



Federal Aid in Wildlife Restoration Grant W-175-R

Final report, June 2022

Montana Blackfoot Elk Study

Dr. Joshua Millspaugh, Professor, University of Montana,
Forestry 108, Missoula, MT 59812
Joshua.millspaugh@mso.umt.edu

Lauren Snobl, Graduate Student, University of Montana,
Forestry 108, Missoula, MT 59812
laurensnobl@gmail.com

Dr. Kelly Proffitt, Research Biologist, Montana Fish, Wildlife & Parks,
1400 S. 19th Ave, Bozeman, MT 59715
kproffitt@mt.gov

Dr. Christopher Hansen, Postdoctoral Research Associate, University of Montana,
Forestry 108, Missoula, MT 59812
christopher.hansen@mso.umt.edu

Jonathan Karlen, Graduate Student, University of Montana,
Forestry 108, Missoula, MT 59812
jonathan.karlen@umconnect.umt.edu

Benjamin Jimenez, Research Technician, Montana Fish, Wildlife & Parks,
3201 Spurgin Road, Missoula, MT 59804

State: Montana

Agencies: Fish, Wildlife & Parks and University of Montana

Grant: Montana Blackfoot Elk Study

Grant #: W-175-R

Time Period: 1 December, 2018– 01 June, 2022

Table of Contents

LIST OF TABLES	5
LIST OF FIGURES	7
EXECUTIVE SUMMARY	12
PROJECT BACKGROUND.....	15
STUDY AREA.....	18
OBJECTIVE 1: COLLECT ELK DIET DATA	21
Methods	21
<i>Field Methods: Pellet Sample Collection.....</i>	<i>21</i>
<i>Lab Methods: DNA Metabarcoding</i>	<i>21</i>
<i>Analytical Methods: Classification Methods for Diet List</i>	<i>21</i>
Results	22
OBJECTIVE 2: EVALUATE ELK BODY CONDITION AND PREGNANCY RATES... 24	
Methods	24
<i>Field Methods.....</i>	<i>24</i>
<i>Analytical Methods.....</i>	<i>24</i>
Results	24
OBJECTIVE 3: EVALUATE AND COMPARE ELK USE OF AREAS THAT BURNED AT DIFFERENT LEVELS OF FIRE SEVERITY..... 27	
Methods	27
Results	27
OBJECTIVE 4: EVALUATE AND COMPARE VEGETATION AND FORAGE RESOURCES IN AREAS THAT BURNED AT DIFFERENT LEVELS OF SEVERITY 31	
Methods	31
<i>Field Methods: Site Selection.....</i>	<i>31</i>
<i>Field Methods: Estimating Phenological Stage-Specific Digestible Energy.....</i>	<i>31</i>
<i>Field Methods: Estimating Forage Quality and Quantity.....</i>	<i>32</i>
<i>Analytical Methods: Landscape Modeling.....</i>	<i>33</i>
<i>Analytical Methods: Phenological Differences Between Fire Severities.....</i>	<i>34</i>
<i>Analytical Methods: Predicted Landscape Level Differences Between Fire Severities.....</i>	<i>34</i>
Results	34

<i>Vegetation Sampling Sites</i>	34
<i>Estimating Forage Quality and Quantity</i>	35
<i>Landscape Modeling</i>	37
<i>Phenological Differences Between Fire Severities</i>	40
<i>Predicted Landscape Level Differences Between Fire Severities</i>	41
OBJECTIVE 5: DEVELOP A RESOURCE SELECTION PROBABILITY FUNCTION MODEL TO EVALUATE THE EFFECTS OF WILDFIRE AND OTHER FACTORS ON SUMMER AND FALL ELK DISTRIBUTIONS	44
Methods	44
<i>Identifying Seasons</i>	44
<i>Trail Cameras and Prevalence</i>	45
<i>Covariates:Nutrition</i>	49
<i>Covariates:Landscape</i>	52
<i>Covariates:Predation Risk/Hunting</i>	52
<i>Covariates:Environmental</i>	53
<i>Resource Selection Probability Function</i>	53
Results	54
<i>Identifying Seasons</i>	54
<i>Frequency of Predator Detections Covariate</i>	57
<i>RSPF:Neonatal/Summer</i>	61
<i>RSPF: Prehunt</i>	65
<i>RSPF: Archery-Only</i>	67
<i>RSPF: Backcountry-Rifle</i>	69
<i>RSPF: Rifle</i>	71
ADDITIONAL ANALYSIS: MAMMAL COMMUNITY USE OF AREAS THAT BURNED AT DIFFERENT LEVELS OF FIRE SEVERITY	76
Methods	76
<i>Field Methods</i>	76
<i>Analytical Methods</i>	76
Results	77
OBJECTIVE 6: RECOMMENDATIONS FOR FIRE MANAGEMENT TO IMPROVE ELK HABITAT	80

<i>Conclusions</i>	80
<i>Recommendations</i>	81
LITERATURE CITED	83

LIST OF TABLES

Table 1. Hunting regulations and hunter pressure found within each of the 10 hunting districts found in the Blackfoot-Clearwater elk range in west-central Montana, USA for 2019 and 2020. Hunter pressure is expressed as the total number of hunter days annually for each hunting period and district estimated using the Montana Fish, Wildlife and Parks harvest survey program from data collected in 2020. *First 10 days: brow-tined bull or antlerless elk for youth only ages 12-15; brow-tined bull for general license; After the first 10 days: Brow-tined or antlerless elk general licenses. **The two hunting districts that have an early backcountry rifle season..... 20

Table 2. Summer and winter elk diet taxa within the Blackfoot-Clearwater region of west-central Montana, USA that met the FOO and RRA thresholds, the final ranking, and the forage ratios for the ITS2 and rbcL markers. Forage ratios were calculated by comparing the RRA value for each marker to the proportion of vegetation plots containing each food item (i.e., RRA/proportion of plots). The * denotes that the taxon did not meet the forage ratio threshold to be included in the final diet. All other taxa are considered a food item. 23

Table 3. Standardized coefficient estimates and standard errors for the top models predicting summer forage quality in each of the forest types in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. Bold face values denote 95% CI not containing 0. Effects of fire severity in dry and mesic forests are in relation to the reference unburned forest (Intercept)..... 38

Table 4. Standardized coefficient estimates and standard errors for the top models predicting summer herbaceous and shrub forage biomass within dry and mesic forests in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. “NB” refers to the negative binomial part of the model that estimates the amount of biomass and “ZI” refers to the zero inflated part of the model that estimates the presences or absence of biomass. Boldface values denote 95% CI not containing zero. Effects of fire severity are in relation to the reference unburned forest (Intercept). 39

Table 5. Covariates used in modeling resource selection for each season in the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Landcover types included unburned conifer forests (not burned or harvested in the last 15 years), low severity burned conifer forests, high severity burned conifer forests, open (grasslands, agricultural areas, and shrublands), closed (deciduous forests and riparian areas), and other (forests burned or harvested between 2002-2017). The “Hunt Method” covariate only applied to the backcountry rifle season because it was the only season when some districts only allowed archery hunting, while other districts had a rifle option (i.e., backcountry districts). 49

Table 6. Model selection results for female elk occupancy (ψ) during Fall: Period 1 (August 24 – September 14, 2019 or August 22 – September 14, 2020), Fall: Period 2 (September 15 – October 25, 2019 or September 15 – October 23, 2020), and Fall: Period 3 (October 26 – December 13, 2019 or October 24 – December 11, 2020) in the Blackfoot-Clearwater region of west-central Montana, USA. Covariates included in models represent: null (.), archery hunting pressure (“archery”), firearms hunting pressure (“rifle”), distance to open road (“road.dist”), landcover type (“landcover”), digestible energy (“DE”), distance to canopy cover >40% (“canopy.dist”), canopy cover (“canopy”), snow water equivalent (“SWE”), and vector ruggedness measure (“rugged”). “K” represents the number of parameters in the model, “AICc”

is Akaike’s Information Criterion adjusted for small sample size, “ $\Delta AICc$ ” is the difference in AICc units between the current model and the most-supported model, and “AICc wt” is the AICc weight of the model. All models included a constant detection probability (p). 58

Table 7. Parameter estimates, 95% credible intervals (LCrI = 2.5% and UCrI = 97.5% quantiles), and *R* values from a neonatal/summer resource selection probability function for female elk in the Blackfoot-Clearwater region of west-central Montana, USA from 2019-2021. “Predator” = frequency of predator detections, “DE” = digestible energy, “Ruggedness” = vector ruggedness measure, “Dist. To Canopy” = distance to canopy >40%, “Dist. To Road” = distance to road, “Dist to Stream” = distance to hydrologic feature, “Land:Unburned” = unburned forest, “Land:Low Severity” = low severity burned forest, “Land”High Severity” = high severity burned forest, “Land:Open” = open landcover, and “Land:Closed” = closed landcover. Each variable is interacted with season (“*Neonate”), with the summer season and the “Land:Other” landcover types used as the reference (i.e., intercept). 62

Table 8. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the prehunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized, distance to road was included in its pseudothreshold form, and the intercept term is the low severity burned forest. . 65

Table 9. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the archery-only hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized and the intercept term is low severity burned forest..... 67

Table 10. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the backcountry-rifle hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized and the intercept term is low severity burned forest in archery only areas. 69

Table 11. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the general rifle hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. The continuous variables are standardized and the intercept term is low severity burned forest..... 71

Table 12. Burn severity descriptions adapted from the protocol of the Blackfoot Clearwater Elk project in west-central Montana. Moderate severity fire classification was not part of the Blackfoot Clearwater Elk Project but was created based on criteria for low and high burn severities. 76

Table 13. Detection frequency (count/100 days) of mammal species detected on trail cameras within each burn severity (unburned, low, moderate, high) of the Rice Ridge Wildfire in west-central Montana, USA between May 2019 and October 2020 (excluding winter). 77

LIST OF FIGURES

- Figure 1.** The Blackfoot-Clearwater elk population annual range (thick, blue outline; calculated using locations of GPS-collared individuals), 2020 hunting districts (thin, black lines), and the perimeter of the Rice Ridge Wildfire (red region) located in the Ovando – Seeley Lake area of west-central Montana, USA (panel a); and the fire severity burn pattern from the 2017 Rice Ridge wildfire (panel b). Burn severity values of 1, 2, 3, and 4 represent “unburned”, “low severity burn”, “moderate severity burn”, and “high severity burn”, respectively. Low and moderate burn severities were combined into a “Low severity” category for all analyses except mammal community structure. Example photos of low and high severity burns from the Rice Ridge Wildfire are provided in panel c. 19
- Figure 2.** Ages of adult female elk ($n = 65$) sampled during 2019 (December 2018 and February 2019; red bars) and 2020 (December 2019; blue bars) in the Blackfoot-Clearwater area of west-central Montana, USA. 25
- Figure 3.** Estimates of percent ingesta-free body fat for elk sampled during 2019 (December 2018 and February 2019) and 2020 (December 2019) in the Blackfoot-Clearwater area of west-central Montana, USA. Box and whisker plots represent minimum, lower quartile, median, upper quartile, and maximum values. 26
- Figure 4.** Spring (April 1 – May 30), Neonatal (May 31 – July 10), Summer (July 11 – August 23), Fall (August 24 – December 13), Winter (December 14 – March 31), and annual locations of female elk (black/colored dots) from December 2018 – February 2022 in the Blackfoot-Clearwater region of west-central Montana, USA. The Rice Ridge Wildfire boundary is shown in red. 28
- Figure 5.** Selection ratios for collared female elk across landcover types, burn severities, and seasons (Spring [April 1 – May 30], Neonatal [May 31 – July 10], Summer [July 11 – August 23], Fall [August 24 – December 13], and Winter [December 14 – March 31]) in the Blackfoot-Clearwater region of west-central Montana, USA. Selection ratios were calculated as the proportion of elk locations within a landcover type divided by the proportion of that landcover type available within the 99% annual home range boundary of collared elk. A selection ratio >1 suggests selection for that landcover type, while a selection ratio <1 suggests avoidance. The horizontal dashed line in the figures represents a selection ratio = 1, suggesting no selection/avoidance. Bar colors represent burn severity, with white, yellow, and red representing unburned, low severity burn, and high severity burn, respectively. 29
- Figure 6.** Female elk selections ratios by landcover type in Spring (April 1 – May 30), Neonatal (May 31 – July 10), Summer (July 11 – August 23), Fall (August 24 – December 13), and Winter (December 14 – March 31) seasons from December 2018 – February 2022 in the Blackfoot-Clearwater region of west-central Montana, USA. Selection ratios > 1 suggest selection for that landcover type, while selection ratios <1 suggest avoidance. Landcover types are shown in the bottom right panel with values representing: 0 = Unburned Other; 1 = Unburned Dry Forest; 2 = Unburned Mesic Forest; 3 = Riparian Woodland and Shrubland; 4 = Montane Grassland; 5 = Deciduous Shrubland; 6 = Deciduous Forest and Woodland; 7 = Irrigated Agriculture; 8 = Low Severity Burned Dry Forest; 9 = Low Severity Burned Mesic Forest; 10 = High Severity Burned Dry Forest; 11 = High Severity Burned Mesic Forest; 12 = Low Severity Burned Other; 13 = High Severity Burned Other. 30

Figure 7. Methods for estimating a) mean digestible energy (DE; i.e., forage quality; kcal/g) and b) mean forage quantity (g/m^2) at each vegetation sampling site in the Blackfoot-Clearwater elk population annual range in west-central Montana, USA. Figure adapted from Proffitt et al. (2019). 33

Figure 8. Proportion of vegetation sampling plots containing each forage species within each fire severity category in dry and mesic forests in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. 35

Figure 9. Median digestible energy measured within each vegetation cover class and month from the vegetation sampling sites (focused on summer forage species) in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5x the IQR is represented by the whiskers, outliers $>1.5x$ IQR are represented by the points outside of the whiskers. 36

Figure 10. Summer median herbaceous and shrub forage biomass (g/m^2) measured within each vegetation cover class and month (focused on the summer forage species) in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5x the IQR is represented by the whiskers, outliers $>1.5x$ IQR are represented by the points outside of the whiskers. 37

Figure 11. The average kg/ha per month for herbaceous forage biomass (panel a) and shrub forage biomass (panel b) within the summer range of the four predicted landscape scenarios in the Blackfoot-Clearwater elk population’s summer range. Panel “c” shows the percent of the Blackfoot-Clearwater elk population’s summer range within the four fire scenarios that meets the threshold of >2.75 kcal/g of forage to be considered adequate for each month. 42

Figure 12. Digestible energy predicted onto the observed mixed severity landscape and the unburned fire scenario for May and August for the Blackfoot-Clearwater elk population summer range in west-central Montana, USA using the top forage quality model. The percent of the landscape that meets adequate forage quality ($\text{DE} > 2.75$ kcal/g) increased from May to August for the predicted observed mixed severity landscape, but percent of the landscape with adequate forage quality decreased in an unburned predicted landscape. 43

Figure 13. Trail camera locations in the Blackfoot-Clearwater region of west-central Montana, USA in 2019 (red dots) and 2020 (blue dots). The Rice Ridge wildfire boundary is depicted in red. 45

Figure 14. Example workflow for estimating individual-based prevalence values for defining informative priors in a Bayesian implementation of a resource selection probability function for elk in the Blackfoot-Clearwater region of west-central Montana, USA. We used trail camera data (1) to produce occupancy probability predictive maps (2), from which we extracted predicted values within individual elk 95% kernel density home range contours (blue, dashed line; 3 and 4). We used the mean occupancy value within an individual home range as the prevalence value for that individual, then used moment matching to induce a beta prior on the prevalence term with mean = prevalence and variance = 0.03 (5 and 6). 48

Figure 15. Decreases in digestible energy (DE; kcal/g) from spring through summer for forbs, grasses, and shrubs (panel a., data from current project and Proffitt et al. [2016, 2019]) and

estimated DE values (panel b.) used for female elk neonatal and summer resource selection analyses in the Blackfoot-Clearwater region of west-central Montana from 2019-2021. The colored region in panel b. is the annual home range of female elk and the black outline is the perimeter of the Rice Ridge wildfire. Box and whisker plots represent minimum, lower quartile, median, upper quartile, and maximum values. 51

Figure 16. Daily movement rate (m/hr; panel a.) and 95% kernel density home range size (ha; panel b) of female elk in the Blackfoot-Clearwater region of west-central Montana, USA from December 2018 – February 2022. Black dots represent mean values across elk, while the black line and error ribbon represent predicted values and 95% confidence interval from loess smoothing. The vertical dashed line represents May 31, the date selected as the start of the “Neonatal” season. 55

Figure 17. Estimation of the temporal “breakpoint” in daily home range size for female elk in the Blackfoot-Clearwater region of west-central Montana, USA. The x-axis represents days past parturition, with a value of 0 representing May 31 and a value of 40 representing July 10. Black dots represent mean daily home range estimates across elk, light gray lines represent slope estimates for line segments from a sample of iterations from the multiple change point model, red dashed lines represent the bounds of the 95% credible interval of slope estimates, and the blue lines represent the distribution of breakpoint estimates from the model. 56

Figure 18. Predicted occupancy probability of female elk during Fall: Period 1 (August 24 – September 14, 2019 or August 22 – September 14, 2020; panel a.), Fall: Period 2 (September 15 – October 25, 2019 or September 15 – October 23, 2020; panel b.), and Fall: Period 3 (October 26 – December 13, 2019 or October 24 – December 11, 2020; panel c.) in the Blackfoot-Clearwater region of west-central Montana, USA. The black outline in each figure represents the 99% annual home range of all collared elk in the region. Red circles represent trail cameras where a female elk was detected, while black exes represent trail cameras where female elk were not detected. Warmer colors represent higher predicted occupancy probability. 59

Figure 19. Observed and estimated frequency of predator (gray wolf, mountain lion, grizzly bear, black bear, coyote) detections (count/day) during the neonatal (May 31 – July 10; panel a.) and summer (July 11 – August 23; panel b.) seasons during 2019 and 2020 in the Blackfoot-Clearwater region of west-central Montana, USA. White exes represent cameras that did not detect predators, while red circles represent cameras where predators were detected. The outlined region with estimated frequency of predator detections represents the annual range of elk in the region. 60

Figure 20. Estimated probability of use during the neonatal (May 31 – July 10; red) and summer (July 11 – August 23; blue, dashed) seasons as a function of a.) elk predator (gray wolf, mountain lion, grizzly bear, black bear, coyote) frequency of detections, b.) digestible energy (kcal/g), c.) terrain ruggedness, d.) distance to canopy cover >40%, e.) distance to road, f.) distance to stream, and g.) landcover category for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2021. The mean posterior distribution is represented by solid lines and the 95% credible intervals are represented by the ribbons/error bars. The reference landcover type used in figures a. through f. is “Other”. 63

Figure 21. Probability of female elk use throughout the Blackfoot-Clearwater region of west-central Montana, USA from 2019-2021 during neonatal (May 31 – July 10; panel a) and summer (July 11 – August 23; panel b) seasons. Lighter colors represent higher probabilities of use, while

darker colors represent lower probabilities of use. The white outline represents the annual home range of elk in the region. 64

Figure 22. Estimated probability of use during the prehunt season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, and e) distance to open road, for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panels b - e assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons. 66

Figure 23. Estimated probability of use during the archery-only season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, e) distance to open road, and f) hunter pressure, for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panels b – f assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons. 68

Figure 24. Estimated probability of use during the backcountry rifle season as a function of: a) landcover category, b) hunt method, c) distance to dense canopy, d) ruggedness, e) digestible energy, f) distance to motorized route, g) hunter pressure, and h) max snow water equivalent (SWE), for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panel a assumes that use occurs in archery only areas, panel b assumes that use occurs in high severity burned forests, and panels c - h assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests in archery-only areas. The 95% credible intervals are represented by the error bars in panels a and b, and gray ribbons in panels c - h. 70

Figure 25. Estimated probability of use during the rifle season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, e) distance to open road, f) hunter pressure, and g) snow water equivalent (SWE), for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. All panels assume all other continuous covariates are fixed at their mean observed value, and use occurs in the open landcover type. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons. 72

Figure 26. Probability of use predicted for the prehunt (panel a), archery-only (panel b), backcountry rifle (panel c), and rifle (panel d) hunt seasons for the Blackfoot-Clearwater elk population fall range in west-central Montana, USA using the RSPF model for each hunt season. Backcountry rifle hunting takes place in hunting districts 150 and 280 and hunting district 282 is by permit only for the rifle season. From the prehunt to the rifle season, female elk transitioned from their backcountry summer range to their front country winter range. 73

Figure 27. Female elk locations (red dots) during the first week of the backcountry rifle season (September 15 – 21), the first week of rifle season (October 25 – 31), the last week of rifle season (November 24 – 30), and post rifle season (December 25 – 31) in the Blackfoot-Clearwater region of west-central Montana in 2019 and 2020. Yellow regions on the map represent the backcountry hunting districts (150 and 280) and the white region represents district 282, which houses the Blackfoot-Clearwater Wildlife Management Area. 74

Figure 28. Proportion of elk locations within district 282 by week in 2019 and 2020 in the Blackfoot-Clearwater region of west-central Montana (black lines). Blue, dashed lines on the secondary axis represent mean snow water equivalent (m) by week (only shown from mid-August to late December). Background colors represent the type of general hunting season occurring during the week, with green, yellow, orange, and red representing no general hunting season, archery-only season, backcountry rifle season (rifle in backcountry districts and archery in front country districts), and general rifle season, respectively. 75

Figure 29. Rarefaction curves for species richness (a.) and Shannon Diversity (b.) of wild mammals as a function of sites sampled with trail cameras within the Rice Ridge Wildfire in west-central Montana, USA between May 2019 and October 2020 (excluding winter). Dots represent observed values, solid lines represent interpolated values, dotted lines represent extrapolated values, and ribbons represent 95% confidence intervals. 79

EXECUTIVE SUMMARY

The purpose of this study was to evaluate the effects of a recent, large-scale wildfire on the elk (*Cervus canadensis*) population in the Blackfoot Clearwater area of west-central Montana. Approximately half of the elk population's summer range was impacted by the Rice Ridge wildfire which occurred during summer 2017. The approximately 623 km² mixed-severity fire included approximately 46% low and moderate severity and 54% high severity burns. Our objective in this project was to evaluate the effects of low severity and high severity wildfire on elk forage and distribution to better understand the effects of wildfire on elk populations.

