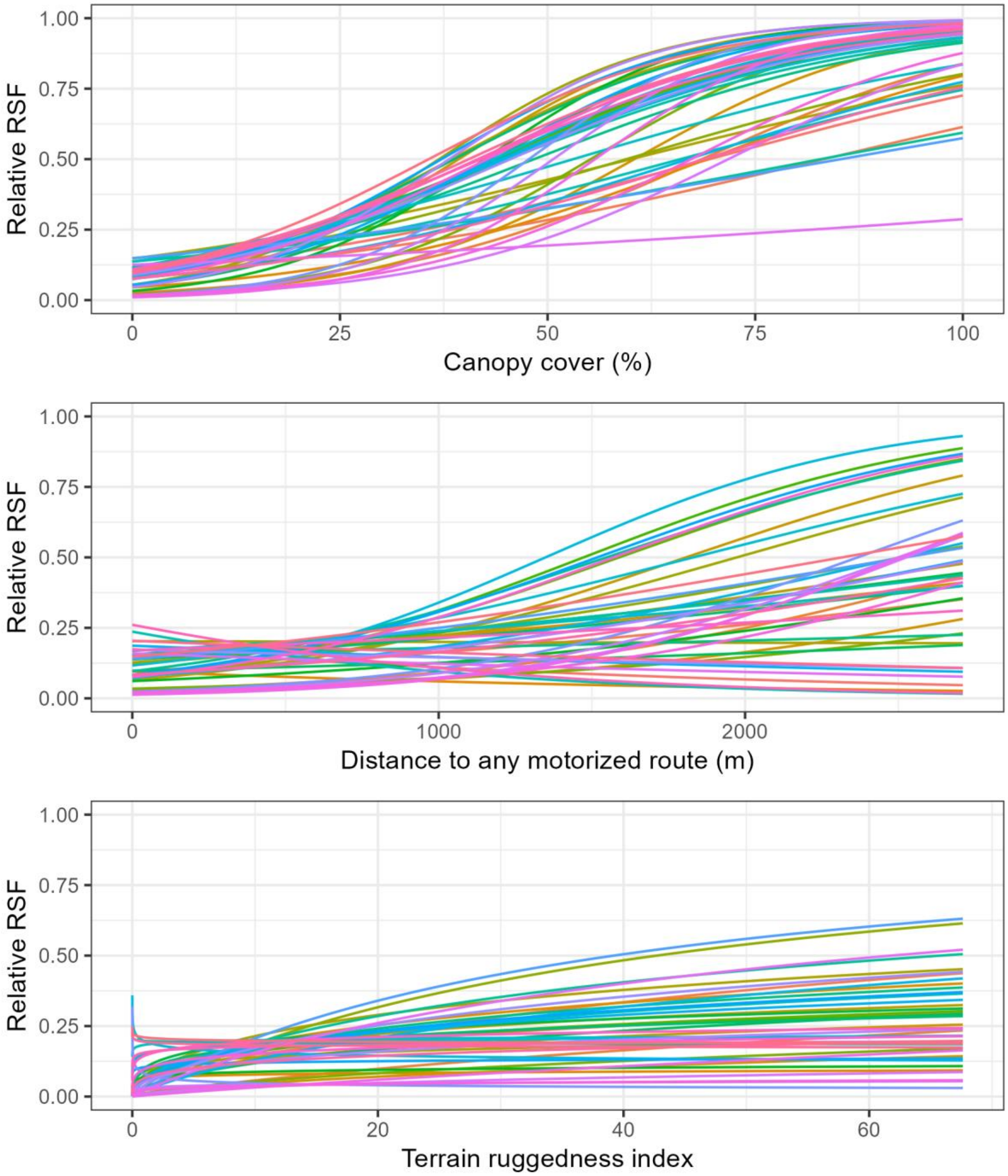

Figure C1. Predicted relative resource selection functions for individual female elk in the Custer Forest area in southeastern Montana, 2021-2023, based on random coefficient estimates from the final resource selection model.

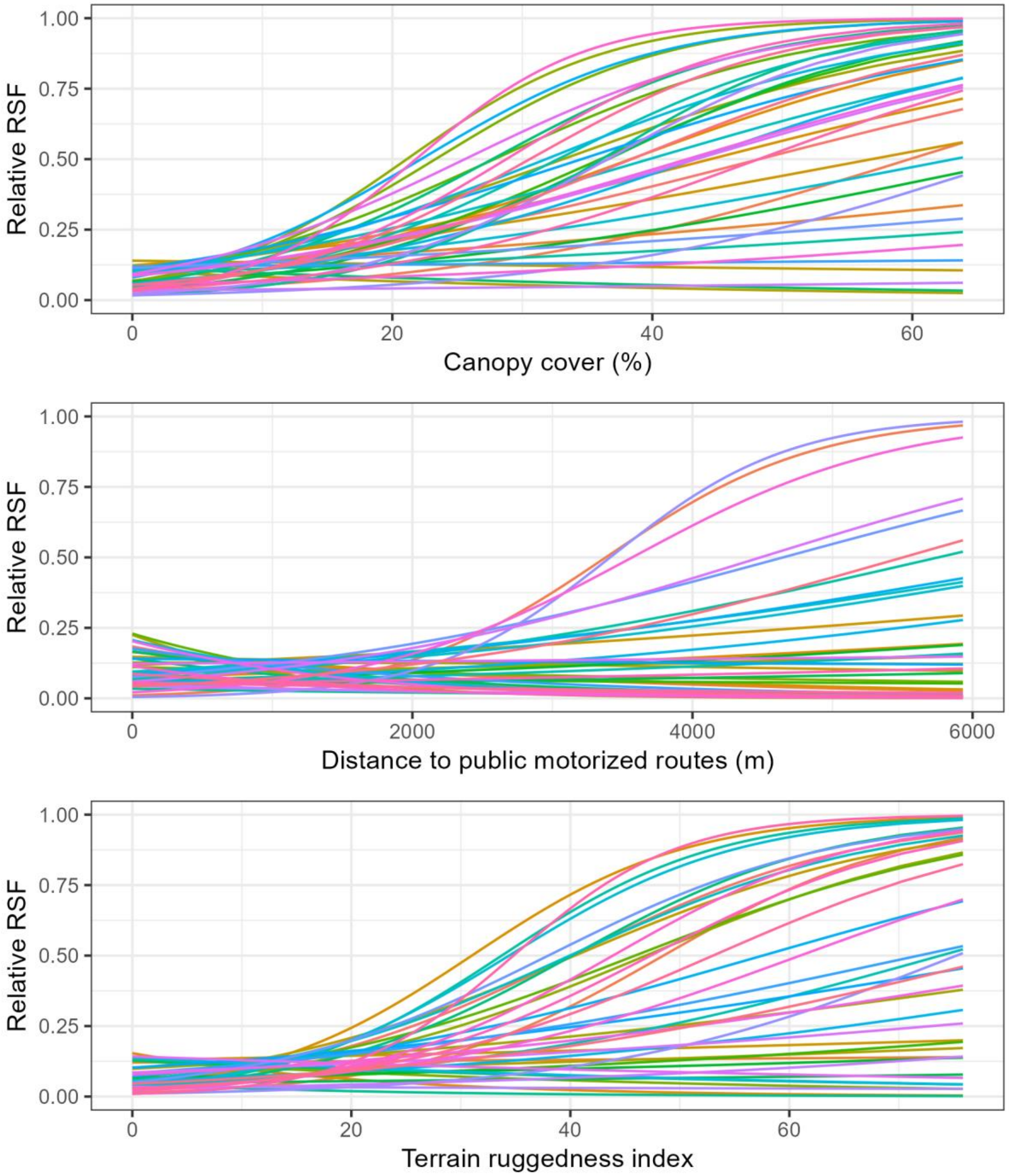

Figure C2. Predicted relative resource selection functions for individual female elk in the Missouri River Breaks area of northeastern Montana, 2021-2023, based on random coefficient estimates from the final resource selection model.