To identify the effects of fire on elk forage, we first identified important food items for elk by collecting composite elk fecal samples and using DNA metabarcoding techniques to determine the primary forage species in summer and winter. The most common diet species within each of the forb, shrub/tree, and graminoid lifeforms in summer were fireweed (*Chamerion angustifolium*), huckleberry (*Vaccinium sp.*), and sedge (*Carex sp.*), while winter diets in each lifeform were yarrow (*Achillea sp.*), western larch (*Larix occidentalis*), and fescue (*Festuca sp.*).

Using elk diet information and vegetation sampling, we developed a landscape nutrition model to predict forage quality and quantity within the summer range. We sampled vegetation across a total of 682 sampling sites, including 353 mesic forest sites (102 unburned, 113 low severity, and 138 high severity) and 329 dry forests sites (98 unburned, 105 low severity, 126 high severity). Forage quality (i.e., digestible energy [DE; kcal/g]) in low and high severity dry forests was 7.9% (95% CI: 2.9 - 12.6%) and 7.6% (2.1 - 12.9%) higher than unburned forests, respectively, while forage quality in low and high severity mesic forests was 16.3% (95% CI: 11.8 – 20.1%) and 14.1% (95% CI: 9.5 – 18.3 %) greater than unburned forests, respectively. Low severity and high severity dry forests had 179% (95% CI: 98 – 291%) and 145% (95% CI: 72 – 250%) greater herbaceous forage biomass compared to unburned forests, respectively, while low and high severity burned mesic forests had 160% (95% CI: 58 – 327%) and 124% (95% CI: 28 – 294%) greater herbaceous forage biomass compared to unburned forests.

To evaluate post-fire effects on elk habitat use, we evaluated elk movements and resource selection using GPS-collared individuals. We captured a total of 71 individual adult (> 1.5 years old) female elk: 19 during December 2018, 12 during February 2019, and 40 during December 2019. We calculated ingesta-free body fat (IFBF) for each animal captured and found IFBF was similar during all three capture periods: December 2018 (mean = 7.26, SD = 1.0, *n* = 19), February 2019 (mean = 8.56, SD = 2.2, *n* = 8) and December 2019 (mean = 8.58, SD = 1.8, *n* = 39), and was within the range of levels typical of populations that are not experiencing nutritional limitations. A total of 8 collared elk died throughout the duration of our study. Annual probability of survival for female elk with harvest included was 0.85 (95% confidence interval [CI] = 0.75 – 0.96) and with harvest excluded was 0.92 (95% CI = 0.85 – 1.0).

From December 2018 – February 2022, we collected a total of 130,422 locations from 57 collared elk in spring (April 1 – May 30), 82,817 locations from 55 collared elk during the neonatal season (May 31 – July 10), 79,704 locations from 51 collared elk in summer (July 11 – August 23), 192,588 locations from 55 collared elk in fall (August 24 – December 13), and 252,893 locations from 58 collared elk in winter (December 14 – March 31). Elk generally had

higher selection ratios in grasslands and irrigated agriculture during early spring, late fall, and winter, while elk had higher selection ratios in burned landcover types during neonatal, summer, and early fall seasons. There were not large differences in elk use of low vs. high-severity burns.

We also deployed 132 motion-activated trail cameras in 2019 and 137 in 2020 at random locations throughout the study area to collect elk occupancy data for resource selection analyses and to identify the effects of wildfire on the broader mammal community. We detected female elk on 126 cameras (47%) from 2019 through 2021. Further, we detected 26 wild mammal species throughout the study area between May 2019 and October 2020 (excluding winter), with cervids being the most-detected species. Combined frequency of detections (count/100 days) of potential predators of elk (gray wolves [*Canis lupus*], mountain lions [*Puma concolor*], grizzly bears [*Ursus arctos*], black bears [*Ursus americanus*], coyotes [*Canis latrans*]) was higher in unburned sites (2.46) compared to low (1.23), moderate (0.55), and high (0.46) severity sites. Predicted species richness and Shannon diversity at 50 camera sites was highest in moderate severity burns (richness = 25.5, CI = 17.4 – 33.5; diversity = 12.5, CI = 5.7 – 10), but confidence intervals overlapped across burn severities.

To evaluate the effects of low severity and high severity wildfire on elk distribution, we developed a resource selection probability function (RSPF) for the neonatal (May 31 – July 10), summer (July 11 – August 23), and fall (August 24–December 1) elk distributions. We modeled female elk resource selection for the neonatal season based on 17,732 used locations and 88,660 available locations from 54 unique elk. We modeled resource selection for the summer season based on 17,097 used locations and 85,485 available locations from 51 unique elk. Female elk generally selected similar resources during the neonatal and summer seasons, although the magnitude of selection varied. Female elk were 55% more likely to use low and high severity burns compared to unburned forests in the neonatal season, but only 48% and 32% more likely to use low and high severity burns in summer, respectively. Among continuous covariates, frequency of predator detections (predicted predator count/day, estimated using trail camera data) had the strongest negative association with elk probability of use during summer, but there was only a small negative association during the neonatal season. The relationship between frequency of predator detections and elk use could have been confounded with elk preference for high elevation, burned areas in summer, where there were fewer predators detected. Thus, we caution interpretation of this finding as it relates to the effect of predators on elk habitat use.

During the fall, we developed a separate RSPF model for each of four hunt seasons, including “Prehunt” (August 24 – September 6, 2019 or August 22 – September 4, 2020), “Archery-Only” (September 7 – 14, 2019 or September 5 – 14, 2020), “Backcountry-Rifle” (September 15 – October 25, 2019 or September 15 – October 23, 2020), and “Rifle” (October 26 – December 1, 2019 or October 24 – November 29, 2020). During the prehunt season, female elk selected burned forests, and there was no difference in selection based on fire severity category. Female elk were 23%, 97%, 83%, and 83% more likely to select both low and high severity burned forests compared to the unburned forest, open, closed, and other landcover types, respectively. Similar to the prehunt season, female elk during the archery-only season selected for burned forests, and there was no difference in selection based on fire severity category. Female elk were 40%, 92%, 77%, and 67% more likely to select low and high severity burned forests over the unburned forest, open, closed, and other landcover types, respectively. Similar to

the prehunt and archery-only seasons, female elk during the backcountry rifle season selected burned forests, and there was no difference in selection between fire severity categories. Female elk were 28%, 16%, 20%, and 57% more likely to select low and high severity burned forests over the unburned forest, open, closed, and other landcover types, respectively. In contrast to the other three seasons, elk avoided burned and unburned conifer forests during the rifle season. Elk were 14-18% more likely to select the open landcover type compared to the remaining five landcover types during the rifle season.

Overall, our results highlight that in years two through four after a large-scale wildfire, elk forage quality and quantity increased during the summer as a function of landscape characteristics and vegetation cover types. We found that fire improved forage quality regardless of fire severity, and that fire severity had variable effects on forage quantity dependent upon forage type and forest type. Fire, in conjunction with spatiotemporal factors (e.g., elevation, topography, precipitation), altered the availability and distribution of elk forage by extending the duration in which elk could access high quality forage throughout the summer. Elk, in turn, selected low and high-severity burned landscapes during neonatal, summer, and early fall seasons. Elk left burned areas in late fall, and a combination of snowpack and hunting pressure became the most important factors associated with elk movements and resource use during rifle hunting. However, given the timing of movements, the effects of snowpack and hunter pressure on elk movements and resource use were confounded because snowpack and rifle hunting pressure increased at the same time.

Overall, we recommend managers allow mesic forests to burn, where possible, given these forests had the largest increase in elk forage quality when burned. There were not large differences in elk forage resources or elk use of different burn severities; thus, managing for specific burn severities may not be necessary. Hunter pressure during the early fall (i.e., archery season and early backcountry rifle season) did not affect elk use of burned areas, as elk did not stop using burned sites until the rifle season. Thus, managers may not need to consider fire when making early-season hunting regulations at the level of hunting pressure we observed. Snowpack and hunter pressure were confounded and both associated with elk movements from burned areas to open grasslands in hunting district 282 in late fall (i.e., rifle season). We therefore cannot disentangle the contribution of hunting pressure on elk resource use during late fall from the effect of snowpack and winter range location, nor provide recommendations on whether managers should consider the effects of fire in harvest management during the rifle season. Effects of fire severity on elk movements and resource use could change over time as burned areas move through different successional stages. Thus, managers should also consider long-term management objectives when managing wildfires for elk habitat.

PROJECT BACKGROUND

Across much of the western United States, changes in seasonal elk (*Cervus canadensis*) distribution and migratory behavior are of concern to wildlife managers, land managers, hunters, and private landowners. In some areas, elk hunters and wildlife managers are observing declines in public-land hunting opportunities and agricultural producers are experiencing increased property damage (Burcham 1956, Haggerty and Travis 2006, Krausman et al. 2014, Fontaine et al. 2019). As such, there is shared interest among wildlife managers, public land managers, hunters using public lands, and private landowners in developing tools that encourage elk to remain on public land ranges and to achieve more desirable distributions across public and private lands (Sittler et al. 2015).

Migratory behaviors of ungulates often lead to seasonal redistribution of animals across the landscape, and across public and private lands, as individuals respond to seasonally variable forage while minimizing risk of predation (Fryxell and Sinclair 1988, Boyce 1991, Berger 2004). In spring, migratory individuals generally depart lower-elevation winter ranges in search of newly emergent, highly digestible forage associated with higher elevation summer ranges, before returning to winter ranges in late fall (Van Soest 1982, Eggeman et al. 2016, Merkle et al. 2016). Annual weather conditions and trends associated with climate change, shifts in land use practices, such as increasing irrigation on low-elevation crop lands, and changes in forest management, such as increased fire suppression on higher-elevation summer ranges, have the potential to alter the distribution of forage across the landscape (Mould and Robbins 1982, Keane et al. 2002, Brown et al. 2004, Lande et al. 2013, Middleton et al. 2013). For example, in the North Sapphire mountains of west-central Montana, elk remaining on lower elevation winter ranges throughout the year had access to higher overall forage quality than elk that migrated to higher elevation summer ranges (Barker et al. 2019). In addition to acting as a primary driver of elk resource selection and distribution (Boyce et al. 2003, Ranglack et al. 2016, Ranglack et al. 2017), the seasonal availability of forage has been shown to have an important effect on ungulate reproduction and survival (Cook, R. C. et al. 2013, Monteith et al. 2014, Cook, J. G. et al. 2016). Understanding factors that influence elk forage and distribution on a year-round basis is important for elk distribution and population management (Found and St. Clair 2016, Barker et al. 2019).

Fire can reshape forest structure and associated vegetation on varying temporal and spatial scales, altering forage quality and quantity on seasonal elk ranges (Fisher and Wilkinson 2005, Noss et al. 2006, Long et al. 2008, Allred et al. 2011, Proffitt et al. 2019). Fire has the potential to change forest age structure and canopy density, and influence soil moisture, temperature, and nitrogen levels, all of which may influence post-fire vegetative composition, and alter the timing and duration of greenup (Krueger 1972, Van Dyke and Darragh 2006, Hebblewhite et al. 2008, Kerns and Day 2018). As a result, fire management has the potential to influence landscape heterogeneity and associated animal distributions on multiple scales (Boyce et al. 2003). Under certain conditions, fire may facilitate regeneration of forb and graminoid species that contain elevated nutrient levels and are easily digestible for elk (Tracy and McNaughton 1991, Smith et al. 2000, Greene et al. 2012, Proffitt et al. 2016). However, post-fire regeneration is not consistent across all habitats or under all conditions, with factors such as pre-fire landcover and habitat type, season, terrain, fire history, and fire severity and duration

shaping the post-fire landscape (Van Dyne and Darragh 1963, Sachro et al. 2005, Lord and Kielland 2015, Proffitt et al. 2019). Further, the effects of prescribed fire may not mimic those of wildfire in magnitude or duration (Proffitt et al. 2019). In the North Sapphire Mountains, recently burned dry forests (i.e., < 6 years), whether prescribed burn or wildfire, contain high quality forage similar in digestible energy to irrigated agricultural lands (Barker et al. 2019). Other studies have suggested divergent effects of prescribed burns vs. wildfire, indicating that the effects of prescribed burning are highly variable, and may not replicate the effects of wildfire (Kerns and Day 2018, Proffitt et al. 2019). Because of the variation in potential effects of fire on a given landscape, the complex suite of factors that may determine post-fire regrowth, and likelihood of increasing fire activity in the future due to climate change, additional large-scale research on the variable effects of fire on elk forage quantity and quality is needed to inform forest management decisions (Brown et al. 2004, Proffitt et al. 2019).

While fire has the potential to positively impact forage availability and increase landscape heterogeneity, wildfire and prescribed burns may also reduce elk security habitat, potentially negating the positive effects on forage quality (Rowland et al. 2000, Hebblewhite et al. 2009). Much as forage acts as an important driver of elk distributions overall, hunter access combined with security habitat strongly influence elk resource selection and spatial distribution during hunting seasons (Proffitt et al. 2009, Wisdom et al. 2018). Elk, especially mature males, have repeatedly been shown to select for denser forest canopy cover and steeper terrain in areas within proximity to roads or other human access during hunting seasons (Lyon 1983, Unsworth et al. 1998, McCorquodale 2003, Lowrey et al. 2020). Many recommendations for forest management to maintain elk have included maintaining forest cover or horizontal visibility and preserving blocks of habitat away from open roads (Christensen et al. 1993, Hillis et al. 1999, Wisdom et al. 2004). However, both prescribed burns and wildfire often decrease hiding cover and increase horizontal visibility, potentially increasing vulnerability to hunter harvest as well as sympatric predators (Rowland et al. 2000, Hebblewhite et al. 2009). In addition, while there has been heated debate over the effects of post-fire management practices (i.e., post-fire logging) on post-fire regeneration (Donato et al. 2006, Newton et al. 2006, Peterson and Dodson 2016), the effects of such practices on ungulates is poorly understood (McIver and Starr 2000, Hebblewhite et al. 2009). Therefore, as management agencies look for ways to maintain elk on public lands during summer and fall seasons, understanding the impacts of fire and fire related activities on elk nutrition and security is important.

Montana Fish, Wildlife and Parks (FWP) and partners initiated this study to evaluate the effects of a large-scale wildfire on elk forage and seasonal distributions. The project area includes the annual range of the Blackfoot-Clearwater elk population. Approximately half of the 1,247 km² elk summer range was burned by low, moderate, or high severity fire during a wildfire in August and September 2017. This project focused on evaluating elk forage and distributions during the first 4 years post-fire. This evaluation of post-fire effects on elk forage and distributions will be widely applicable to management of elk populations and elk habitat throughout this region of the Rocky Mountains.

During the 4-year period covered by Federal Aid in Wildlife Restoration grant W-175-R to FWP, our primary objectives were to:

1. Collect elk diet data.
2. Evaluate elk body condition and pregnancy rates.
3. Evaluate and compare elk use of areas that burned at different levels of fire severity.
4. Evaluate and compare vegetation and forage resources in areas that burned at different levels of fire severity.
5. Develop a resource selection probability function model to evaluate the effects of wildfire and other factors on summer and fall elk distributions.
6. Provide preliminary recommendations or guidelines for fire management that improve elk forage quality, security, and/or elk use of treatment areas.

In addition to the above objectives, we also took advantage of the large volume of remote camera photos to evaluate mammal community use of areas that burned at different levels of fire severity, to better understand the effects of wildfire on the broader mammal community.

STUDY AREA

This study was conducted in west-central Montana in the Ovando-Seeley Lake area and focused on the Blackfoot-Clearwater (BC) elk population (Figure 1a). Elevations in the region ranged from 1,150 m to 2,600 m with varied topography including flat bottomland, foothills, and steep and rugged mountain slopes. Annual precipitation ranged from 380 mm in valley bottoms to 1,500 mm in the mountains with most precipitation falling as snow in the winter. Mean temperatures for July and January were 17.22°C and -6.1°C, respectively (Prism Climate Group, <https://prism.oregonstate.edu/>).

Approximately half of the elk population's summer range was impacted by the Rice Ridge Fire, which started due to a lightning strike on July 24, 2017, and continued to burn through September 7, 2017. The approximately 623 km² mixed-severity fire included approximately 46% low and moderate severity and 54% high severity burns (Figure 1b). Fire has historically impacted the study area, with 23 fires occurring between 1985 and 2015 ranging in size of area burned from 0.05 km² to 96 km². In total, 238 km² were burned, with the majority, 208 km², burning before 2010. Throughout the majority of this report, fire severity is described as low severity (comprised of low and moderate severity) and high severity, based on designations by the Rapid Assessment of Vegetation Condition after Wildfire (RAVG, <https://fsapps.nwcg.gov/ravg/>). Separate moderate fire severity designations were only included in mammal community analyses to better identify whether intermediate levels of burn severity were more beneficial to the mammal community, akin to the intermediate disturbance hypothesis (Connell 1978).

Pre-fire forest communities were dominated by Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland, with the dominant conifers being Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest also made up a large portion of the study area, and these forests were dominated by lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*). The main lower elevational habitats included irrigated agriculture, cattle-grazed pastures, riparian areas, deciduous shrublands, and montane grasslands dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), rough fescue (*Festuca campestris*), or Idaho fescue (*Festuca idahoensis*).

The BC elk population was estimated at approximately 1,000 animals between 2018-2020 and has an annual range occupying 13% private property, 10% state-owned land including the Blackfoot-Clearwater Wildlife Management Area, and 75% federal land including portions of the Lolo National Forest, Flathead National Forest, and the Bob Marshall Wilderness Complex. Sympatric ungulate species included mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*). Large predators within the region included grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), mountain lion (*Puma concolor*), and gray wolf (*Canis lupus*).

The range of the BC elk population spanned 10 hunting districts with variable hunting regulations (Table 1). For the eight front country hunting districts, archery hunting took place during a six-week season in September and early October, followed by a five-week general rifle

hunting season during late October and November. For the two backcountry hunting districts, an approximately one-week archery season took place in the beginning of September, followed by an approximately 11-week rifle season where both archery and rifle hunting methods were allowed. For archery season, hunter pressure varied by hunting district and ranged from 155 to 2,857 hunter-days annually. For rifle season, hunter pressure ranged from 740 to 8,898 hunter-days annually (Table 1).

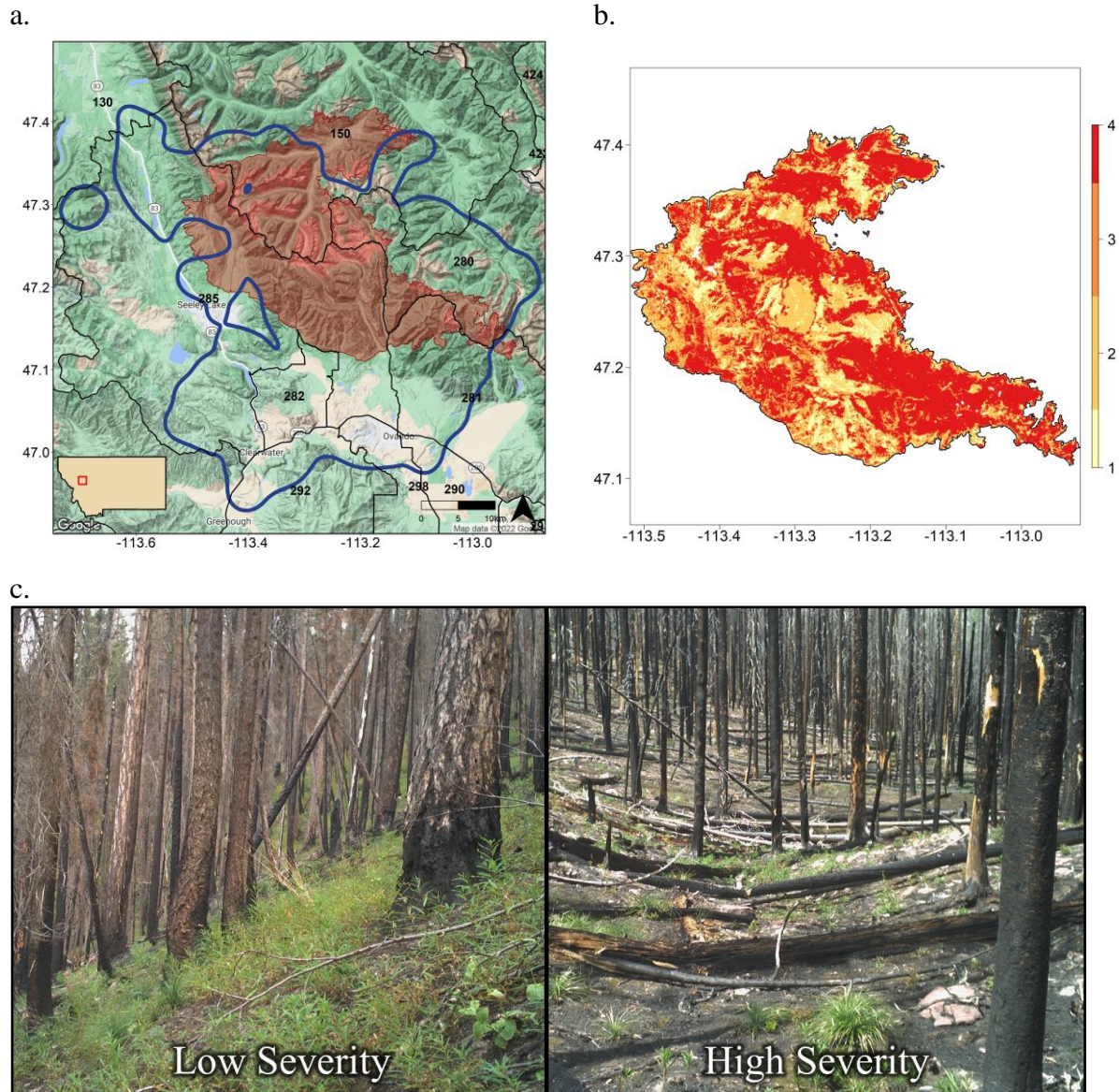


Figure 1. The Blackfoot-Clearwater elk population annual range (thick, blue outline; calculated using locations of GPS-collared individuals), 2020 hunting districts (thin, black lines), and the perimeter of the Rice Ridge Wildfire (red region) located in the Ovando – Seeley Lake area of west-central Montana, USA (panel a); and the fire severity burn pattern from the 2017 Rice Ridge wildfire (panel b). Burn severity values of 1, 2, 3, and 4 represent “unburned”, “low severity burn”, “moderate severity burn”, and “high severity burn”, respectively. Low and moderate burn severities were combined into a “Low severity” category for all analyses except mammal community structure. Example photos of low and high severity burns from the Rice Ridge Wildfire are provided in panel c.

Table 1. Hunting regulations and hunter pressure found within each of the 10 hunting districts found in the Blackfoot-Clearwater elk range in west-central Montana, USA for 2019 and 2020. Hunter pressure is expressed as the total number of hunter days annually for each hunting period and district estimated using the Montana Fish, Wildlife and Parks harvest survey program from data collected in 2020. *First 10 days: brow-tined bull or antlerless elk for youth only ages 12-15; brow-tined bull for general license; After the first 10 days: Brow-tined or antlerless elk general licenses. **The two hunting districts that have an early backcountry rifle season.

Hunting District	Regulations			Hunter Pressure	
	Archery	Rifle	Permits & Licenses	Archery	Rifle
285	Brow-tined Bull or Antlerless Elk	Brow-tined Bull; Brow-tined Bull or Antlerless Elk only youth 12-15 and PTHFV	Elk B License 285-01, Antlerless Elk, quota = 30	2304.6	8898.4
282	Brow-tined Bull or Antlerless Elk	No General Rifle, permit/License only	Elk Permit 282-10 Brow-tined Bull or Antlerless elk for Youth 12-15, quota = 1; Elk Permit 282-00, Antlerless Elk, quota = 25	408.5	957.3
150*	Brow-tined Bull	Brow-tined Bull**	None	154.9	2233.6
281	Brow-tined Bull or Antlerless Elk	Brow-tined Bull - General; Brow-tined Bull or Antlerless Elk - Youth 12-15	Elk Permit 281-01, Antlerless Elk, quota = 10	2856.5	5871.7
292	Brow-tined Bull or Antlerless Elk	Brow-tined Bull - General; Brow-tined Bull or Antlerless Elk only youth 12-15 and PTHFV	Elk B License: 292-01, Antlerless Elk, quota = 100	2279.2	6758.8
280*	Brow-tined Bull or Antlerless Elk	Brow-tined Bull or Antlerless Elk**	None	457.2	740.1
298	Brow-tined Bull or Antlerless Elk	Brow-tined Bull or Antlerless Elk	Elk B License 290-01, Antlerless Elk, quota = 300	607.1	1333.4
130	Brow-tined Bull or Antlerless Elk	Brow-tined Bull	None	2068.3	6204.7
290	Brow-tined Bull or Antlerless Elk	Antlerless Elk	Elk B License 290-01, Antlerless Elk, quota = 300	900.3	1461.9
283	Brow-tined Bull or Antlerless Elk	Brow-tined Bull	None	1453.5	4204

OBJECTIVE 1: COLLECT ELK DIET DATA

Methods

Field Methods: Pellet Sample Collection—To identify important food items for elk, we collected composite elk fecal samples and used DNA metabarcoding techniques to determine the primary forage species in summer and winter. We defined a composite fecal sample as collecting 2 fresh, moist pellets per pellet group from 10 individual pellet groups that were >1 meter apart for a total of 20 pellets per sample. We collected summer samples in two separate ways to achieve spatially and temporally balanced sampling: 1) we selected areas used by GPS-collared female elk <24 hours prior without replacement, and 2) we opportunistically collected fresh pellets. The second option for collecting fecal samples ensured a large sample size because of difficulty in accessing areas used by GPS-collared female elk within a short window of time to guarantee the pellets were from the designated season. We evaluated winter diet from pellet samples collected during winter elk captures in 2018 and 2019. Two pellets per elk were composited into winter samples.

We combined composite samples in two separate ways: 1) we combined 10 individual pellet groups within a 300 m² area into one composite sample, or 2) we combined pellets that were collected at a similar date if there were not enough pellet groups within a 300 m² area. We froze samples and then randomly selected two pellets, placed them into a vial containing a liquid salt-based DNA stabilizer, and then sent samples to the Species from Feces-Bat Ecology and Genetics Lab (Northern Arizona University, Flagstaff, Arizona) for DNA metabarcoding analysis.

Lab Methods: DNA Metabarcoding.—We identified forage species using fecal DNA metabarcoding techniques. DNA metabarcoding identifies a standardized region from DNA in the pellet samples, cross-references the standardized region (further referred to as variants) to a database to identify the plant species, and then returns the relative quantities (further referred to as reads) of plant species in elk diets. Fecal material was subsampled from inside the pellet to avoid including external DNA. The lab extracted and amplified DNA from two markers: the ITS2 region of nuclear 18S DNA (Chen et al. 2010, Yao et al. 2010) and a 334 base chloroplast region of rbcL (Erickson et al. 2017). The lab processed sequencing reads separately for each marker. For each marker, the lab removed variants if the variant was observed in only one sample or was observed in less than 1% of a sample's composition to avoid including exogenous DNA (Ando et al. 2018). The lab classified variants against curated databases to identify plant species for ITS2 (Banchi et al. 2020) and rbcL markers (Bell et al. 2017).

Analytical Methods: Classification Methods for Diet List.—To identify the important forage species in the summer and winter diets, we employed two different methods, frequency of occurrence (FOO) and relative read abundance (RRA). The FOO method is frequently considered the conservative approach as a food item is included in the diet list based upon a threshold for the percentage of samples that contain the food item. The FOO approach, therefore, limits the effect of taxa-specific biases that impact marker signal (e.g., differential digestibility, PCR priming bias, etc.). However, solely utilizing FOO can artificially inflate the importance of rare food items, potentially biasing both forage quality and quantity results (Ford et al. 2016,

Deagle et al. 2018). The RRA method has been used as a surrogate for relative biomass consumed and is based upon the percentage of reads for each food item. The population level RRA is calculated by averaging the sample specific RRA values with equal weight given to each sample. Interpreting RRA as the amount of biomass consumed is cautioned against as the taxa-specific biases highlighted earlier could influence read abundance. However, the real food items should dominate, providing utility in filtering out exogenous DNA or plant species eaten in small quantities despite high availability (Deagle et al. 2018).

We used a 10% FOO threshold and 1% RRA threshold for the food item to be included in the winter and summer diet. We separately analyzed the ITS2 and rbcL markers for the RRA threshold. To be included in the diet, we required each food item to meet the FOO threshold and at least one marker's RRA threshold. We did not include taxa only identified to the family level in the final diet. To further filter our diet list to important food items, we compared RRA to the proportion of vegetation plots containing each food item by developing a modified forage ratio (i.e., RRA/proportion of plots). Elk select plant species that are more palatable and nutritious, and therefore, elk diets vary as a function of forage availability. We selected a modified forage ratio threshold of 0.05 within at least one marker for inclusion in the diet to remove plant species that are widely available yet eaten at low quantities. To provide a metric of importance in the diet, we ranked food items by first giving each food item a rank for FOO and RRA separately if they met the thresholds, and then added the FOO ranking and lowest RRA marker ranking (either ITS2 or rbcL) together. We then classified food items ordinally based upon the lowest summed rankings.

Results

For the summer diet, 19 taxa met the FOO and RRA thresholds and 18 taxa met the modified forage ratio threshold and were included in the summer diet. For the winter diet, 16 taxa met the FOO and RRA thresholds and 15 taxa met the modified forage ratio threshold and were included in the winter diet (Table 2). The most common diet species within each of the respective lifeforms (forb, shrub/tree, graminoid) in summer was fireweed (*Chamerion angustifolium*), huckleberry (*Vaccinium sp.*), and sedge (*Carex sp.*), while the most common diet species within each lifeform in winter were yarrow (*Achillea sp.*), western larch (*Larix occidentalis*), and fescue (*Festuca sp.*).

Table 2. Summer and winter elk diet taxa within the Blackfoot-Clearwater region of west-central Montana, USA that met the FOO and RRA thresholds, the final ranking, and the forage ratios for the ITS2 and rbcL markers. Forage ratios were calculated by comparing the RRA value for each marker to the proportion of vegetation plots containing each food item (i.e., RRA/proportion of plots). The * denotes that the taxon did not meet the forage ratio threshold to be included in the final diet. All other taxa are considered a food item.

Season	Taxon	Final rank	Forage Ratio ITS2	Forage Ratio rbcL
Summer	<i>Chamerion angustifolium</i>	1	0.92	0.79
	<i>Iliamna rivularis</i>	2	3.97	2.16
	<i>Vaccinium</i> sp.	2	0.02	0.12
	<i>Fragaria</i> sp.	3	0.004	0.25
	<i>Rubus</i> sp.	4	0.89	0.32
	<i>Potentilla</i> sp.	5	1.32	0.28
	<i>Rosa</i> sp.	6	0.11	0.21
	<i>Carex</i> sp.	7	-	0.06
	<i>Eurybia</i> sp.	7	0.12	-
	<i>Menziesia</i> sp.	7	0.17	-
	<i>Arctostaphylos uva-ursi</i>	8	0.23	0.32
	<i>Arnica</i> sp.*	8	0.03	0.002
	<i>Salix</i> sp.	8	-	0.16
	<i>Centaurea</i> sp.	9	0.26	-
	<i>Alopecurus</i> sp.	10	NA	-
	<i>Rhododendron</i> sp.	10	-	1
	<i>Geum</i> sp.	11	1.22	0.25
<i>Geranium</i> sp.	12	0.24	1.16	
<i>Tragopogon</i> sp.	13	0.51	0.06	
Winter	<i>Festuca</i> sp.	1	4.53	3.21
	<i>Larix occidentalis</i>	2	-	6.48
	<i>Poa</i> sp.	2	0.65	3.11
	<i>Salix</i> sp.	2	2.28	0.54
	<i>Cornus sericea</i>	3	-	2.88
	<i>Achillea</i> sp.	4	0.54	-
	<i>Rubus</i> sp.	5	1.08	-
	<i>Pinus</i> sp.	6	-	0.19
	<i>Geum</i> sp.	6	3.94	-
	<i>Arctostaphylos uva-ursi</i>	7	-	0.26
	<i>Allium</i> sp.	8	1.14	-
	<i>Ulmus</i> sp.	9	-	-
	<i>Fraxinus</i> sp.	9	-	-
	<i>Carex</i> sp.*	10	0.007	0.03
	<i>Populus</i> sp.	10	-	0.31
<i>Centaurea</i> sp.	11	0.35	-	

OBJECTIVE 2: EVALUATE ELK BODY CONDITION AND PREGNANCY RATES

Methods

Field Methods.—We completed 2 years of elk capture, GPS collaring, and sampling: 2019 (December 2018 and February 2019 captures) and 2020 (December 2019 captures). We captured elk by a combination of helicopter netgunning and chemical immobilization following approved MTFWP animal capture protocols (IACUC FWP13-2018). Each captured elk was outfitted with Iridium remote upload global positioning system (GPS) radio-collars (Lotek Wireless, model LiteTrack Iridium 420, New Market, Ontario, Canada) programmed to record a location every hour, transmit a mortality notification 6 hours post-mortality, and drop off after 2 years.

We calculated ingesta-free body fat (IFBF) for each animal from measurements of chest girth and scaled estimates of maximum rump fat obtained using a portable ultrasound machine (Cook et al. 2010, Cook et al. 2016). IFBF represents an index of nutritional resources acquired by individuals and reflects forage quality within individuals' ranges. We assessed lactation status during the December captures, but not during the February 2019 captures because some calves were weaned by that time. We collected blood during all captures to determine pregnancy status based on the presence of pregnancy-specific protein-B in the blood serum (Noyes et al. 1997). We used blood serum to screen for exposure to a suite of diseases previously detected in Montana, including brucellosis (*Brucella abortus*) and leptospirosis (*Leptospira*). We extracted a lower incisor for cementum aging analysis. We collected nasal swabs during the 2019 captures to screen for exposure to *Mycoplasma ovipneumonia*.

Analytical Methods.—We estimated annual survival of female elk using the Kaplan-Meier estimator (Kaplan and Meier 1958) within the “survival” package (Therneau 2021) in Program R. We considered the elk-specific day of capture as the first day of “exposure”, while the last day of exposure was the day the elk either died, the collar dropped, or the collar stopped transmitting. We calculated survival in two ways: 1) we treated human harvest as a mortality (“harvest included”) and 2) we censored elk from the analysis on the day they were harvested (“harvest excluded”). For each analysis, we censored elk from analysis the day their fate became unknown (e.g., collar dropped).

Results

We captured a total of 68 unique individual adult (> 1.5 years old) female elk: 19 during December 2018, 9 during February 2019, and 40 during December 2019. We recaptured an additional 3 elk during February 2019 to replace malfunctioning GPS collars. The average age of elk sampled during 2019 (December 2018 and February 2019; mean = 8.9 years, SD = 4.8, range = 2 – 19 years, $n = 28$) was similar to the average age of elk sampled during 2020 (December 2019; mean = 8.6 years, SD = 4.4, range = 2 – 17 years, $n = 37$; Figure 2). We did not detect exposure to brucellosis or *Mycoplasma ovipneumonia* ($n = 71$), but we did detect *Leptospira pamona* in one animal sampled during December 2019.

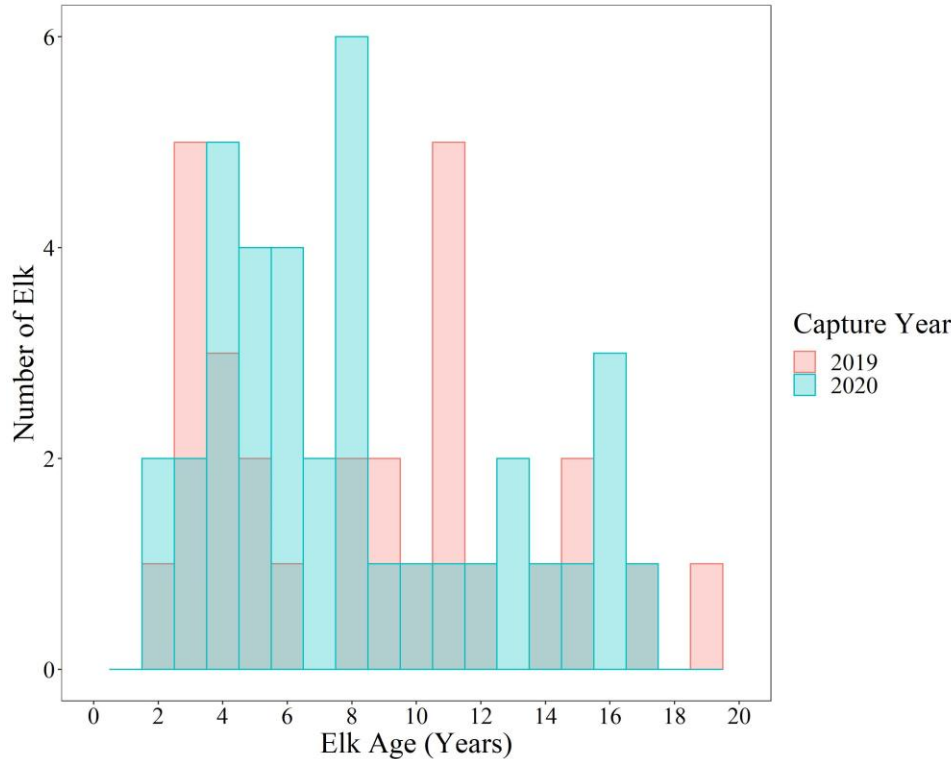


Figure 2. Ages of adult female elk ($n = 65$) sampled during 2019 (December 2018 and February 2019; red bars) and 2020 (December 2019; blue bars) in the Blackfoot-Clearwater area of west-central Montana, USA.

We found IFBF was similar during all three sampling events: December 2018 (mean = 7.26, SD = 1.0, $n = 19$), February 2019 (mean = 8.56, SD=2.2, $n = 8$) and December 2019 (mean = 8.58, SD=1.8, $n = 39$; Figure 3). The high variability in February 2019 likely reflected the small sample size. December IFBF in 2019 and 2020 was similar to other elk herds in western Montana sampled in early winter 2012–2018. Non-lactating elk had slightly higher IFBF levels than lactating elk, a pattern similar to other herds. The overall pregnancy rate of captured adult female elk was 0.90 (95% confidence interval [CI] = 0.82–0.97, $n = 67$).

A total of 8 collared elk died throughout the duration of our study; 3 were harvested by hunters, 3 had natural causes of mortality unrelated to predation, 1 was predated by a grizzly bear, and 1 had an unknown cause of mortality. Annual probability of survival for female elk with harvest included was 0.85 (95% CI = 0.75 – 0.96) and with harvest excluded was 0.92 (95% CI = 0.85 – 1.0).

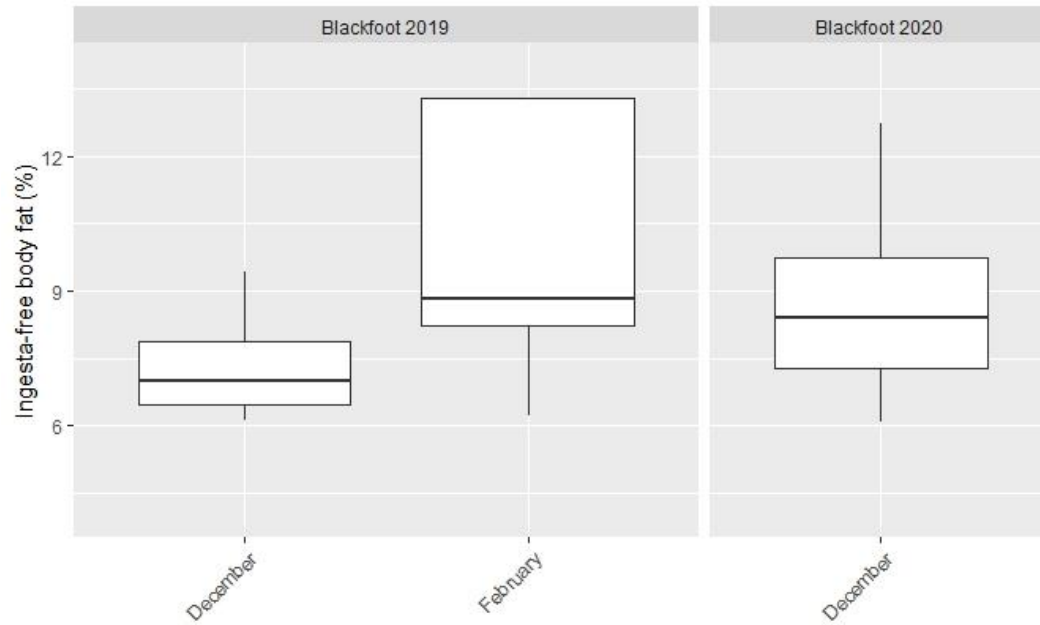


Figure 3. Estimates of percent ingesta-free body fat for elk sampled during 2019 (December 2018 and February 2019) and 2020 (December 2019) in the Blackfoot-Clearwater area of west-central Montana, USA. Box and whisker plots represent minimum, lower quartile, median, upper quartile, and maximum values.

OBJECTIVE 3: EVALUATE AND COMPARE ELK USE OF AREAS THAT BURNED AT DIFFERENT LEVELS OF FIRE SEVERITY

Methods

To evaluate elk use of landcover types and fire severities throughout the study area, we first developed a 99% kernel density annual home range boundary of all collared female elk, using the `adehabitatHR` package (Calenge 2006) in Program R with the “href” bandwidth selector. We used the 2016 Montana MSDI Land Cover (<http://geoinfo.msl.mt.gov>) dataset and the Rapid Assessment of Vegetation Condition after Wildfire (RAVG, <https://fsapps.nwcg.gov/ravg/>) product to identify landcover types and burn severities within the annual home range boundary. We classified landcover types into unburned conifer forests, low severity burned conifer forests, high severity burned conifer forests, open (grasslands, agricultural areas, and shrublands), closed (deciduous forests and riparian areas), and other (forests burned or harvested between 2002-2017).

We calculated the proportion of landcover types/burn severities used by female elk by identifying the number of elk locations within each landcover type for each season, then dividing by the total number of elk locations in that season. We defined 5 seasonal periods as: Spring (April 1 – May 30), Neonatal (May 31 – July 10; see Objective 5), Summer (July 11 – August 23), Fall (August 24 – December 13), and Winter (December 14 – March 31). To identify the proportion of landcover type/burn severity available within the annual range, we placed 1,000,000 random points within the annual elk home range boundary and identified the landcover type/burn severity for each random point. Then, we determined the proportion of each landcover type/burn severity available by dividing the number of points within each landcover type by 1,000,000 (the total number of random points). Finally, we calculated a seasonal selection ratio for each landcover type/burn severity by dividing the proportion of used locations in a landcover type/burn severity by the proportion of available locations within that landcover type/burn severity (e.g., Manly et al. 2003). Thus, selection ratios >1 suggested a landcover type was used more, relative to what was available, while selection ratios <1 suggested a landcover type was used less, relative to what was available.

Results

After removing locations with poor accuracy (dilution of precision >10 ; D'Eon and Delaporte 2005), we collected a total of 130,422 locations from 57 collared elk in spring, 82,817 locations from 55 collared elk during the neonatal season, 79,704 locations from 51 collared elk in summer, 192,588 locations from 55 collared elk in fall, and 252,893 locations from 58 collared elk in winter. Of these locations, 4,621 were from 2018; 141,420 from 2019; 385,648 from 2020; 202,411 from 2021; and 4,324 from 2022 (Figure 4). Elk generally had higher selection ratios in grasslands and irrigated agriculture during spring, fall, and winter, while elk had higher selection ratios in burned landcover types during neonatal and summer seasons (Figure 5). Thus, elk used open landcover types in the Blackfoot valley bottom more in early spring, late fall, and winter, and used burned areas in higher-elevation regions during neonatal and summer seasons (Figure 6). There were not large differences in elk use of low vs. high-severity burns.