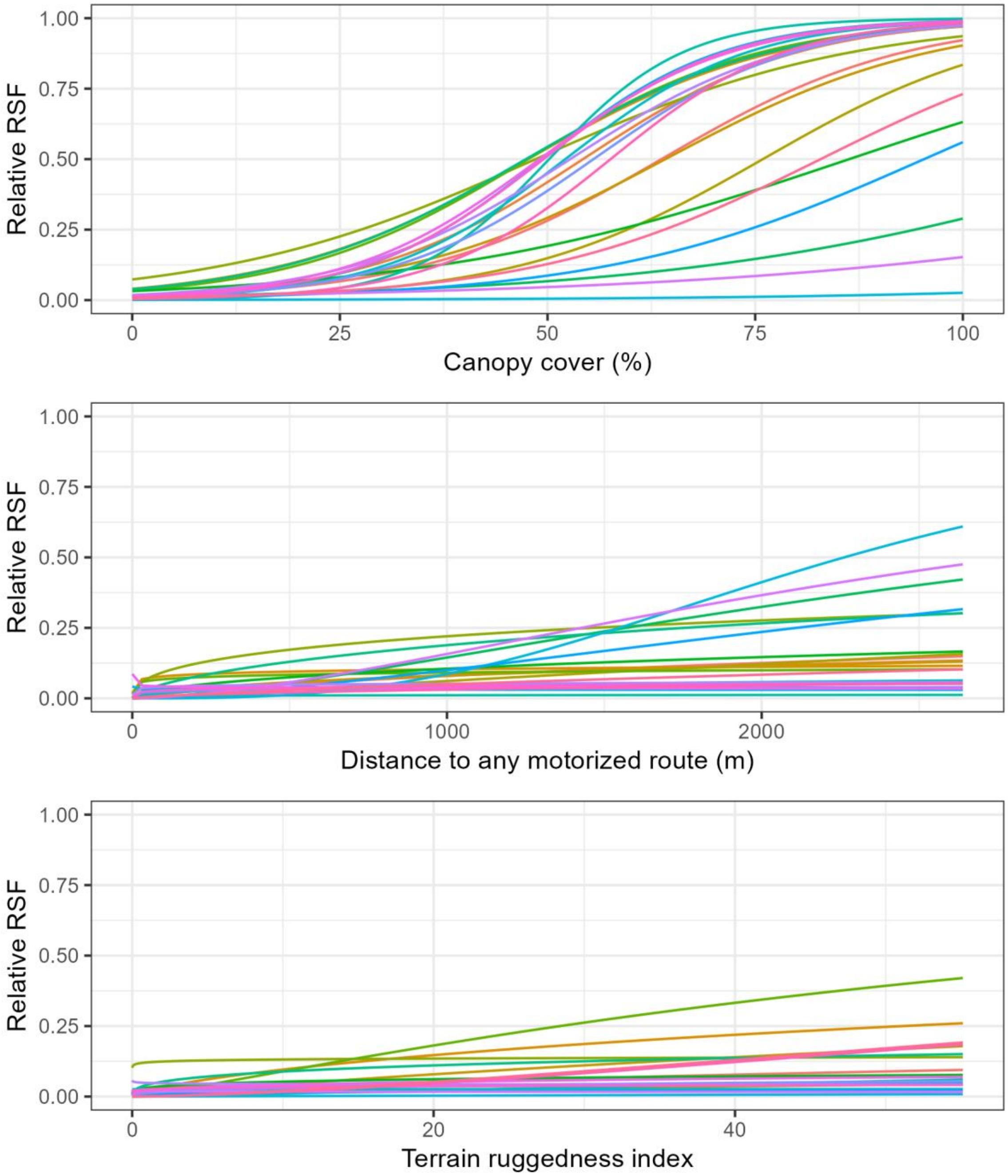

Figure C3. Predicted relative resource selection functions for individual male elk in the Custer Forest area of southeastern Montana, 2021-2023, based on random coefficient estimates from the final resource selection model.

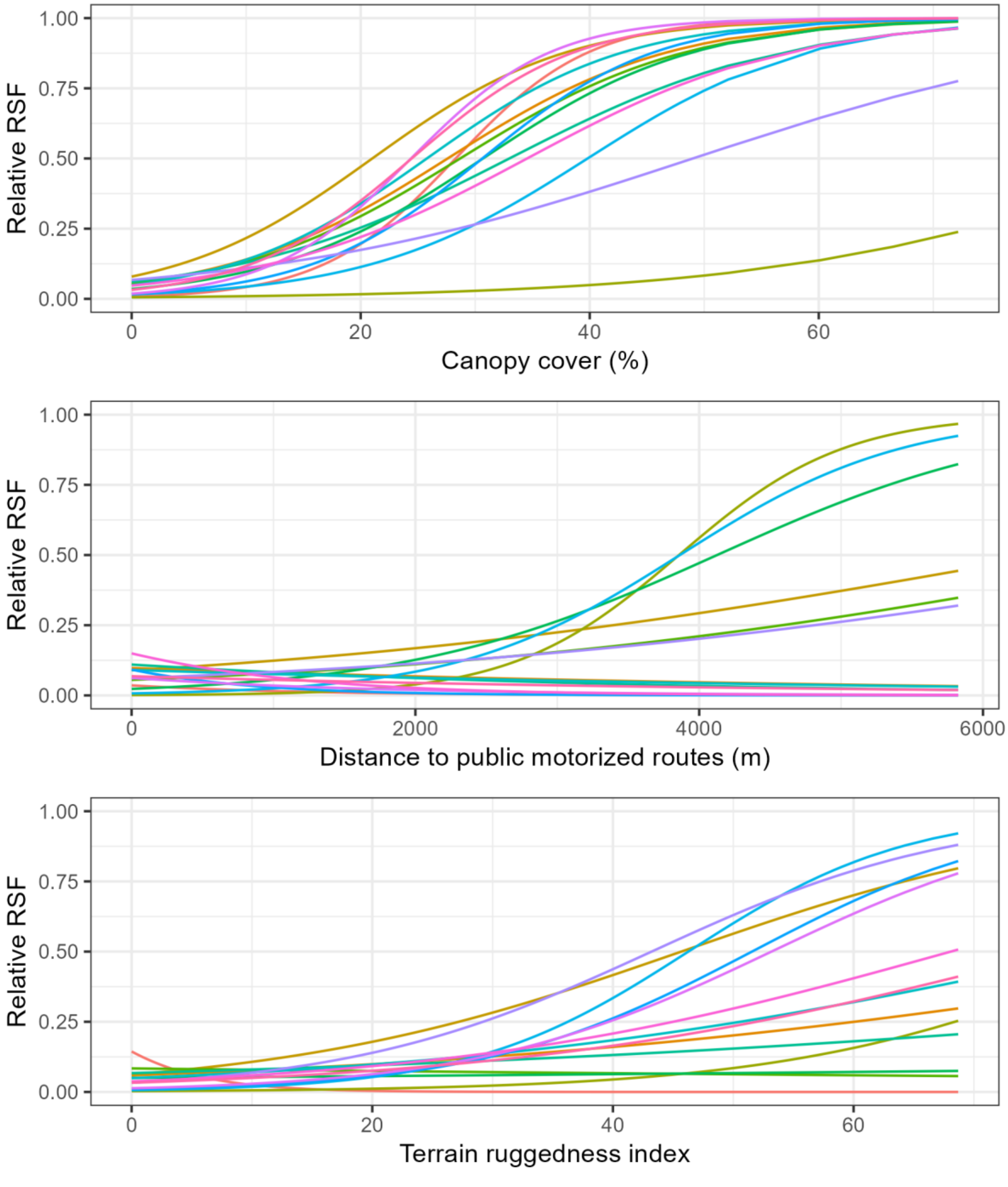

Figure C4. Predicted relative resource selection functions for individual male elk in the Missouri River Breaks area of northeastern Montana, 2022-2023, based on random coefficient estimates from the final resource selection model.

# REFERENCES CITED

Aikens, E. O., K. L. Monteith, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and M. J. Kauffman. 2020a. Drought reshuffles plant phenology and reduces the foraging benefit of green-wave surfing for a migratory ungulate. Global Change Biology 26:4215–4225.

Aikens, E. O., A. Mysterud, J. A. Merkle, F. Cagnacci, I. M. Rivrud, M. Hebblewhite, M. A. Hurley, W. Peters, S. Bergen, J. De Groeve, S. P. H. Dwinnell, B. Gehr, M. Heurich, A. J. M. Hewison, A. Jarnemo, P. Kjellander, M. Kröschel, A. Licoppe, J. D. C. Linnell, E. H. Merrill, A. D. Middleton, N. Morellet, L. Neufeld, A. C. Ortega, K. L. Parker, L. Pedrotti, K. M. Proffitt, S. Saïd, H. Sawyer, B. M. Scurlock, J. Signer, P. Stent, P. Šustr, T. Szkorupa, K. L. Monteith, and M. J. Kauffman. 2020b. Wave-like Patterns of Plant Phenology Determine Ungulate Movement Tactics. Current Biology 30:3444-3449.e4.

Allred, B. W., B. T. Bestelmeyer, C. S. Boyd, C. Brown, K. W. Davies, M. C. Duniway, L. M. Ellsworth, T. A. Erickson, S. D. Fuhlendorf, T. V. Griffiths, V. Jansen, M. O. Jones, J. Karl, A. Knight, J. D. Maestas, J. J. Maynard, S. E. McCord, D. E. Naugle, H. D. Starns, D. Twidwell, and D. R. Uden. 2021. Improving Landsat predictions of rangeland fractional cover with multitask learning and uncertainty. Methods in Ecology and Evolution 12:841–849.