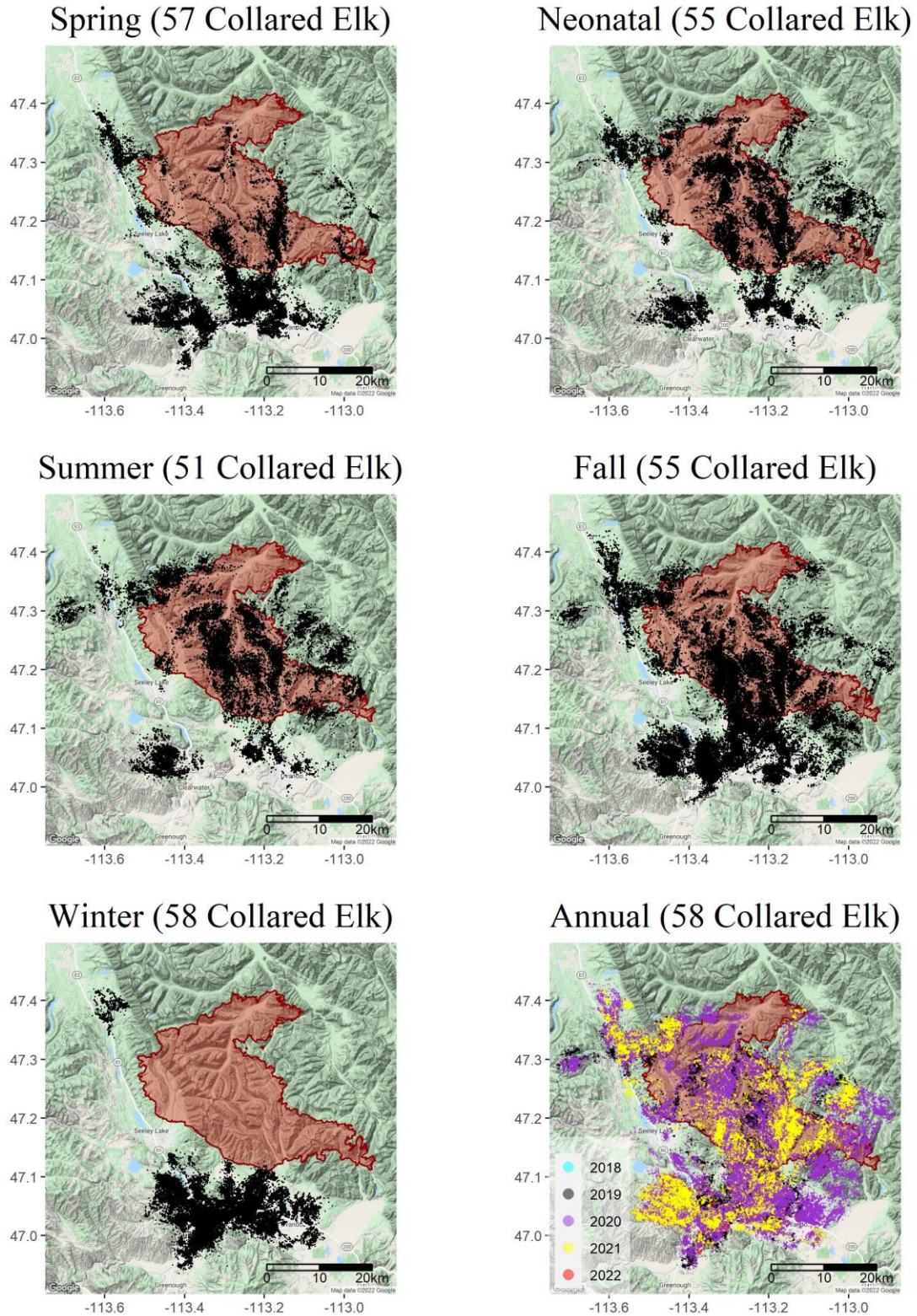


Figure 4. Spring (April 1 – May 30), Neonatal (May 31 – July 10), Summer (July 11 – August 23), Fall (August 24 – December 13), Winter (December 14 – March 31), and annual locations of female elk (black/colored dots) from December 2018 – February 2022 in the Blackfoot-Clearwater region of west-central Montana, USA. The Rice Ridge Wildfire boundary is shown in red.

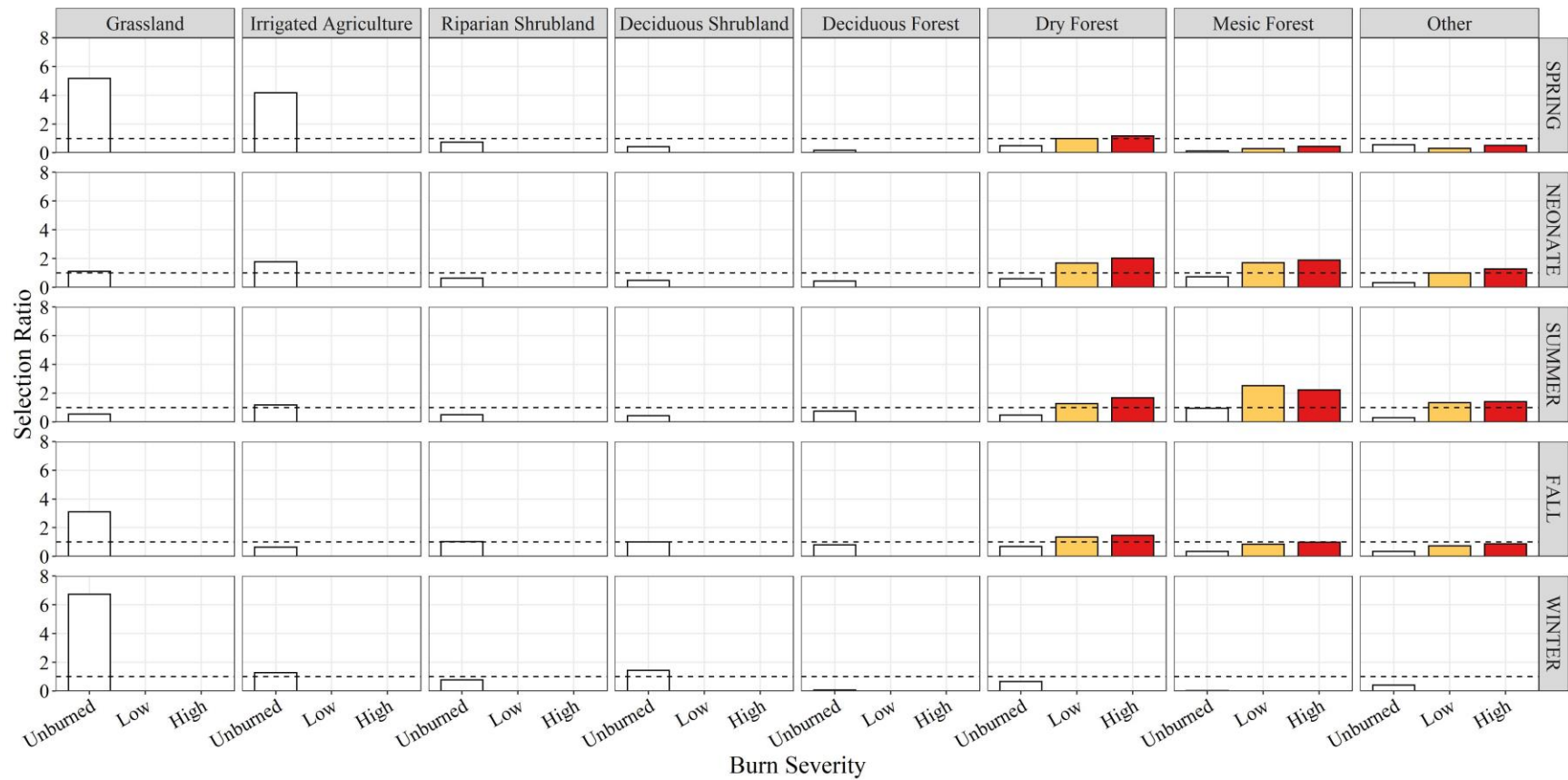


Figure 5. Selection ratios for collared female elk across landcover types, burn severities, and seasons (Spring [April 1 – May 30], Neonatal [May 31 – July 10], Summer [July 11 – August 23], Fall [August 24 – December 13], and Winter [December 14 – March 31]) in the Blackfoot-Clearwater region of west-central Montana, USA. Selection ratios were calculated as the proportion of elk locations within a landcover type divided by the proportion of that landcover type available within the 99% annual home range boundary of collared elk. A selection ratio >1 suggests selection for that landcover type, while a selection ratio <1 suggests avoidance. The horizontal dashed line in the figures represents a selection ratio = 1, suggesting no selection/avoidance. Bar colors represent burn severity, with white, yellow, and red representing unburned, low severity burn, and high severity burn, respectively.

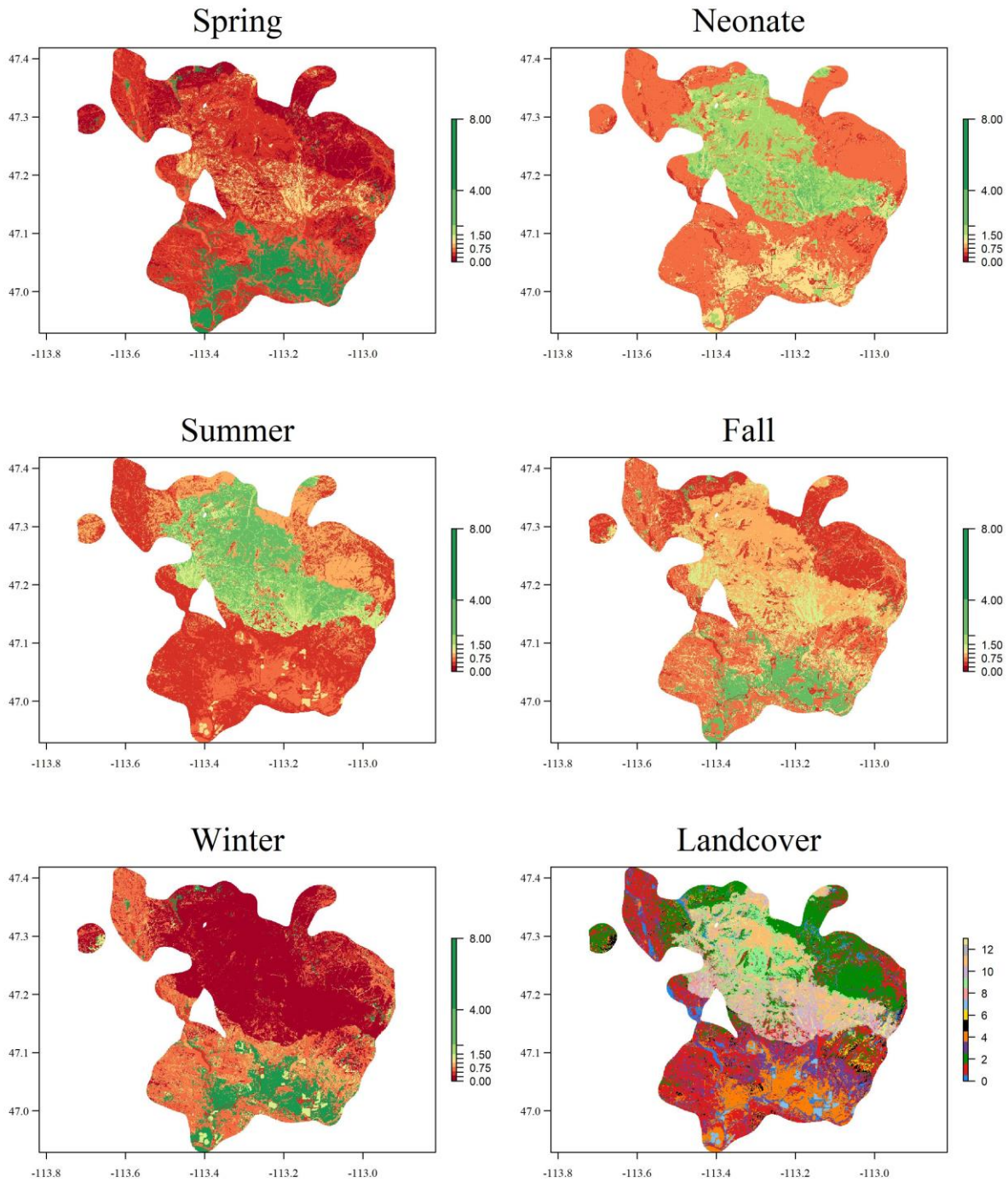


Figure 6. Female elk selections ratios by landcover type in Spring (April 1 – May 30), Neonatal (May 31 – July 10), Summer (July 11 – August 23), Fall (August 24 – December 13), and Winter (December 14 – March 31) seasons from December 2018 – February 2022 in the Blackfoot-Clearwater region of west-central Montana, USA. Selection ratios > 1 suggest selection for that landcover type, while selection ratios < 1 suggest avoidance. Landcover types are shown in the bottom right panel with values representing: 0 = Unburned Other; 1 = Unburned Dry Forest; 2 = Unburned Mesic Forest; 3 = Riparian Woodland and Shrubland; 4 = Montane Grassland; 5 = Deciduous Shrubland; 6 = Deciduous Forest and Woodland; 7 = Irrigated Agriculture; 8 = Low Severity Burned Dry Forest; 9 = Low Severity Burned Mesic Forest; 10 = High Severity Burned Dry Forest; 11 = High Severity Burned Mesic Forest; 12 = Low Severity Burned Other; 13 = High Severity Burned Other.

OBJECTIVE 4: EVALUATE AND COMPARE VEGETATION AND FORAGE RESOURCES IN AREAS THAT BURNED AT DIFFERENT LEVELS OF SEVERITY

Methods

We developed a landscape nutrition model predicting forage quality and quantity within the BC elk population summer range following similar methods as Proffitt et al. (2016, 2019). First, we collected fecal samples and used DNA metabarcoding to determine the primary summer forage species (Species from Feces-Bat Ecology and Genetics Lab, Northern Arizona University, Flagstaff, AZ, USA; see Objective 1). Next, we sampled vegetation across a gradient of fire severity and vegetation types to estimate forage quality and quantity. All sampling was conducted from May-August of 2019 and 2020, years two and three postfire. Finally, we developed summer landscape nutrition models that predicted forage quality and quantity as a function of spatial and temporal covariates. To understand the effects of variable fire conditions, we used the summer range boundary to estimate the availability of forage quality, herbaceous forage biomass, and shrub forage biomass available to elk within four different fire severity scenarios.

Field Methods: Site Selection.—We selected vegetation sampling sites based on a generalized random tessellation stratified sampling approach (Stevens and Olsen 2004) within six vegetation cover types of interest to elk. Fire severity and extent for the Rice Ridge Wildfire was determined using the Rapid Assessment of Vegetation Condition after Wildfire product (RAVG, <https://fsapps.nwcg.gov/ravg/>). The six vegetation cover types included conifer dominated mesic forest types (dominated by subalpine fir and Engelmann spruce) and conifer dominated dry forest types (dominated by lodgepole pine, ponderosa pine, Douglas fir, and western larch) each with three fire severity categories (unburned, low severity, and high severity). We focused our summer sampling on mesic and dry forests as they comprise greater than 70% of the vegetation cover types found within the elk population's summer range. We additionally sampled five other vegetation cover types not impacted by fire (deciduous forest, deciduous shrubland, grassland, irrigated agriculture, riparian), in August only, which comprised approximately 18% of the summer range.

Field Methods: Estimating Phenological Stage-Specific Digestible Energy.—To estimate the phenological stage-specific digestible energy (DE) of elk forage species, we collected forage species in each of the phenological stages (newly emergent, flowering, fruiting, and cured) to determine dry matter digestibility (DMD) using sequential detergent fiber analysis. We collected forage samples from either burned or unburned forests throughout the study area and we defined a composite sample as five individual plants from the same burn type and species-phenological stage. Composite forage samples included both leaves and stems as well as flowers and fruits when present. We immediately dried samples at 55°C for approximately 36 hours and sent samples to the Wildlife Habitat and Nutrition Laboratory (Pullman, WA, USA). The lab uses the Ankom method (Ankom Fiber Analyzer 200/220, Ankom Technology, Fairport, NY, USA) to report values including neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), acid insoluble ash (AIA), and protein precipitation measured using bovine serum albumin (BSA). Sodium sulfite was used in assays for forb and shrub samples, but not grass samples. From these values, DMD is calculated for forage species

while accounting for species containing tannins (shrubs and some forbs), a complex group of chemicals known to reduce DMD and protein in ruminants (Robbins et al. 1987a, b, Hanley et al. 1992), using the following equation from Robbins et al. (1987a, b):

$$\text{DMD} = [(0.9231 e^{-0.0451 * ((\text{ADL}/\text{NDF}) * 100)} - 0.03 * \text{AIA})(\text{NDF})] + [(-16.03 + 1.02 \text{NDS}) - 2.8 * 11.82 \text{BSA}] \quad (\text{Eq. 1})$$

where NDS is the neutral detergent soluble measured at 100 – %NDF. For each forage species, DMD is then converted to DE, a metric to determine forage quality, using the following equation from Cook et al. (2016):

$$\text{DE} = \left(\frac{\text{DMD}}{100} \right) \times \text{GE} \quad (\text{Eq. 2})$$

where GE is the gross energy content determined by bomb calorimetry and estimated as 4.53 kcal/g for forbs, graminoids, and deciduous shrubs and 4.8 kcal/g for evergreen shrubs (Cook et al. 2016).

Field Methods: Estimating Forage Quality and Quantity.—At each vegetation sampling site described above, we set a 40 m transect along the contour of the slope. To estimate forage quality (DE; kcal/g), at the 0, 10, 20, 30, and 40 m marks, we recorded species composition within a 1 m² quadrat. For each quadrat, we separated the forage species from the recorded species composition, and then divided the forage species cover proportionally amongst the identified phenological stages. We calculated DE of the quadrat by multiplying the proportion of the species in the phenological stage by the phenological stage-specific DE (see above) and then summed. We averaged the five quadrats to get the sampling site’s mean DE (Figure 7).

To estimate mean forage quantity (g/m²) per sampling site, we embedded a 0.5 m² clip plot within the 1 m² quadrat at the 0, 20, and 40-meter marks of the transect. We clipped all graminoids and forbs between 1-2 cm from the ground to represent the available foraging height to elk and placed in separate bags. For shrubs, we clipped all leaves and soft-green stems, representing new growth, below the 2 m mark and placed in another bag. We collected all live and senesced vegetation; however, we did not include previous years’ litter. We dried samples at 55°C for 36 hours and then measured for dry weight. First, we allocated dried biomass within each lifeform (forbs, shrubs, and graminoids) across species based on rescaled percent cover. Second, we filtered to forage species and summed biomass. Lastly, we averaged biomass across all clip plots and then scaled up to square meters to estimate mean forage quantity (Figure 7). Because ocular estimates of percent cover for each species may vary from actual biomass, our results for forage quality and quantity should be interpreted as relative between fire severity classes rather than absolute.

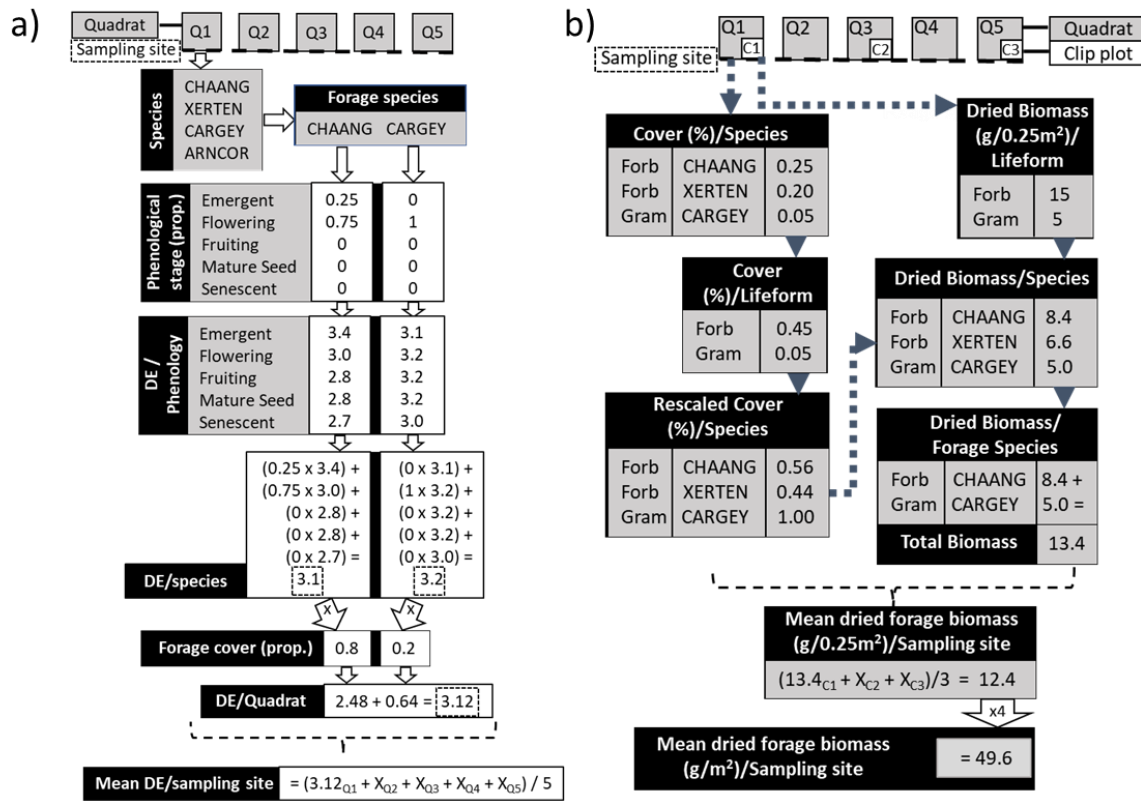


Figure 7. Methods for estimating a) mean digestible energy (DE; i.e., forage quality; kcal/g) and b) mean forage quantity (g/m²) at each vegetation sampling site in the Blackfoot-Clearwater elk population annual range in west-central Montana, USA. Figure adapted from Proffitt et al. (2019).