Basille, M., B. V. Moorter, I. Herfindal, J. Martin, J. D. C. Linnell, J. Odden, R. Andersen, and J.-M. Gaillard. 2013. Selecting Habitat to Survive: The Impact of Road Density on Survival in a Large Carnivore. PLOS ONE 8:e65493.

van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723–735.

Bocinsky, R. K. 2023. FedData: Functions to Automate Downloading Geospatial Data Available from Several Federated Data Sources. <http://CRAN.R-project.org/package=FedData>.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research 59:185–193.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Burcham, M., W. D. Edge, and C. L. Marcum. 1999. Elk Use of Private Land Refuges. Wildlife Society Bulletin (1973-2006) 27:833–839.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science and Business Media, New York, New York, USA.

Christensen, A. G., L. J. Lyon, and J. W. Unsworth. 1993. Elk management in the Northern Region: Considerations in forest plan updates or revisions. Gen. Tech. Rep. INT-303. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 10 p. 303. <https://research.fs.usda.gov/treesearch/35132>. Accessed 20 Jul 2024.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking Elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of Summer-Autumn Nutrition and Parturition Date on Reproduction and Survival of Elk. Wildlife Monographs 155:1–61.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

DeVoe, J. D., K. M. Proffitt, M. S. Mitchell, C. S. Jourdonnais, and K. J. Barker. 2019. Elk forage and risk tradeoffs during the fall archery season. The Journal of Wildlife Management 83:801–816.

Donovan, G., and P. Champ. 2009. The Economic Benefits of Elk Viewing at the Jewell Meadows Wildlife Area in Oregon. Human Dimensions of Wildlife 14:51–60.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Eliason, S. L. 2008. A Statewide Examination of Hunting and Trophy Nonhuman Animals: Perspectives of Montana Hunters. Society & Animals 16:256–278.

Garrott, R. A., P. J. White, and F. G. R. Watson. 2008. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Academic Press.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gude, J. A., J. A. Cunningham, J. T. Herbert, and T. Baumeister. 2012. Deer and elk hunter recruitment, retention, and participation trends in Montana. The Journal of Wildlife Management 76:471–479.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.

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

Hijmans, R. J. 2024. terra: Spatial Data Analysis. <http://CRAN.R-project.org/package=terra>.

Hillis, J., M. Thompson, J. Canfield, L. Lyon, C. Marcum, P. Dolan, and D. McCleerey. 1991. Defining elk security: the Hillis Paradigm. Pages 38–43 in. Proceedings of a Symposium on Elk Vulnerability. Montana State University, Bozeman, USA.

Hobbs, N. T. 1996. Modification of Ecosystems by Ungulates. The Journal of Wildlife Management 60:695–713.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61:65–71.

Jones, M. O., N. P. Robinson, D. E. Naugle, J. D. Maestas, M. C. Reeves, R. W. Lankston, and B. W. Allred. 2021. Annual and 16-Day Rangeland Production Estimates for the Western United States. Rangeland Ecology & Management 77:112–117.

Lowrey, B., J. Devoe, K. M. Proffitt, and R. A. Garrott. 2020. Hiding Without Cover? Defining Elk Security in a Beetle-Killed Forest. The Journal of Wildlife Management 84:138–149.

Mabille, G., C. Dussault, J.-P. Ouellet, and C. Laurian. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. Oecologia 170:965–977.

Mackie, R. J. 1970. Range Ecology and Relations of Mule Deer, Elk, and Cattle in the Missouri River Breaks, Montana. Wildlife Monographs 3–79.

Manly, B. F., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Springer Science & Business Media.

McCool, S. F. 1996. Wildlife viewing, natural area protection, and community sustainability and resiliency. Natural Areas Journal 16:147–151.

Mikle, N. L., T. A. Graves, and E. M. Olexa. 2019. To forage or flee: lessons from an elk migration near a protected area. Ecosphere 10:e02693.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and Hunter Space-Use Sharing in South Dakota. The Journal of Wildlife Management 64:994–1003.

Montana Department of Fish, Wildlife and Parks. 2023. Montana Statewide Elk Management Plan. Montana Fish, Wildlife and Parks, Wildlife Division, Helena, USA. <https://fwp.mt.gov/conservation/wildlife-management/elk/elk-management-plan>.

Morris, D. W. 1989. Density-dependent habitat selection: Testing the theory with fitness data. Evolutionary Ecology 3:80–94.

Morrison, M. L., B. Marcot, and W. Mannan. 2012. Wildlife-Habitat Relationships: Concepts and Applications. Island Press.