Analytical Methods: Landscape Modeling.—We developed summer landscape nutrition models that predicted forage quality using linear models and forage quantity using zero-inflated negative binomial models (ZINB) as a function of spatial and temporal covariates. We modeled dry and mesic forests separately to understand the unique factors that impact nutrition within each forest type (Diaz et al. 1998, Hollingsworth et al. 2013). Additionally, we separately modeled herbaceous (forbs and graminoids) and shrub forage biomass to understand the distinct drivers that influence the amount of forage based on lifeform. Spatial covariates evaluated to predict forage DE quality and quantity included fire severity (unburned, low severity, and high severity), aspect, percent tree canopy cover, compound topography index, distance to unburned patch, elevation, patch size, and solar radiation. Temporal covariates included precipitation and week. We standardized continuous covariates by subtracting their mean and dividing by their standard deviation and we assumed covariates were measured without error. We screened covariates for collinearity and removed covariates if they were strongly correlated.

We hypothesized that the effect of patch size and distance to unburned patches on forage quality and quantity would differ based on fire severity. Therefore, we included interaction terms to understand the effect of fire severity on patch size and distance to unburned patches (Heinselman 1981, Turner et al. 1997). We also included an interaction term between elevation and week to account for the progression of vegetation emergence at higher elevations across the

summer season. We converted our quantity measurements to an integer by multiplying by 100 to meet the assumptions of zero-inflated negative binomial models. Our primary goal was to determine which combination of the spatial and temporal covariates best predicted DE, herbaceous forage biomass, and shrub forage biomass in each of the forest types. We considered all subsets of plausible covariates and selected the most parsimonious model using Akaike's Information Criterion for small sample sizes (Burnham and Anderson 2002). For forage quality we used R^2 values from the top models to assess goodness of fit, and for forage quantity we used posterior predictive checks to assess predictive capability.

From the top forage quality models, we assessed the effects of covariates based on the sign and magnitude of standardized coefficient estimates, and we compared prediction estimates for fire severities by holding all other covariates at their mean value. From the top forage quantity models, we back-transformed coefficient estimates by exponentiating the value and compared the effects of fire severity by holding all other covariates at their average levels.

Analytical Methods: Phenological Differences Between Fire Severities.—To evaluate if vegetation in the burn was in earlier phenological stages throughout the summer, we tested for differences in phenological stage between fire severity categories using a Poisson regression. We developed a site-level phenological metric for forb, graminoid, and shrub forage species as our response variable. At each vegetation sampling site, we multiplied the proportion of each species in each phenological stage by the ordinal value for each phenological stage (1 for emergent to 5 for senescent) and then averaged across forage species within each lifeform for each site. We included an interaction term between fire severity (unburned, low severity, and high severity) and month (May, June, July, and August) as a predictor variable. If phenology differed between fire severity categories, we would expect 95% confidence intervals of fire severity coefficients to not overlap within each month.

Analytical Methods: Predicted Landscape Level Differences Between Fire Severities.—To investigate potential effects of fire severity on the nutritional landscape, we used the unstandardized coefficient estimates from the top landscape nutrition models to predict forage quality and quantity within the Rice Ridge fire perimeter across four fire severity scenarios: 1) an unburned landscape, 2) a landscape burned completely by a low severity fire, 3) a landscape burned completely by a high severity fire, and 4) the observed landscape impacted by mixed severity fire. For each of the four predicted fire severity scenarios, we calculated the area (km^2) and percent of the BC elk population's summer range within mesic and dry forests that meets the nutritional requirements for lactating female elk throughout the summer. We classified adequate nutrition as > 2.75 kcal/g and inadequate nutrition as < 2.74 kcal/g (Cook et al. 2004, Cook et al. 2016). For herbaceous and shrub forage biomass we calculated the mean kg/ha within mesic and dry forests for each predicted landscape throughout the summer.

Results

Vegetation Sampling Sites.—We sampled a total of 682 vegetation sampling sites within 353 mesic forest sites (102 unburned, 113 low severity, and 138 high severity) and 329 dry forests sites (98 unburned, 105 low severity, 126 high severity). The most common forage taxa varied within mesic and dry forests and fire severity (Figure 8).

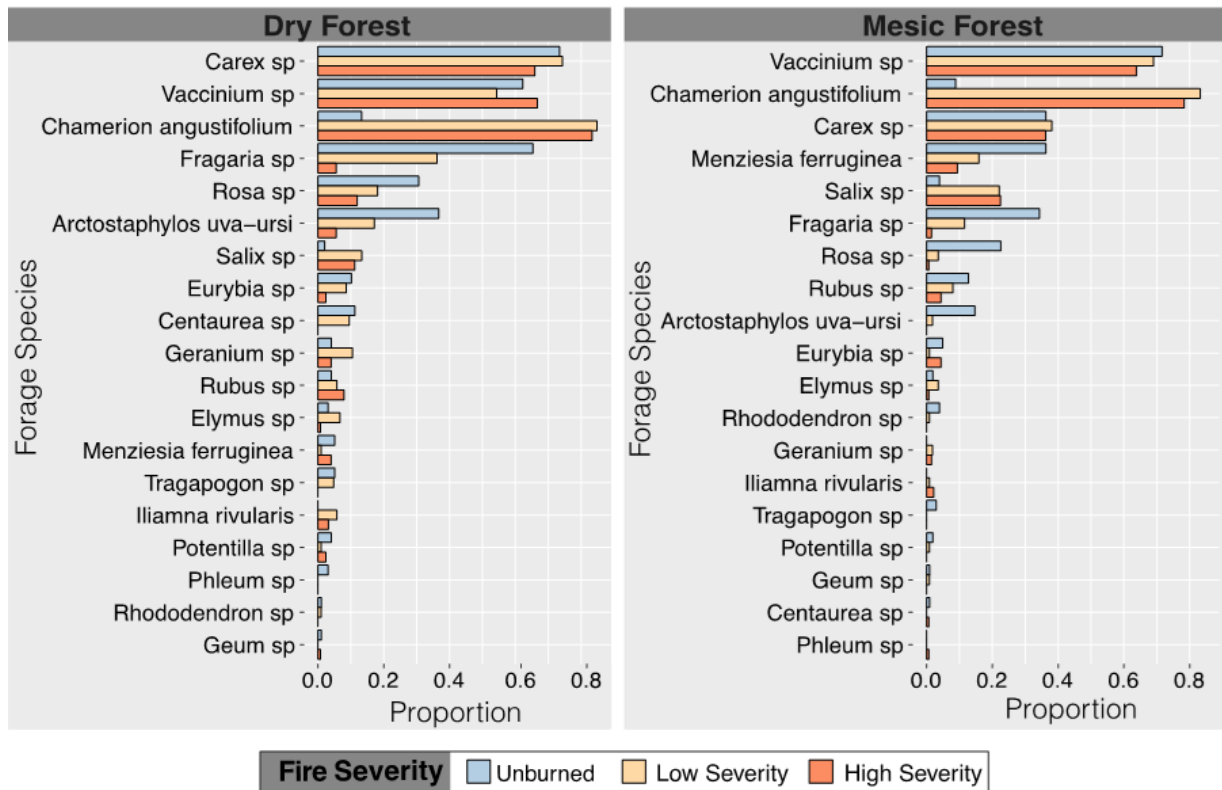


Figure 8. Proportion of vegetation sampling plots containing each forage species within each fire severity category in dry and mesic forests in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020.

Estimating Forage Quality and Quantity.—Median summer DE was 3.00 kcal/g (25 – 75% quantiles: 2.65 – 3.22) and varied by fire severity, vegetation cover type, and month (Figure 9). Median DE for both dry and mesic forests burned by low severity (3.04 and 3.03 kcal/g, respectively) and high severity (2.98 and 2.91 kcal/g, respectively) was higher than unburned forests (2.75 and 2.59 kcal/g, respectively).

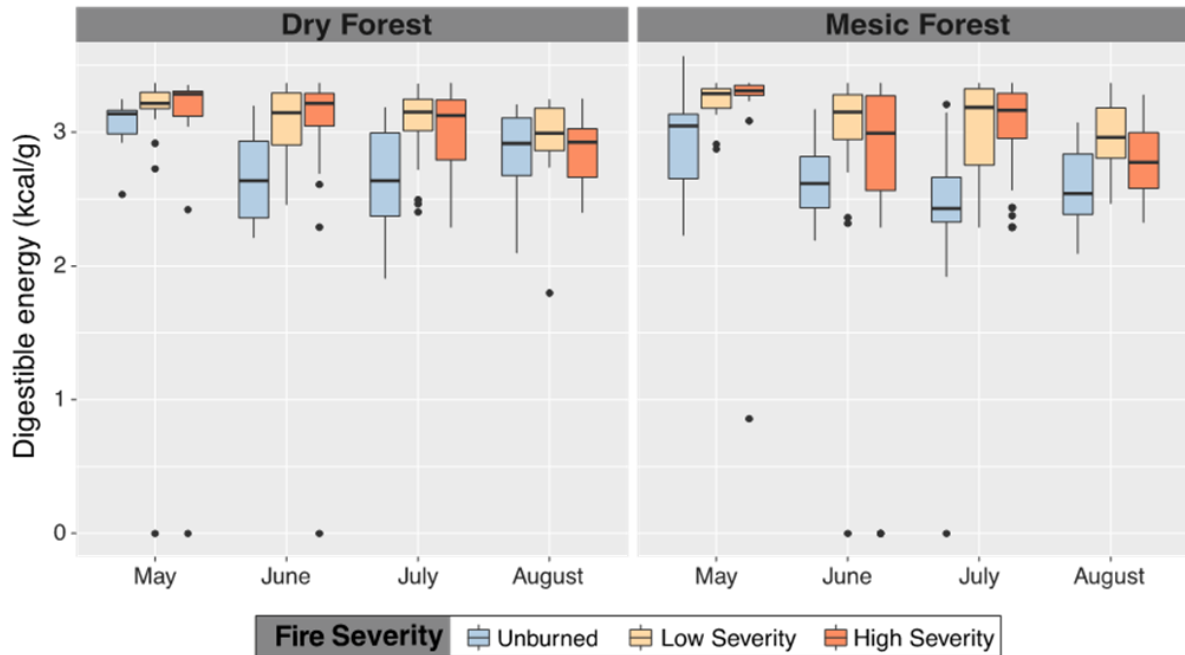


Figure 9. Median digestible energy measured within each vegetation cover class and month from the vegetation sampling sites (focused on summer forage species) in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5x the IQR is represented by the whiskers, outliers >1.5x IQR are represented by the points outside of the whiskers.

Median summer herbaceous and shrub forage biomass was 7.96 g/m^2 (25 - 75% quantiles: $0.2 - 27.21$) and 0.00 g/m^2 (25 - 75% quantiles: $0.00 - 5.66$), respectively, and varied based on fire severity, vegetation cover type, and month (Figure 10). Median herbaceous forage biomass for both dry and mesic forests burned by low severity (21.4 and 12.5 g/m^2 , respectively) and high severity (9.89 and 7.83 g/m^2 , respectively) was higher than unburned forests (2.93 and 0.00 g/m^2 , respectively). Median shrub forage biomass for both dry and mesic forests was higher in unburned forests (7.15 and 6.06 g/m^2 , respectively) than forests burned by both low and high severity (0.00 g/m^2 for all burned forests).

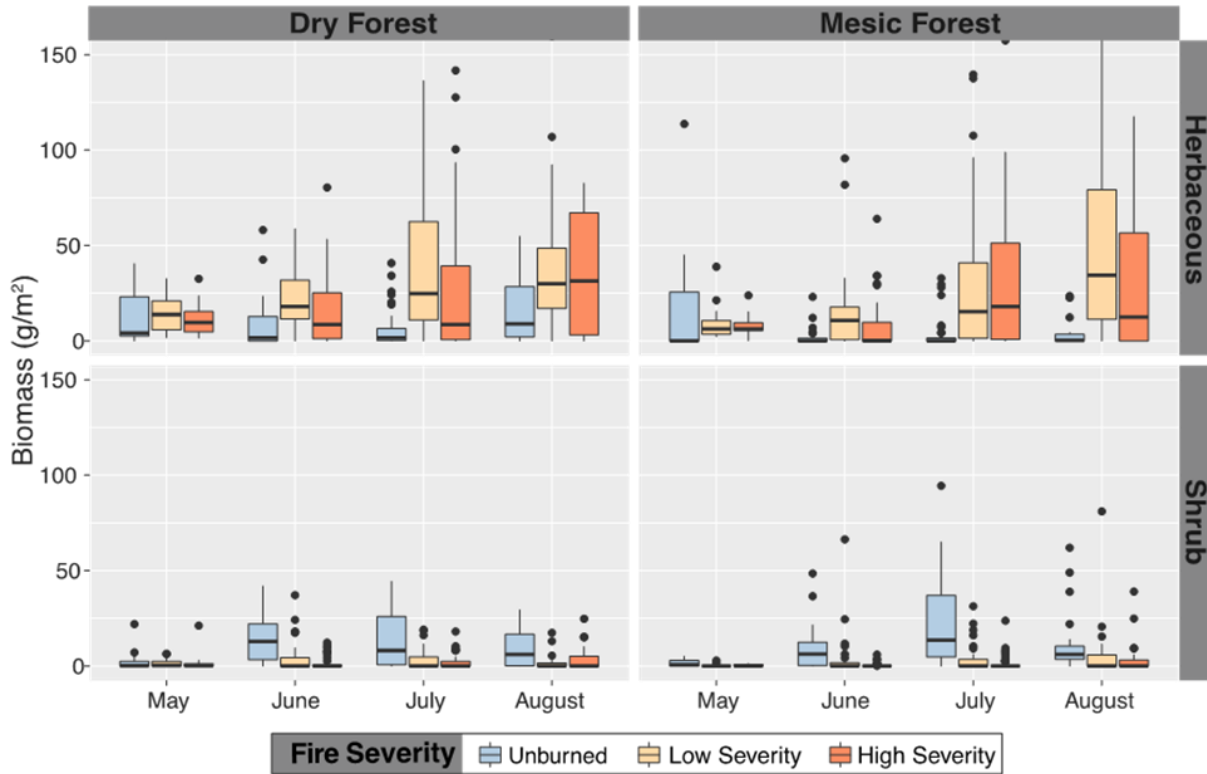


Figure 10. Summer median herbaceous and shrub forage biomass (g/m^2) measured within each vegetation cover class and month (focused on the summer forage species) in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. The median is represented by the horizontal lines through the boxes, the interquartile range (IQR) is represented by the length of the box, 1.5x the IQR is represented by the whiskers, outliers $>1.5x$ IQR are represented by the points outside of the whiskers.

Landscape Modeling.—Within dry forests, the top model predicting forage quality included the covariates fire severity, percent tree canopy cover, slope, solar radiation, and the interaction of week and elevation ($R^2 = 0.16$; Table 3). Forage quality in low and high severity forests was 7.9% (95% CI: 2.9 - 12.6%) and 7.6% (2.1 - 12.9%) higher than unburned forests, respectively. There was no difference in forage quality between low and high severity burned forests, as confidence intervals between fire severities overlapped. Digestible energy decreased by 2.2% (95% CI: 0.1 - 4.5%) for every standard deviation increase in percent tree canopy cover, decreased by 2.2% (95% CI: 0.5 - 4%) for every standard deviation increase in solar radiation, and increased by 3.9% (95% CI: 2.2 - 6.1%) for every standard deviation increase in slope. In May, DE decreased by 6.5% (95% CI: 4.3 - 9.0 %) for every standard deviation increase in elevation, but as time progressed, DE increased with elevation by 2.2% (95% CI: 0.4 - 4%).

Table 3. Standardized coefficient estimates and standard errors for the top models predicting summer forage quality in each of the forest types in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. Bold face values denote 95% CI not containing 0. Effects of fire severity in dry and mesic forests are in relation to the reference unburned forest (Intercept).

Covariate	Dry Forests	Mesic Forests
Intercept	2.77 (0.052)	2.63 (0.046)
Low Severity	0.22 (0.067)	0.43 (0.062)
High Severity	0.21 (0.077)	0.37 (0.060)
Elevation	-0.18 (0.033)	-0.16 (0.028)
Week	0.002 (0.025)	-0.025 (0.03)
Week*Elevation	0.061 (0.027)	0.093 (0.03)
Slope	0.11 (0.027)	--
Canopy Cover	-0.064 (0.031)	--
Solar Radiation	-0.060 (0.024)	--
Monthly Precip	--	0.061(0.025)
Weekly Precip	--	--
Aspect	--	--
CTI	--	--
Patch Size*Fire Severity	--	--
Summer Precip	--	--
R ²	0.16	0.21

Within mesic forests, the top model predicting forage quality included the covariates fire severity, monthly precipitation, and the interaction term of week and elevation and their main effects ($R^2 = 0.21$; Table 3). Forage quality in low severity burned forests was 16.3% (95% CI: 11.8 – 20.1%) greater than unburned forests, and forage quality in high severity burned forests was 14.1% (95% CI: 9.5 – 18.3 %) greater than unburned forests. Low severity burned mesic forests trended to have 2% greater forage quality compared to high severity burned mesic forests, however, confidence intervals between fire severities overlapped. Digestible energy increased by 2.3% (95% CI: 0.4 – 4.2%) for every standard deviation increase in precipitation. Digestible energy within mesic forests in May decreased by 6.1% (95% CI: 3.8 - 8%) for every standard deviation increase in elevation, but as the time progressed, DE increased with increasing elevation by 3.4% (95% CI: 1.3 – 5.7%).

Within dry forests, the top model predicting the presence/absence of herbaceous forage biomass (the zero inflated part of the model) included fire severity and elevation (Table 4). The odds of low severity and high severity burned forests having no herbaceous forage biomass were 93% (95% CI: 72 – 98%) and 65% (95% CI: 19 – 85%) lower than unburned forests, respectively. The covariates predicting the amount of herbaceous forage biomass (the negative binomial part of the model) included fire severity, elevation, and week. Low severity and high severity burned forests had 179% (95% CI: 98 – 291%) and 145% (95% CI: 72 – 250%) greater herbaceous forage biomass compared to unburned forests, respectively. There was no

significant difference in predicting the presence/absence or amount of herbaceous forage biomass between low severity and high severity burned forests as the confidence intervals widely overlapped.

Table 4. Standardized coefficient estimates and standard errors for the top models predicting summer herbaceous and shrub forage biomass within dry and mesic forests in the Blackfoot-Clearwater elk summer range in west-central Montana, USA from 2019-2020. “NB” refers to the negative binomial part of the model that estimates the amount of biomass and “ZI” refers to the zero inflated part of the model that estimates the presences or absence of biomass. Boldface values denote 95% CI not containing zero. Effects of fire severity are in relation to the reference unburned forest (Intercept).

		Herbaceous Biomass		Shrub Biomass	
Covariate		Dry Forest	Mesic Forest	Dry Forest	Mesic Forest
NB	Intercept	7.077 (0.14)	7.34 (0.22)	7.37 (0.16)	7.26 (0.11)
	Low Severity	1.02 (0.17)	0.95 (0.25)	-0.72 (0.20)	-0.43 (0.19)
	High Severity	0.90 (0.17)	0.81 (0.29)	-0.98 (0.25)	-1.29 (0.20)
	Canopy	--	-0.25 (0.12)	0.034 (0.11)	--
	Elevation	-0.24 (0.086)	-0.35 (0.10)	0.21 (0.11)	0.31 (0.077)
	Slope	--	--	-0.24 (0.10)	--
	Week	0.35 (0.068)	0.53 (0.10)	--	0.49 (0.095)
	Week*Elevation	--	0.32 (0.13)	--	--
	Aspect	--	0.25 (0.098)	--	--
	CTI	--	--	--	--
	Patch Size*Fire Severity	--	--	--	--
	Monthly Precipitation	--	--	--	--
	Weekly Precipitation	--	--	--	--
	Solar Radiation	--	--	--	--
	Summer Precipitation	--	--	--	--
ZI	Intercept	-0.99 (0.27)	0.11 (0.24)	-0.57 (0.30)	-1.40 (0.25)
	Low Severity	-2.62 (0.69)	-2.89 (0.42)	0.96 (0.36)	1.90 (0.32)
	High Severity	-1.04 (0.42)	-1.91 (0.35)	0.84 (0.42)	2.39 (0.32)
	Canopy	--	-	-0.35 (0.18)	--
	Elevation	0.83 (0.21)	1.32 (0.19)	0.41 (0.14)	--
	Weekly Precipitation	--	--	-0.27 (0.12)	--
	Week	--	--	--	-0.27 (0.13)
	Slope	--	--	--	--
	Week*Elevation	--	--	--	--
	CTI	--	--	--	--
	Aspect	--	--	--	--
	Patch Size*Fire Severity	--	--	--	--
	Monthly Precipitation	--	--	--	--
	Solar Radiation	--	--	--	--
	Summer Precipitation	--	--	--	--

Within mesic forests, the top model predicting the presence/absence of herbaceous forage biomass included fire severity and elevation (Table 4). There was 94% (95% CI: 87 – 98%) and 85% (95% CI: 70 – 93%) lower odds of low severity and high severity burned forests having no herbaceous forage biomass compared to unburned forests, respectively. The covariates predicting the amount of herbaceous forage biomass included fire severity, aspect, percent tree canopy cover, elevation, and the interaction term of week and elevation (Table 4). Low severity and high severity burned forests had 160% (95% CI: 58 – 327%) and 124% (95% CI: 28 – 294%) greater herbaceous forage biomass compared to unburned forests. There was no significant difference in predicting the presence/absence or amount of herbaceous forage biomass between low severity and high severity forests as the confidence intervals widely overlapped.

Within dry forests, the top model predicting the presence/absence of shrub forage biomass included fire severity, percent tree canopy cover, elevation, and weekly precipitation (Table 4). The odds that low severity and high severity burned forests had no shrub forage biomass was 161% (95% CI: 28 – 431%) and 131% (95% CI: 2 – 422%) greater than unburned forests, respectively. The covariates predicting the amount of shrub forage biomass included fire severity, percent tree canopy cover, elevation, and slope (Table 4). Low severity and high severity burned forests had 51% (95% CI: 28 - 67%) and 62% (95% CI: 39 - 77%) lower shrub forage biomass compared to unburned forests, respectively. There was no significant difference in predicting the presence/absence or amount of shrub forage biomass between low severity and high severity forests as the confidence intervals widely overlapped.

Within mesic forests, the top model predicting the presence/absence of shrub forage biomass included fire severity and week (Table 4). The odds that low severity and high severity burned forests had no shrub forage biomass was 572% (95% CI: 262 – 1148%) and 993% (95% CI: 489 – 1927%) greater compared to unburned forests, respectively. The covariates predicting the amount of shrub forage biomass included fire severity, elevation, and week (Table 4). Low severity and high severity burned forests had 35% (95% CI: 6 – 55%) and 72% (95% CI: 59 – 81%) lower shrub forage biomass compared to unburned forests, respectively. There was a significant difference in the amount of shrub forage biomass between low and high severity burned forests where low severity burned forests had approximately 57% more shrub forage biomass compared to high severity burned forests.