Muff, S., J. Signer, and J. Fieberg. 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology 89:80–92.

Mysterud, A., and R. A. Ims. 1998. Functional Responses in Habitat Use: Availability Influences Relative Use in Trade-Off Situations. Ecology 79:1435–1441.

Oregon State University. 2024. PRISM Climate Group. <https://prism.oregonstate.edu>. Accessed 16 Jul 2024.

Paterson, J. T., K. M. Proffitt, N. J. DeCesare, J. A. Gude, and M. Hebblewhite. 2022. Evaluating the summer landscapes of predation risk and forage quality for elk (Cervus canadensis). Ecology and Evolution 12:e9201.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. Journal of Wildlife Management 73:345–356.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. The Journal of Wildlife Management 77:514–524.

Proffitt, K. M., S. Thompson, D. Henry, B. Jimenez, and J. A. Gude. 2016. Hunter access affects elk resource selection in the Missouri breaks, Montana. The Journal of Wildlife Management 80:1167–1176.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2017. Security areas for elk during archery and rifle hunting seasons. The Journal of Wildlife Management 81:778–791.

Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2022. Modeling broad-scale patterns of elk summer resource selection in Montana using regional and population-specific models. Ecosphere 13:e4311.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Science 5:23–27.

Rosenzweig, M. L. 1991. Habitat Selection and Population Interactions: The Search for Mechanism. The American Naturalist 137:S5–S28.

Robinson, N. P., M. O. Jones, A. Moreno, T. A. Erickson, D. E. Naugle, and B. W. Allred. 2019. Rangeland Productivity Partitioned to Sub-Pixel Plant Functional Types. Remote Sensing 11:1427.

Sergeyev, M., B. R. McMillan, L. K. Hall, K. R. Hersey, C. D. Jones, and R. T. Larsen. 2022. Reducing the refuge effect: using private-land hunting to mitigate issues with hunter access. The Journal of Wildlife Management 86:e22148.

Sergeyev, M., B. R. McMillan, K. R. Hersey, and R. T. Larsen. 2020. The influence of habitat use on harvest vulnerability of cow elk (Cervus canadensis). PLOS ONE 15:e0242841.

Skovlin, J. M., P. Zager, and P. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–556 in. North American elk: ecology and management. Smithsonian Institute Press, Washington, D.C., USA.

Stewart, C. M., B. Keller, and C. R. Williamson. 2013. Keys to managing a successful archery deer hunt in an urban community: a case study. Human-Wildlife Interactions 7:132–139.

Stewart, D. G., W. D. Gulsby, S. S. Ditchkoff, and B. A. Collier. 2022. Spatiotemporal patterns of male and female white-tailed deer on a hunted landscape. Ecology and Evolution 12. <https://onlinelibrary.wiley.com/doi/10.1002/ece3.9277>. Accessed 9 Oct 2022.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. Behavioural Processes 120:30–39.

Thornton, M. M., R. Shrestha, Y. Wei, P. E. Thornton, S.-C. Kao, and B. E. Wilson. 2022. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1. ORNL DAAC. <https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=2129>. Accessed 9 Jan 2024.

Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Canadian Journal of Zoology 87:1129–1137.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk Habitat Selection on the Clearwater National Forest, Idaho. The Journal of Wildlife Management 62:1255–1263.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk Mortality in the Clearwater Drainage of Northcentral Idaho. The Journal of Wildlife Management 57:495–502.

U.S. Census Bureau. 2018. U.S. Census 2018 TIGER/Line files machine-readable data files. U.S. Census Bureau, Washington, D.C., USA. <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>. Accessed 8 Mar 2024.

U.S. Geological Survey. 2023a. National Hydrography Dataset. <https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products>. Accessed 31 Mar 2024.

U.S. Geological Survey. 2023b. 3D Elevation Program 30-Meter Resolution Digital Elevation Model. <https://www.usgs.gov/the-national-map-data-delivery>. Accessed 18 Dec 2023.

U.S. Geological Survey (USGS) Gap Analysis Project (GAP). 2022. Protected Areas Database of the United States (PAD-US). U.S. Geological Survey data release. <https://doi.org/10.5066/P9Q9LQ4B>. Accessed 4 Apr 2024.

Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of Archery Hunter Numbers and Opening Dates on Elk Movement. The Journal of Wildlife Management 67:717–728.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An Experimental Test of the Effects of Predation Risk on Habitat Use in Fish. Ecology 64:1540–1548.

Worton, B. J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70:164–168.