Phenological Differences Between Fire Severities.—There were minimal differences in phenology between fire severity categories in May and June for forage species in each lifeform. In July, low and high severity burned forests were in significantly earlier phenological stages compared to unburned forests for each lifeform, suggesting that forage species were continuing to emerge in July in burned forests. Approximately 10-20% more burned sampling sites were classified as having early phenology (emergent and flowering) compared to unburned sampling sites in July. In August, phenological differences varied as a function of lifeform and fire severity. For forbs, unburned forests had an earlier phenological stage compared to low and high severity burned forests. Unburned sampling sites had approximately 39% and 48% more sampling sites with forbs classified as early phenology compared to low and high severity burned forests, respectively. For graminoids and shrubs in August, low and high severity burned forests had significantly earlier phenological stages compared to unburned forests.

Approximately 12-19% more burned sampling sites were classified as early phenology compared to unburned sites.

Predicted Landscape Level Differences Between Fire Severities.—The percent of the summer range with adequate DE varied based on month and fire severity scenario (Figure 11). For the observed mixed severity, low severity, and high severity predicted scenarios, percent adequate DE generally increased during summer and did not vary substantially between the three fire severity scenarios. In general, approximately half of the landscape had adequate DE throughout the summer for each of the predicted fire severity scenarios. For the unburned scenario, the majority of the landscape provided inadequate DE. For the unburned predicted landscape, percent adequate DE was substantially lower compared to the three predicted burned landscape scenarios, and the percent of adequate DE across the summer range decreased from month to month. For example, the unburned landscape had 18%, 24%, 29%, and 36% less of the landscape with adequate DE compared to the landscape burned with the observed mixed-severity conditions from May – August, respectively (Figure 12). The low severity landscape had 2.9%, 4.3%, 5.0%, and 0.2% more of the landscape with adequate DE compared to a high severity landscape in May, June, July, and August, respectively.

The mean kg/ha of herbaceous and shrub forage biomass within dry and mesic forests in the summer range increased throughout the summer and varied based on fire severity scenario (Figure 11). Herbaceous forage biomass did not substantially vary across the observed mixed severity, low severity, and high severity predicted landscapes but was substantially lower across each month for the unburned landscape. For example, the observed mixed severity predicted landscape compared to the unburned predicted landscape had 66%, 68%, 41%, and 42% more herbaceous forage biomass (kg/ha) in May, June, July, and August, respectively. The low severity predicted landscape had approximately 10% more herbaceous forage biomass compared to a high severity predicted landscape at each time step. Shrub forage biomass for each of the four predicted landscapes was highest in the unburned landscape, and greater in the low severity predicted landscape compared to the high severity predicted landscape. The low severity predicted landscape had approximately 17%, 15%, 22%, and 24% greater shrub forage biomass compared to a high severity predicted landscape in May, June, July, and August, respectively.

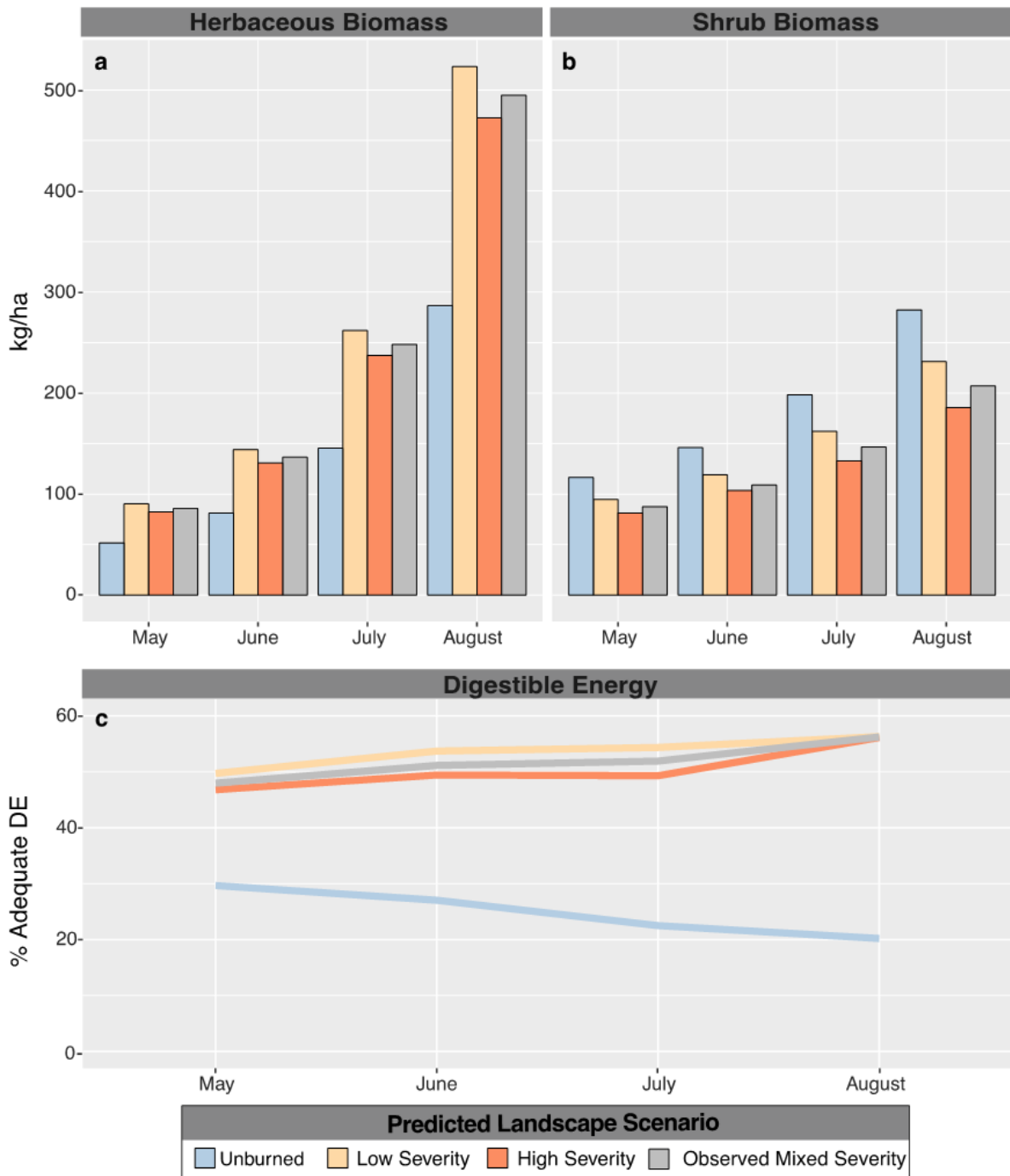


Figure 11. The average kg/ha per month for herbaceous forage biomass (panel a) and shrub forage biomass (panel b) within the summer range of the four predicted landscape scenarios in the Blackfoot-Clearwater elk population’s summer range. Panel “c” shows the percent of the Blackfoot-Clearwater elk population’s summer range within the four fire scenarios that meets the threshold of ≥ 2.75 kcal/g of forage to be considered adequate for each month.

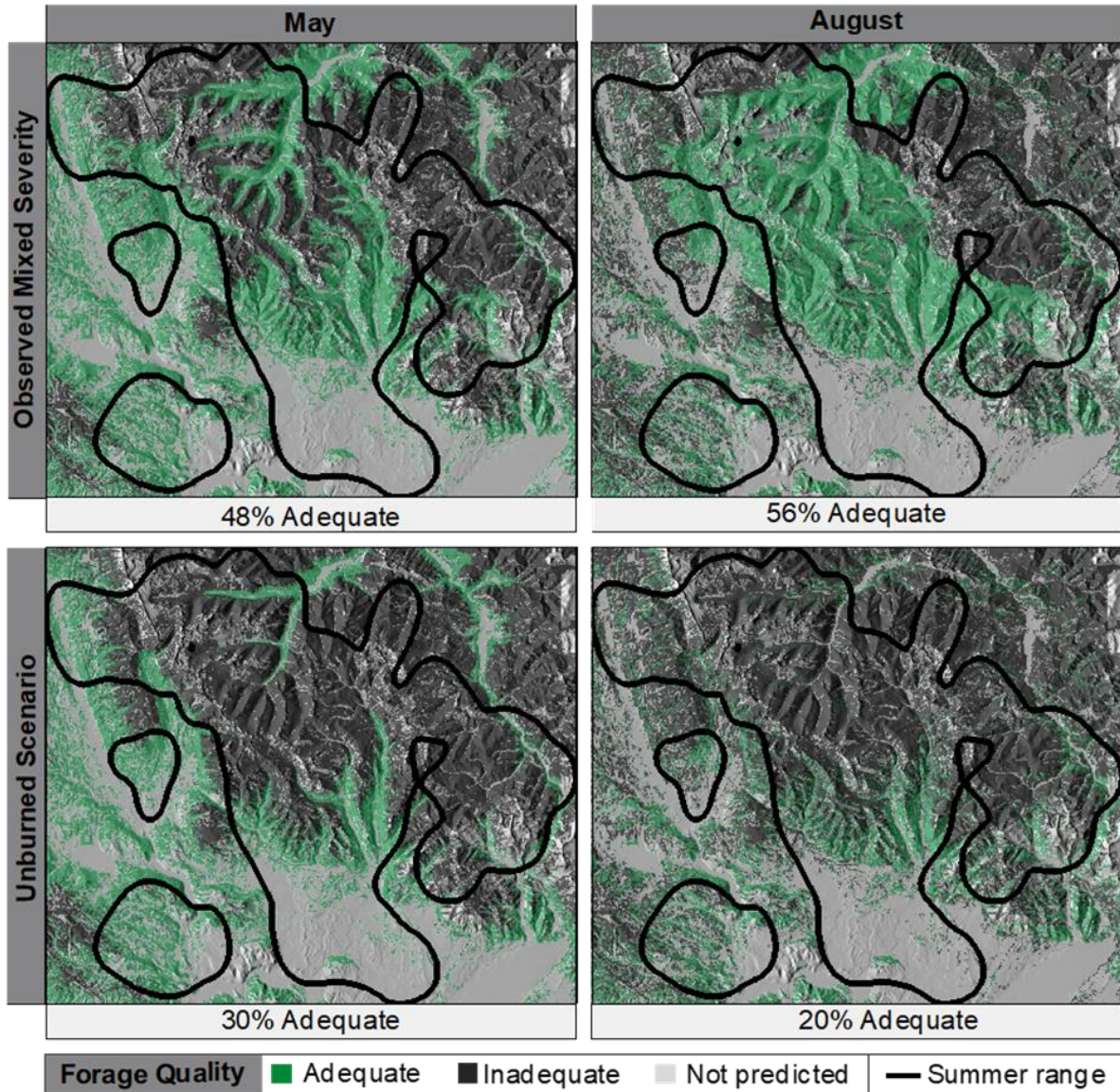


Figure 12. Digestible energy predicted onto the observed mixed severity landscape and the unburned fire scenario for May and August for the Blackfoot-Clearwater elk population summer range in west-central Montana, USA using the top forage quality model. The percent of the landscape that meets adequate forage quality ($DE \geq 2.75$ kcal/g) increased from May to August for the predicted observed mixed severity landscape, but percent of the landscape with adequate forage quality decreased in an unburned predicted landscape.

OBJECTIVE 5: DEVELOP A RESOURCE SELECTION PROBABILITY FUNCTION MODEL TO EVALUATE THE EFFECTS OF WILDFIRE AND OTHER FACTORS ON SUMMER AND FALL ELK DISTRIBUTIONS

Methods

To evaluate female elk use of the Blackfoot-Clearwater region, we developed and fit Resource Selection Probability Functions (RSPF; Rota et al. 2013) for neonatal, summer, and fall hunting seasons. The estimated parameter coefficients in a RSPF allow prediction of the absolute probability that a site will be used; thus, they are more intuitive and useful for informing habitat management.

Identifying Seasons.—Elk may make tradeoffs in selection between sites with high-quality forage resources and sites with low risk of predation (DeVoe et al. 2019, Berg et al. 2021). These tradeoffs could be most evident during the neonatal period, when nutritional demands of maternal elk are high and neonates are at greatest risk of predation. Thus, we divided the summer period (May 31 – August 23) into two seasons, “Neonatal” and “Summer”, to identify whether there were tradeoffs in selection throughout the summer, as resource requirements and availability changed.

We used similar methods as those outlined in Berg et al. (2021) and Brook (2010) to classify neonatal and summer seasons. First, we determined the start of the neonatal season (i.e., parturition) by identifying the date in spring when the average movement rate/day and 95% daily home range size across collared female elk was lowest. We estimated movement rate by calculating the Euclidean distance between subsequent elk GPS locations and dividing by the time between locations. We calculated daily home range sizes by calculating individual daily 95% kernel density home ranges using the “adehabitatHR” package (Calenge 2006) and the “href” bandwidth selector in Program R. We used LOESS smoothing across mean daily movement rates and home ranges to estimate the date with the lowest amount of movement in spring/early summer.

Next, we determined the end of the neonatal season by identifying a temporal “breakpoint” in average daily elk home range size between the mean date of parturition and August 1 (Berg et al. 2021). This “breakpoint” represented the break in time between when elk neonates were gaining mobility (“Neonatal” season) vs. when elk had established a summer home range and daily home range sizes reached an asymptote (“Summer” season). We identified this breakpoint using a Bayesian implementation of a multiple change point analysis with the “mcp” package (Lindeløv 2020) in Program R.

Elk resource use may change throughout the fall as weather and hunting pressure changes. Thus, we defined four fall seasons based around hunting seasons, including “Prehunt” (August 24 – September 6, 2019 or August 22 – September 4, 2020), “Archery-Only” (September 7 – 14, 2019 or September 5 – 14, 2020), “Backcountry-Rifle” (September 15 – October 25, 2019 or September 15 – October 23, 2020), and “Rifle” (October 26 – December 1, 2019 or October 24 – November 29, 2020).

Trail Cameras and Prevalence.—RSPFs require the estimation of a “prevalence” term, equivalent to the average probability of use by the species of interest across sample units within the study area (Rota et al. 2013). Prevalence may be estimated from use-availability data; however, prior information about species prevalence may improve model convergence and fit. Thus, we used trail camera data to estimate seasonal elk prevalence across our study area for use in seasonal elk RSPFs.

We deployed 138 motion-activated Reconyx Hyperfire 2 trail cameras in 2019 and 133 trail cameras in 2020 at random locations (Figure 13) generated using a generalized random tessellation stratified approach in Program R (Dumelle et al. 2022). We placed cameras at approximately chest height (~1.4 m), parallel to the ground, facing a direction that offered the largest viewshed. We set cameras to take bursts of 5 photos each time triggered, with no lag time between triggers, 24 hours per day. Cameras were active for at least 14 days; if a camera failed (e.g., camera knocked down, battery/SD card failure, etc.), we censored that camera from further analysis. After we retrieved cameras, we identified elk and all other mammal species in photos using Timelapse Image Analysis system (Greenberg et al. 2019). All trail camera field methodology was approved through the University of Montana Institutional Animal Care and Use Committee (protocol identification number: 015-18JMWB-031618).

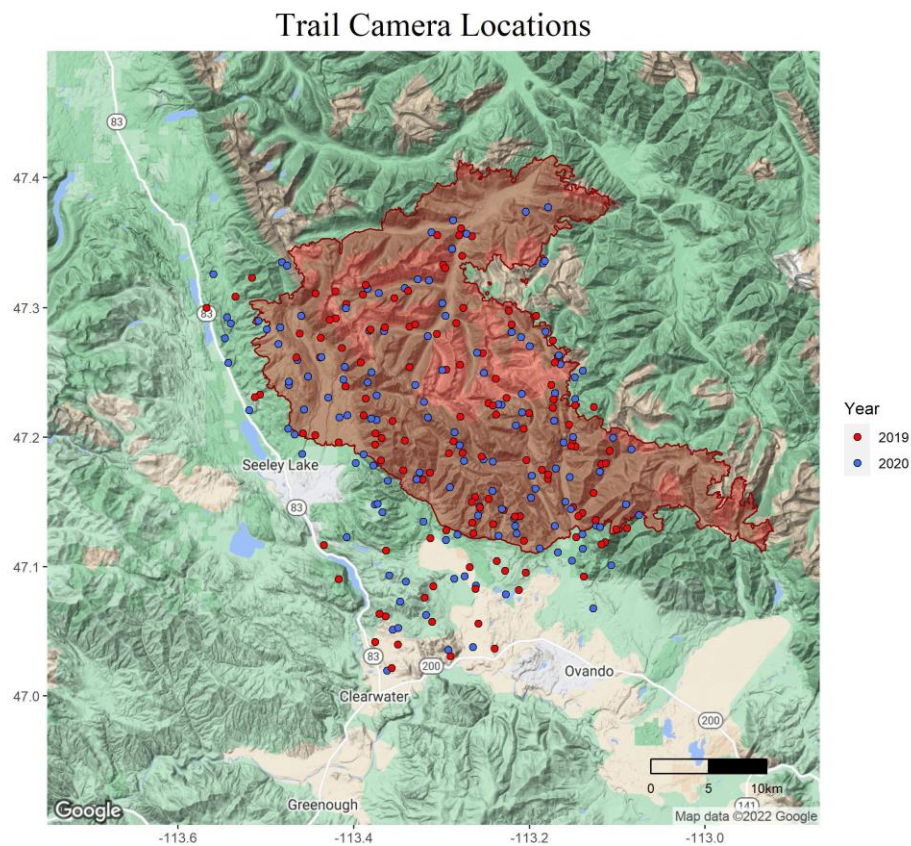


Figure 13. Trail camera locations in the Blackfoot-Clearwater region of west-central Montana, USA in 2019 (red dots) and 2020 (blue dots). The Rice Ridge wildfire boundary is depicted in red.

We separated trail camera data into seasonal periods, based on logical biological and environmental/anthropogenic factors driving elk movement patterns and resource use. Seasons included: Neonatal (May 31 – July 10), Summer (July 11 – August 22), Fall: Period 1 (August 24 – September 14, 2019 or August 22 – September 14, 2020), Fall: Period 2 (September 15 – October 25, 2019 or September 15 – October 23, 2020), and Fall: Period 3 (October 26 – December 13, 2019 or October 24 – December 11, 2020). Fall periods coincided with the prehunt and archery-only hunt seasons (Fall: Period 1), backcountry-rifle hunt season (archery hunting in front country districts and rifle hunting in backcountry districts; Fall: Period 2), and the rifle hunt season (Fall: Period 3) in 2019 and 2020. We did not break up camera trap data into the same four fall seasons as the GPS data (described above) because there were not enough camera trap data during some seasons for fitting occupancy models. We grouped camera data from 2019 and 2020 to increase sample size and improve inference related to elk prevalence.

For each seasonal period, we divided the camera activity period into 7-day “surveys” and identified whether a female elk was detected (i.e., photo taken) during each survey, resulting in binary “detection histories” for each camera. Further, we identified spatial covariates for each camera that could affect elk use of the site. Covariates included archery hunter pressure, rifle hunter pressure, hunt method (archery or firearm), snow water equivalent (SWE), digestible energy (DE), tree canopy cover, distance to tree canopy cover >40%, distance to open road, vector ruggedness measure (Sappington et al. 2007, Lowrey et al. 2020), and land cover category. Covariates such as DE and SWE varied temporally, so we calculated the mean covariate values throughout each seasonal period and used those values for analysis. Before fitting models, we centered and scaled all continuous covariates and determined whether covariates were correlated using Pearson’s correlation coefficient (r ; Pearson 1895). We removed covariates from models if they were strongly correlated.

We fit a suite of occupancy models (MacKenzie et al. 2002) for each seasonal period using the elk detection histories as the response and the uncorrelated covariates described above as predictors of elk use. We assumed constant detection probability in each model. We compared models within a model set using Akaike’s Information Criterion adjusted for small sample size (AICc; Akaike 1973, Burnham and Anderson 2002), assuming the model with the lowest AICc was most supported (Burnham and Anderson 2002). We used parameter coefficients from the most-supported model to make a predictive map of elk occupancy for each period throughout the study area.

We used the “adehabitatHR” package (Calenge 2006) and elk location data to calculate 95% kernel density home ranges for each elk within each seasonal period. We considered prevalence to be equivalent to occupancy, given both metrics describe the probability a site is used; thus, we estimated individual-based seasonal period elk prevalence by calculating the mean occupancy value within each elk home range boundary (Figure 14). We used prevalence estimates from Fall: Period 1 for the prehunt and archery seasons, prevalence estimates from Fall: Period 2 for the backcountry-rifle season, and prevalence estimates from Fall: Period 3 for the rifle season in our RSPF model.

We used individual prevalence estimates to create informative beta priors for the prevalence term in a Bayesian implementation of an RSPF. Specifically, we used moment matching to induce a prior on the prevalence term with mean = prevalence and variance = variance, such that:

$$a = prevalence * \left(\frac{prevalence * (1 - prevalence)}{variance} - 1 \right)$$

$$b = a * (1 - prevalence) / prevalence \quad (\text{Eq. 3})$$

$$pi \sim dbeta(a, b)$$

where a and b are shape parameters for the beta distribution, “prevalence” is the individual-based elk prevalence, variance is the variance of the individual-based elk prevalence and pi is the prior distribution for the prevalence term. We used a variance of 0.03 in RSPF models because it allowed for a relatively informative prevalence prior, while inducing some uncertainty, in case prior knowledge of elk prevalence was inaccurate.

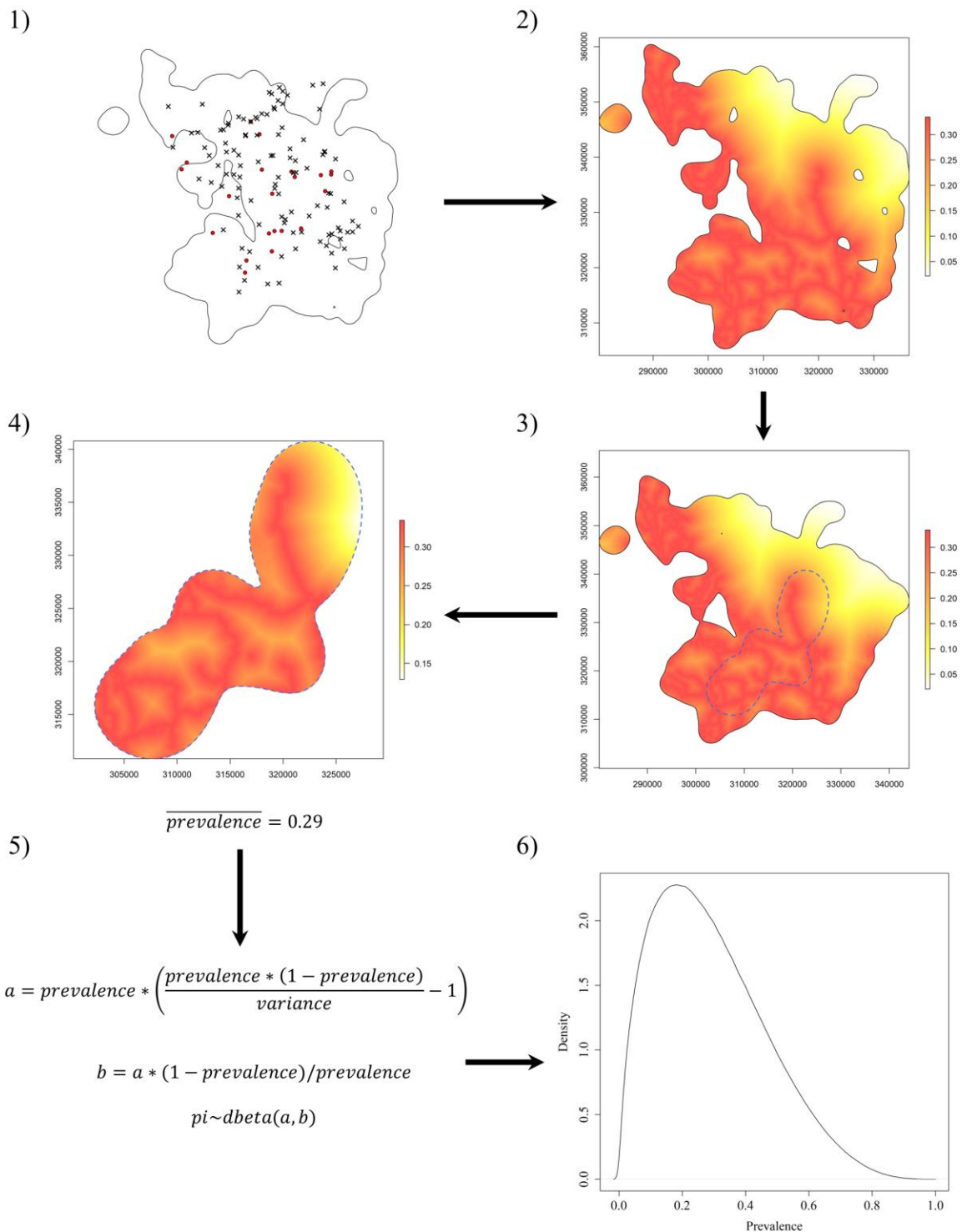


Figure 14. Example workflow for estimating individual-based prevalence values for defining informative priors in a Bayesian implementation of a resource selection probability function for elk in the Blackfoot-Clearwater region of west-central Montana, USA. We used trail camera data (1) to produce occupancy probability predictive maps (2), from which we extracted predicted values within individual elk 95% kernel density home range contours (blue, dashed line; 3 and 4). We used the mean occupancy value within an individual home range as the prevalence value for that individual, then used moment matching to induce a beta prior on the prevalence term with mean = prevalence and variance = 0.03 (5 and 6).

Covariates: Nutrition.—We identified 12 covariates to describe the influence of nutritional, landscape, predation/hunting risk, and environmental factors on elk resource use during the neonatal, summer, and fall seasons for the BC elk population (Table 5). For nutritional resources, we evaluated forage quality (digestible energy/g of forage, kcal/g; DE) that we extracted from landscape models developed from elk diet and vegetation sampling conducted from spring-fall (Objective 4; Snobl et al. In press). DE was not measured in grasslands, shrublands, and other landscape categories outside of the forest during spring. Thus, we estimated DE at unsampled sites during the neonatal season using the estimated DE at the site in August and the predicted decrease in DE from spring through summer, based on other studies in Montana (Proffitt et al. 2016, Proffitt et al. 2019). For example, a site with forbs/grasses and an estimated DE of 2.84 in summer would receive a DE of 3.12 in spring, given DE of forbs/grasses were predicted to decrease by a factor of 0.91 from spring through summer (e.g., Figure 15). Given the uncertainty in DE estimates in spring and summer, we only used one DE estimate per site, rather than the weekly estimates that were produced during the fall seasons.

Table 5. Covariates used in modeling resource selection for each season in the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Landcover types included unburned conifer forests (not burned or harvested in the last 15 years), low severity burned conifer forests, high severity burned conifer forests, open (grasslands, agricultural areas, and shrublands), closed (deciduous forests and riparian areas), and other (forests burned or harvested between 2002-2017). The “Hunt Method” covariate only applied to the backcountry rifle season because it was the only season when some districts only allowed archery hunting, while other districts had a rifle option (i.e., backcountry districts).

Covariate	Description	Source	Season(s)	Reference
Nutrition				
Forage quality	Digestible energy (kcal/g)	Nutrition Model	All	Cook et al. (2004, 2013), Proffitt et al. (2019)
Landscape				
Canopy Cover	Percent canopy cover	Rangeland Analysis Platform	All	Ranglack et al. (2017), DeVoe et al. (2019), Lowrey et al. (2020)
Distance to cover	Distance (m) to areas with canopy cover \geq 40%	Rangeland Analysis Platform	All	Proffitt et al. (2016)
Distance to motorized route	Distance (m) to motorized routes designated as open to public use	USFS travel management plans	All	Hillis (1991), Ranglack et al. (2017), Spitz et al. (2018), Lowrey et al. (2020)
Landcover type	Unburned forest, low severity burned forest, high severity burned forest, open, closed, other	Montana MSDI Land Cover and RAVG products	All	

Terrain Ruggedness	A measure of terrain ruggedness capturing variability in slope and aspect	Vector Ruggedness Measure (VRM)	All	Lowrey et al. (2020)
Distance to Stream	Distance (m) to hydrological feature	USGS National Hydrography dataset	Neonatal, Summer	Cleveland et al. (2012)
Hunting				
Hunter Access	Areas that permit public hunter access vs areas that restrict or prohibit public hunter access	Block Management Program and Public land	Archery-only, Backcountry-Rifle, Rifle	Proffitt et al. (2013)
Hunt Method	Archery vs Rifle	FWP hunting regulations – Backcountry Rifle Season	Backcountry-Rifle	
Hunt Pressure	Estimated number of hunter days for each district/hunting method	FWP harvest reports	Archery-only, Backcountry-Rifle, Rifle	Ranglack et al. (2017)
Predator				
Frequency of Predator Detections	Estimated combined count/day of predators	Trail camera data from study.	Neonatal, Summer	Berg et al. (2021)
Environmental				
SWE	Maximum SWE value for each pixel for each week	SNOWDAS	Backcountry-Rifle, Rifle	Ranglack et al. (2017)

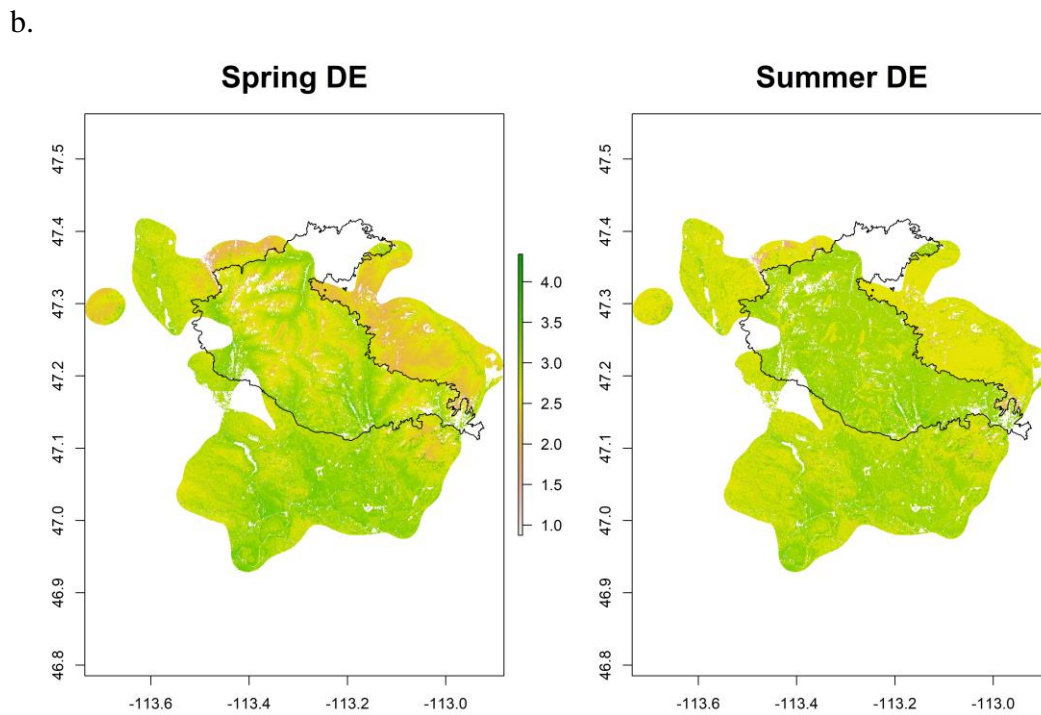
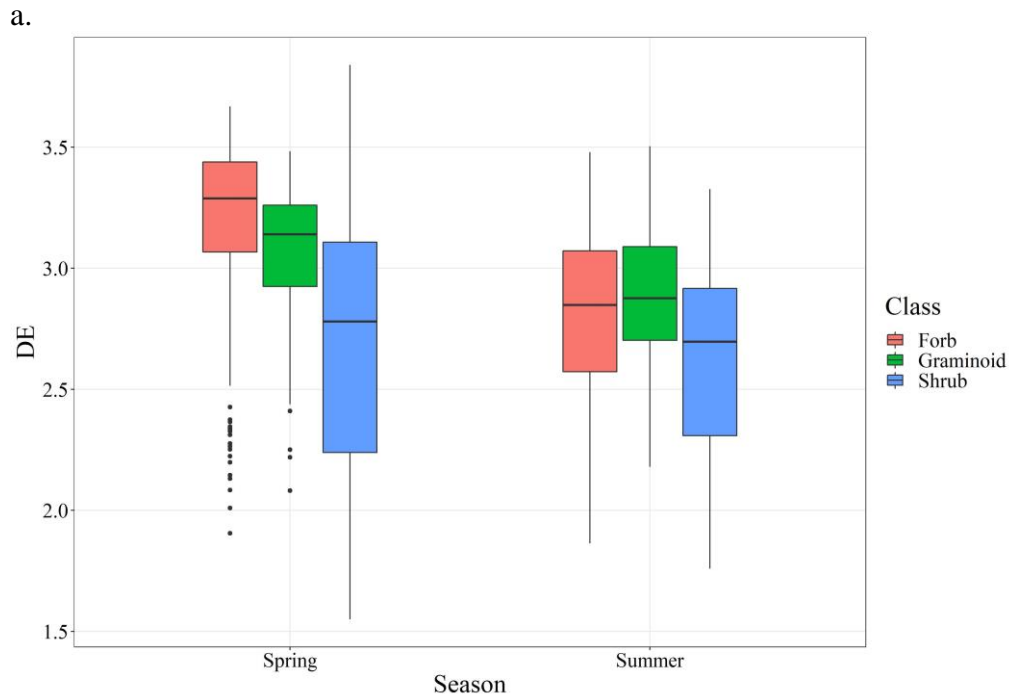


Figure 15. Decreases in digestible energy (DE; kcal/g) from spring through summer for forbs, grasses, and shrubs (panel a., data from current project and Proffitt et al. [2016, 2019]) and estimated DE values (panel b.) used for female elk neonatal and summer resource selection analyses in the Blackfoot-Clearwater region of west-central Montana from 2019-2021. The colored region in panel b. is the annual home range of female elk and the black outline is the perimeter of the Rice Ridge wildfire. Box and whisker plots represent minimum, lower quartile, median, upper quartile, and maximum values.

Covariates:Landscape—We included five landscape variables in our analysis. To characterize potential dense cover areas, we used percent canopy cover from the Rangeland Analysis Platform (<https://rangelands.app/>) and classified dense cover as areas with canopy cover > 40% (Jones et al. 2018, Allred et al. 2021). We used distance to dense cover as a covariate (Proffitt et al. 2016, DeVoe et al. 2019). To understand the influence of roads, we used distance (m) to motorized routes that were categorized as open to motorized use (Hillis et al. 1999, Ranglack et al. 2017, Spitz et al. 2018, Lowrey et al. 2020). To understand the influence of vertical vegetative structure on elk security, we used landcover type using the 2016 Montana MSDI Land Cover (<http://geoinfo.msl.mt.gov>) dataset and the Rapid Assessment of Vegetation Condition after Wildfire (RAVG, <https://fsapps.nwcg.gov/ravg/>) product. We classified landcover types into unburned conifer forests (not burned or harvested in the last 15 years), low severity burned conifer forests, high severity burned conifer forests, open (grasslands, agricultural areas, and shrublands), closed (deciduous forests and riparian areas), and other (forests burned or harvested between 2002-2017). To understand the impact of terrain on elk resource selection, we used the vector ruggedness measure (further referred to as ruggedness), which incorporates variation in aspect and slope to provide a unitless measure of terrain ruggedness (Sappington et al. 2007, Lowrey et al. 2020). Finally, we included the distance to hydrologic feature (e.g., stream) to identify whether distance to water source influenced elk selection (Cleveland et al. 2012).

Covariates:Predation Risk/Hunting.—To quantify predation risk during neonatal and summer seasons, we estimated the predicted frequency of predator detections of all potential elk neonate predators (gray wolf, mountain lion, grizzly bear, black bear, coyote [*Canis latrans*]) at a site for each season using data from trail cameras. We separated camera deployments into either “Neonatal” or “Summer” based on the dates they were active (Neonatal = May 31 – July 10; Summer = July 11 – August 23) and censored cameras that were active for <14 days. For each camera, we grouped pictures taken <60 seconds apart into “independent” sequences, then counted the number of unique detections of each predator species in each sequence (Hansen 2021) and summed predator counts across sequences throughout the duration of the camera deployment.

We identified spatial covariates that could affect frequency of predator detections at a site, including landcover type/burn severity, vector ruggedness measure (Sappington et al. 2007, Lowrey et al. 2020), canopy cover, distance to canopy cover >40%, elevation, and distance to hydrologic feature (e.g., stream). We fit a suite of negative binomial models with predator count as the response and the covariates described above as predictors to identify the factors that best explained the frequency of predator detections. We included an “offset” term in models equivalent to the natural log of the duration a camera was active to account for different exposure times across cameras. We used the “dredge” function in the “MuMIn” package (Barton 2020) to fit all possible models and ranked models based on Akaike’s Information Criterion adjusted for small sample size (AICc; Akaike 1973, Burnham and Anderson 2002). We maintained models with $\Delta AICc \leq 2$ and performed a repeated cross-validation analysis to identify which model best predicted “pseudo-independent” data. Specifically, we repeated a 10-fold cross validation 100 times for each model and calculated the mean R^2 and root mean squared error (RMSE) across iterations, using the “caret” package (Kuhn 2021). We used parameter estimates from the model with the highest cross-validated R^2 value to create a

predictive map of predator detection frequency across the study area to use as the predation risk covariate.

We evaluated three variables related to hunting that may affect elk resource selection: hunting method, hunter pressure, and hunter access. To understand the impacts of having multiple hunting methods on the landscape at the same time, we included a covariate for hunting method (i.e., archery-only vs archery or rifle) during the backcountry rifle hunt season model. The hunt method covariate was a binary categorical variable, with districts that allowed rifle hunting during the backcountry rifle hunt season (i.e., backcountry districts) receiving a value of 1 and districts that only allowed archery methods during the season receiving a 0. We included a hunter pressure variable that we estimated using data from the Montana Fish, Wildlife and Parks harvest survey program. For the archery-only and rifle seasons, we used the total number of hunter days within each hunt district for each method to represent relative hunter pressure. For the backcountry rifle season, within the eight front country hunting districts (only allowed archery during the backcountry-rifle season) we used the total number of archery hunter days and within the two backcountry rifle hunting districts we used the total number of rifle hunter days. We classified hunter access into “accessible” or “unknown” categories. We classified public lands that allowed hunting and any private lands enrolled in the State of Montana’s Block Management Program as accessible. Privately owned lands with varying levels of restrictions on hunting access were classified as unknown.

Covariates: Environmental.—We evaluated the influence of one environmental covariate, SWE, to represent the influence of snowpack on selection. We calculated the maximum SWE value per pixel during each week using data from the Snow Data Assimilation System (SNOWDAS).

We scaled and screened all covariates for collinearity, and we only included covariates with that were not correlated. For each seasonal model, we only included the covariates that were hypothesized to impact resource selection during that season (Table 5).

Resource Selection Probability Function.—We developed seasonal resource selection probability functions using a use-availability design. For used points in our analysis, we retained GPS location data for elk that had collected GPS locations for at least half of the season and excluded all collar locations when the dilution of precision reading was >10 (D'Eon and Delparte 2005). To reduce spatial autocorrelation in the data, we retained only GPS locations with a five-hour interval between relocations (Hansteen et al. 1997). We identified available points within each seasonal home range (neonatal, summer, fall) using a 95% kernel density estimator contour based on the combined individual locations using the *adehabitatHR* package (Calenge 2006). We randomly generated available points for individuals at a 1:5 (used:available) ratio for each season, as a 1:5 ratio sufficiently characterized the distribution of covariates to help avoid potential modeling convergence issues (Northrup et al. 2013, Lula et al. 2020).

We estimated the absolute probability that an elk used sample unit i (ψ_i) as:

$$\psi_i = \frac{\exp(\beta_0 + \ln(\frac{n_1}{\pi n_a} + 1) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})}{1 + \exp(\beta_0 + \ln(\frac{n_1}{\pi n_a} + 1) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})} \quad (\text{Eq. 4})$$

where β_0 is the intercept parameter, n_1 is the number of used locations in the analysis, n_a is the number of available locations in the analysis, π is a “prevalence” term equivalent to the average probability of use by elk across sample units, and β_1, \dots, β_j are the parameter coefficients associated with the j covariates (Rota et al. 2013). Further, we estimated probability of observing use (θ_i) in a use-availability design, conditional on a sample unit being used, using:

$$\theta_i = \frac{n_1}{n_1 + \pi n_a} \quad (\text{Eq. 5})$$

We fit seasonal RSPF models within a Bayesian framework using the R2jags package (Su and Yajima 2015) in R. We fit one global model for the neonatal and summer seasons, with season included as an interaction with all covariates, and we fit separate global models for each fall season. We included unique elk identification as a random effect so that a separate model intercept was calculated for each elk (β_{0i}), drawn from a normal distribution with a population mean μ_{β_0} and standard deviation σ_{β_0} : $\beta_{0i} \sim N(\mu_{\beta_0}, \sigma_{\beta_0})$. We used vague hyperpriors ($\mu_{\beta_0} \sim N(0, 31.6)$; $\sigma_{\beta_0} \sim \text{Unif}(0, 20)$) to allow broad sampling of parameter space.

For fall seasons, we used elk-specific prevalence estimates to induce a beta prior for prevalence in the RSPF model (see *Trail Cameras and Prevalence* above). However, we found model convergence was improved for the neonate/summer model when prevalence was treated as a random variable. Thus, for the neonatal/summer model, we assumed each elk-specific prevalence value (π_i) was drawn from a beta distribution: $\pi_i \sim \text{Beta}(a, b)$ with relatively vague population-level hyperpriors ($a, b \sim \text{Gamma}(2, 1)$).

We included scaled covariates described above as fixed effect predictors in the models and included vague priors for each covariate (j): $\beta_j \sim N(0, 31.6)$. We estimated posterior distributions of predictors by running 3 Markov Chain Monte Carlo (MCMC) chains, each for 150,000 iterations, with a burn-in of 50,000, and thinning of 10. We determined that predictors influenced the response if 95% credible intervals (between 2.5% and 97.5% quantiles) of posterior distributions of parameter estimates did not overlap zero. We identified whether models converged by ensuring \hat{R} values were < 1.1 (Gelman and Rubin 1992) and by examining posterior distributions and MCMC chains.

Results

Identifying Seasons.—Female elk daily movement rates varied throughout the year and, during spring/summer, were predicted to be lowest on May 29 (236.71 m/hr, SE = 4.34), while home range sizes were predicted to be lowest on June 2 (84.82 ha, SE = 7.66; Figure 16). Thus, we chose May 31 as the start of the “Neonatal” season. The breakpoint between “Neonatal” and “Summer” seasons was estimated as 40.9 days past parturition (95% credible interval: 28.3 – 52.0; Figure 17); thus, we designated the end of the “Neonatal” season as July 10.

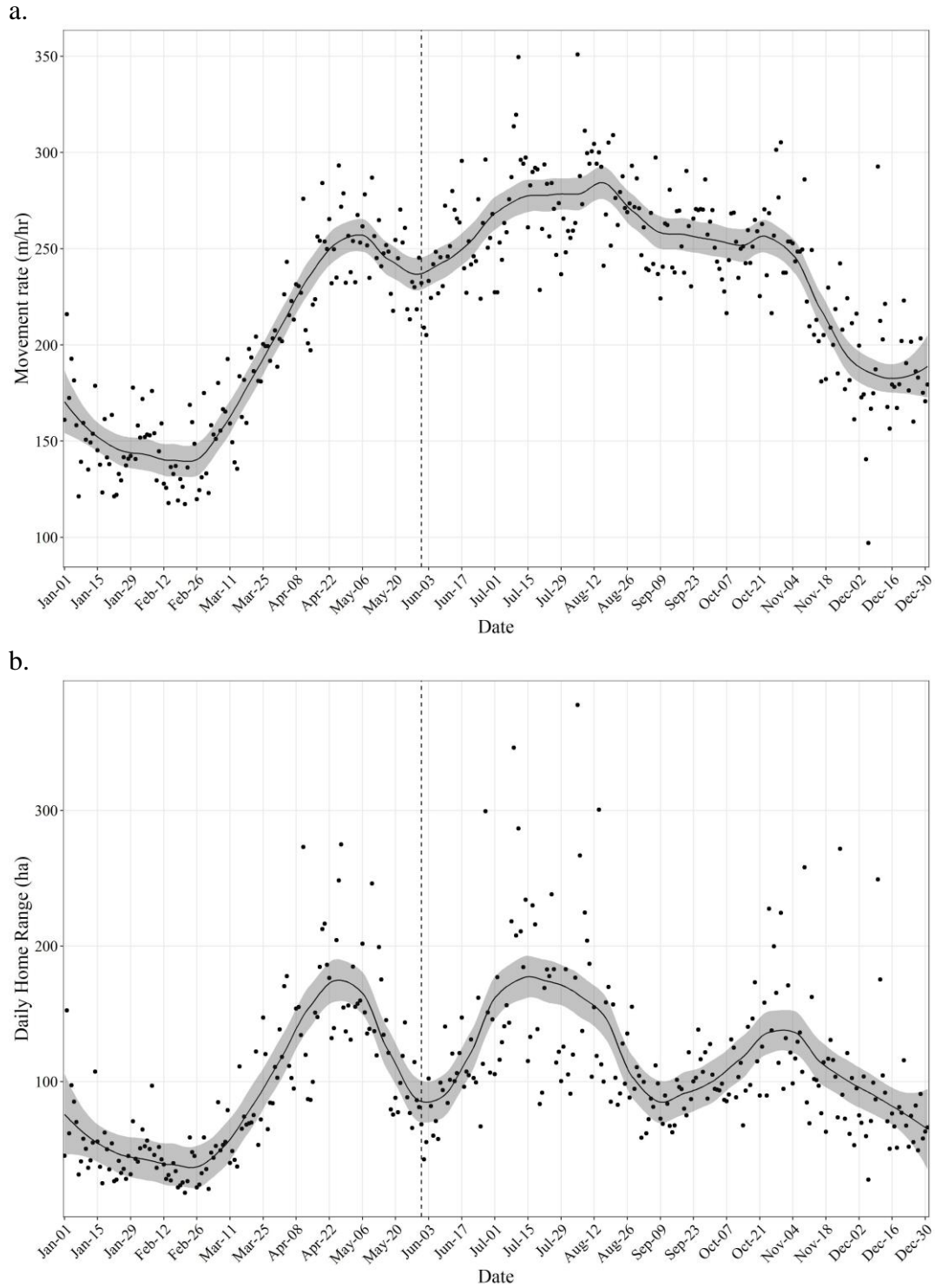


Figure 16. Daily movement rate (m/hr; panel a.) and 95% kernel density home range size (ha; panel b) of female elk in the Blackfoot-Clearwater region of west-central Montana, USA from December 2018 – February 2022. Black dots represent mean values across elk, while the black line and error ribbon represent predicted values and 95% confidence interval from loess smoothing. The vertical dashed line represents May 31, the date selected as the start of the “Neonatal” season.

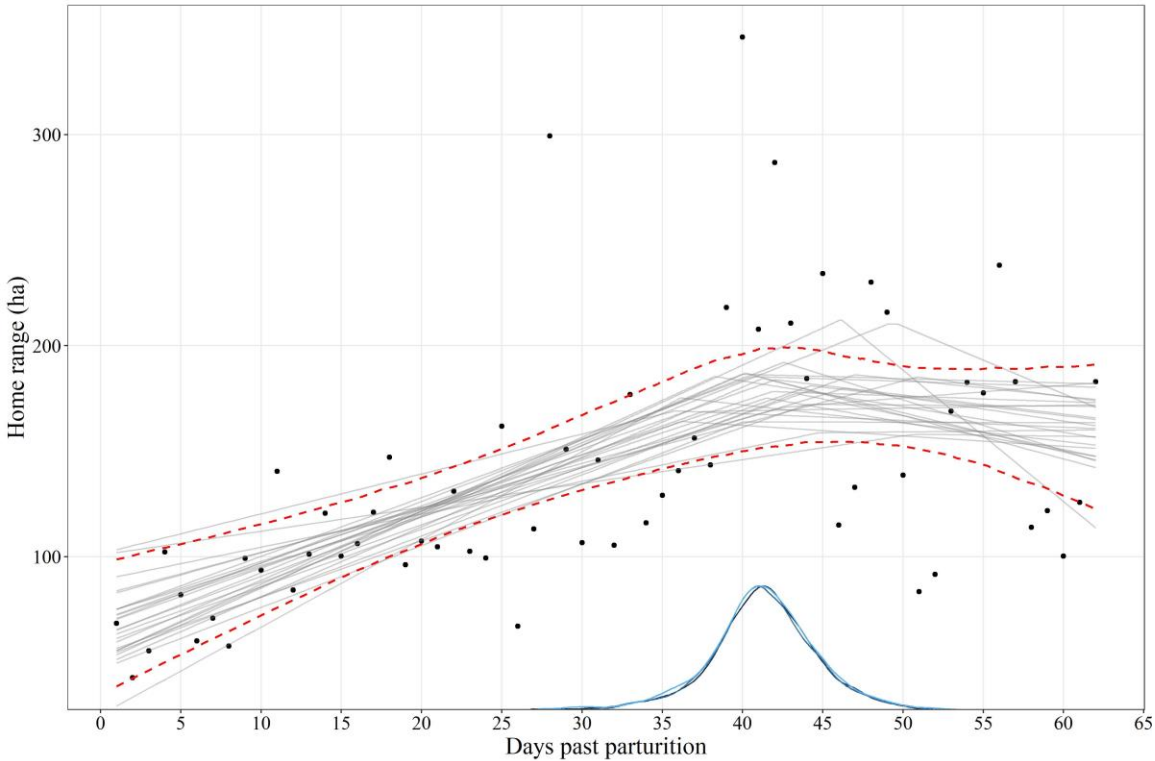


Figure 17. Estimation of the temporal “breakpoint” in daily home range size for female elk in the Blackfoot-Clearwater region of west-central Montana, USA. The x-axis represents days past parturition, with a value of 0 representing May 31 and a value of 40 representing July 10. Black dots represent mean daily home range estimates across elk, light gray lines represent slope estimates for line segments from a sample of iterations from the multiple change point model, red dashed lines represent the bounds of the 95% credible interval of slope estimates, and the blue lines represent the distribution of breakpoint estimates from the model.

Trail Cameras and Prevalence.—In total, we detected female elk on 126 of 269 cameras (47%) from 2019 through 2021. Trail cameras were active for an average of 32.0 days (range = 15 – 41 days) during the neonatal season, 29.7 days (range = 14 – 43.8 days) during summer, and 34.4 days (range = 14 – 49 days) during fall seasons. We detected female elk at 36.3% of sites ($n = 49/135$) during the neonatal season, 27.3% of sites ($n = 38/139$) during the summer season, 21.4% of sites ($n = 18/84$) during Fall: Period 1, 16.7% of sites ($n = 22/132$) during Fall: Period 2, and 12.4% of sites ($n = 15/121$) during Fall: Period 3.

Neonatal/Summer RSPF models converged better when including prevalence as a random variable in the model, so we only estimated individual elk prevalence during the fall seasons. We compared 9 candidate occupancy models during Fall: Period 1 and the most supported occupancy model included only the archery hunting pressure covariate (Table 6). However, the effect of archery pressure on occupancy was not strong ($\beta = 1.10$, $SE = 0.80$). Predicted elk occupancy probability varied from 0.18 – 0.77 across the study area and was highest within accessible hunting districts at lower elevations, where archery pressure was highest (Figure 18). Detection probability during this period was constant at 0.20 ($SE = 0.12$).

We compared 13 candidate occupancy models during Fall: Period 2 (Table 6) and the most supported model included only the distance to road covariate ($\beta = -0.70$, $SE = 0.39$). Predicted elk occupancy varied from 0 to 0.33 across the study area and was highest closer to roads, generally at lower elevations (Figure 18). Detection probability during this period was constant at 0.24 ($SE = 0.071$).

We compared 11 candidate occupancy models during Fall: Period 3 (Table 6) and the most supported model included firearms hunting pressure ($\beta = -4.22$, $SE = 4.88$) and SWE ($\beta = -9.42$, $SE = 6.02$). Predicted elk occupancy varied from 0 to 0.88 and was highest in hunting district 282 that restricted firearms hunting access and occurred at lower elevations, where there was less snow (Figure 18). Detection probability during this period was constant at 0.29 ($SE = 0.057$).

We estimated individual-based prevalence for hunt period home ranges of 46 unique elk for 55 elk years for the prehunt, archery-only, and backcountry rifle (9 elk were surveyed during 2019 and 2020) and 43 unique elk for 52 elk years for the rifle season. Estimated prevalence for the prehunt and archery-only periods were similar with $\bar{\pi} = 0.61$ ($SD = 0.15$) and $\bar{\pi} = 0.61$ ($SD = 0.17$), respectively. Estimated prevalence for the backcountry rifle season was lower than the first two hunt seasons with $\bar{\pi} = 0.27$ ($SD = 0.03$). For the rifle season, estimated prevalence was $\bar{\pi} = 0.51$ ($SD = 0.19$).

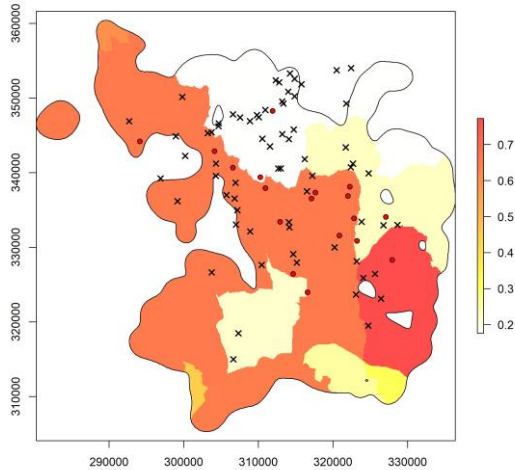
Frequency of Predator Detections Covariate.—Mean frequency of predator detections at camera sites was 0.011 predators/day ($SD = 0.026$; range = 0 – 0.157, $n = 135$) during the neonatal season and 0.013 ($SD = 0.044$; range = 0 – 0.429, $n = 139$) during summer. The most supported predator detection model during the neonatal season ($R^2 = 0.21$, $RMSE = 0.74$) only included tree cover, which had a positive association with predator detections ($\beta = 0.50$, $SE = 0.17$). The most supported predator detection model during summer ($R^2 = 0.19$, $RMSE = 0.76$) included elevation ($\beta = -0.41$, $SE = 0.23$), distance to road ($\beta = -0.46$, $SE = 0.29$), distance to hydrologic feature ($\beta = -0.30$, $SE = 0.24$), and fire severity, with low severity burns ($\beta = -0.45$, $SE = 0.56$) and high severity burns ($\beta = -1.14$, $SE = 0.54$) having fewer predicted predator detections than unburned sites (Figure 19).

Table 6. Model selection results for female elk occupancy (ψ) during Fall: Period 1 (August 24 – September 14, 2019 or August 22 – September 14, 2020), Fall: Period 2 (September 15 – October 25, 2019 or September 15 – October 23, 2020), and Fall: Period 3 (October 26 – December 13, 2019 or October 24 – December 11, 2020) in the Blackfoot-Clearwater region of west-central Montana, USA. Covariates included in models represent: null (\cdot), archery hunting pressure (“archery”), firearms hunting pressure (“rifle”), distance to open road (“road.dist”), landcover type (“landcover”), digestible energy (“DE”), distance to canopy cover >40% (“canopy.dist”), canopy cover (“canopy”), snow water equivalent (“SWE”), and vector ruggedness measure (“rugged”). “K” represents the number of parameters in the model, “AICc” is Akaike’s Information Criterion adjusted for small sample size, “ Δ AICc” is the difference in AICc units between the current model and the most-supported model, and “AICc wt” is the AICc weight of the model. All models included a constant detection probability (p).

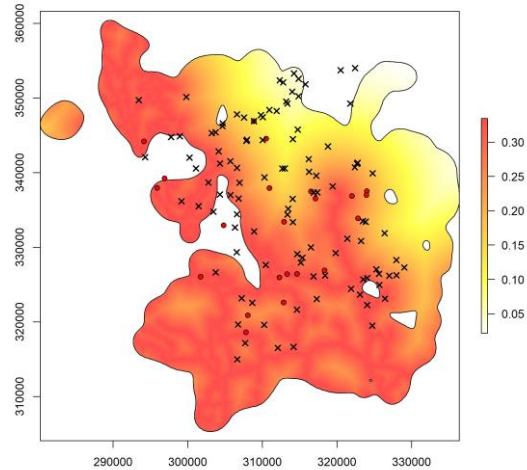
Season	Model	K	AICc	Δ AICc	AICc wt
Fall: Period 1	$\psi(\text{archery}) p(\cdot)$	3	131.48	0.00	0.35
	$\psi(\text{road.dist}) p(\cdot)$	3	132.16	0.68	0.25
	$\psi(\text{landcover}) p(\cdot)$	7	133.47	2.00	0.13
	$\psi(\text{DE}) p(\cdot)$	3	134.22	2.74	0.09
	$\psi(\text{canopy.dist}) p(\cdot)$	3	135.32	3.84	0.05
	$\psi(\cdot) p(\cdot)$	2	135.41	3.93	0.05
	$\psi(\text{canopy}) p(\cdot)$	3	135.53	4.05	0.05
	$\psi(\text{SWE}) p(\cdot)$	3	137.33	5.86	0.02
	$\psi(\text{rugged}) p(\cdot)$	3	137.49	6.02	0.02
Fall: Period 2	$\psi(\text{road.dist}) p(\cdot)$	3	190.96	0.00	0.35
	$\psi(\text{hunt.method}) p(\cdot)$	3	192.88	1.92	0.14
	$\psi(\cdot) p(\cdot)$	2	193.40	2.44	0.10
	$\psi(\text{SWE}) p(\cdot)$	3	193.48	2.52	0.10
	$\psi(\text{hunt.method} + \text{archery}) p(\cdot)$	4	193.62	2.66	0.09
	$\psi(\text{archery}) p(\cdot)$	3	195.22	4.26	0.04
	$\psi(\text{canopy}) p(\cdot)$	3	195.23	4.27	0.04
	$\psi(\text{canopy.dist}) p(\cdot)$	3	195.23	4.27	0.04
	$\psi(\text{rugged}) p(\cdot)$	3	195.36	4.40	0.04
	$\psi(\text{DE}) p(\cdot)$	3	195.46	4.50	0.04
	$\psi(\text{landcover}) p(\cdot)$	7	197.95	6.99	0.01
	$\psi(\text{canopy} + \text{canopy.dist} + \text{road.dist} + \text{rugged} + \text{land}) p(\cdot)$	11	205.24	14.28	0.00
	$\psi(\text{Global}) p(\cdot)$	15	213.49	22.53	0.00
Fall: Period 3	$\psi(\text{rifle} + \text{SWE}) p(\cdot)$	4	140.94	0.00	1.00
	$\psi(\text{rifle}) p(\cdot)$	3	154.07	13.13	0.00
	$\psi(\text{SWE}) p(\cdot)$	3	156.22	15.28	0.00
	$\psi(\text{landcover}) p(\cdot)$	7	172.19	31.25	0.00
	$\psi(\text{canopy} + \text{canopy.dist} + \text{road.dist} + \text{rugged} + \text{land}) p(\cdot)$	11	174.72	33.78	0.00
	$\psi(\text{road.dist}) p(\cdot)$	3	181.23	40.29	0.00

$\psi(\text{rugged}) p(\cdot)$	3	191.00	50.06	0.00
$\psi(\cdot) p(\cdot)$	2	192.31	51.37	0.00
$\psi(\text{canopy}) p(\cdot)$	3	194.20	53.26	0.00
$\psi(\text{canopy.dist}) p(\cdot)$	3	194.39	53.45	0.00
$\psi(\text{DE}) p(\cdot)$	3	194.40	53.46	0.00

a. Fall: Period 1



b. Fall: Period 2



c. Fall: Period 3

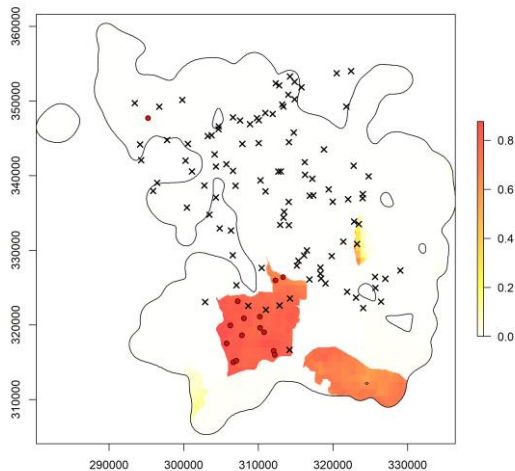
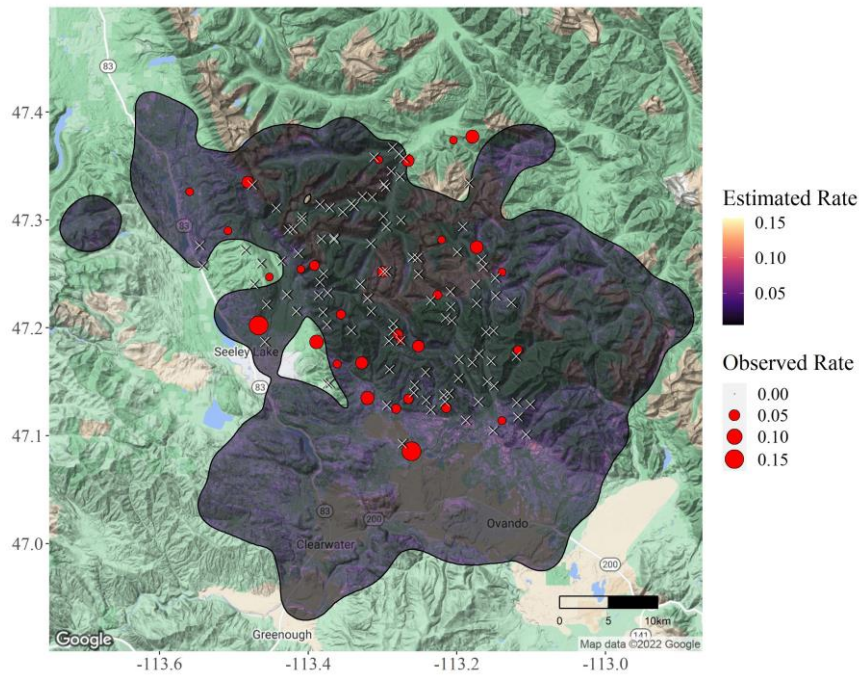


Figure 18. Predicted occupancy probability of female elk during Fall: Period 1 (August 24 – September 14, 2019 or August 22 – September 14, 2020; panel a.), Fall: Period 2 (September 15 – October 25, 2019 or September 15 – October 23, 2020; panel b.), and Fall: Period 3 (October 26 – December 13, 2019 or October 24 – December 11, 2020; panel c.) in the Blackfoot-Clearwater region of west-central Montana, USA. The black outline in each figure represents the 99% annual home range of all collared elk in the region. Red circles represent trail cameras where a female elk was detected, while black exes represent trail cameras where female elk were not detected. Warmer colors represent higher predicted occupancy probability.

a.



b.

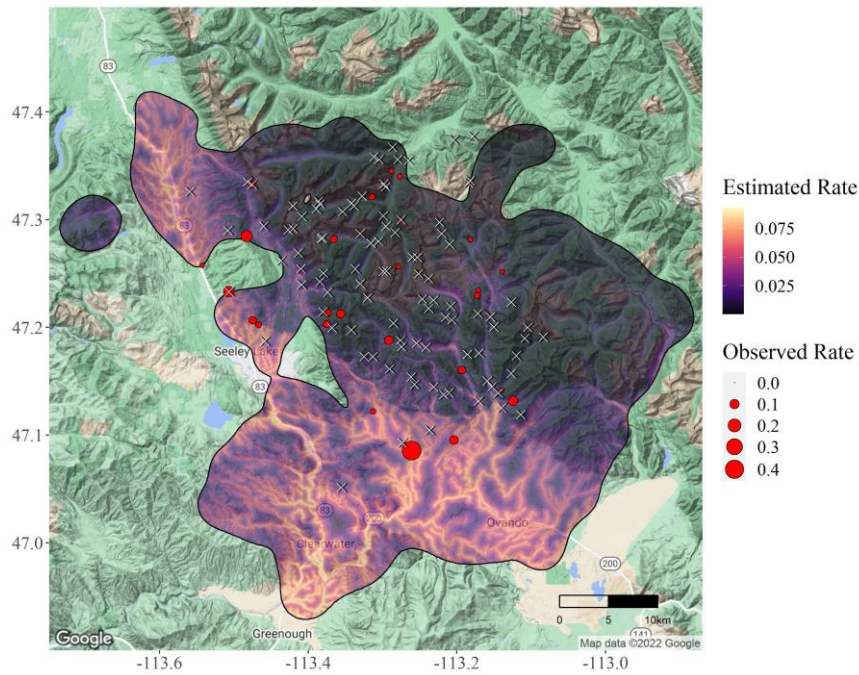


Figure 19. Observed and estimated frequency of predator (gray wolf, mountain lion, grizzly bear, black bear, coyote) detections (count/day) during the neonatal (May 31 – July 10; panel a.) and summer (July 11 – August 23; panel b.) seasons during 2019 and 2020 in the Blackfoot-Clearwater region of west-central Montana, USA. White exes represent cameras that did not detect predators, while red circles represent cameras where predators were detected. The outlined region with estimated frequency of predator detections represents the annual range of elk in the region.

RSPF:Neonatal/Summer.—We modeled female elk resource selection for the neonatal season based on 17,732 used locations and 88,660 available locations from 54 unique elk. We modeled resource selection for the summer season based on 17,097 used locations and 85,485 available locations from 51 unique elk. All parameters in the model adequately converged ($\hat{R} < 1.1$) and the model estimated mean prevalence was 0.48 (95% credible interval [CrI] = 0.41 – 0.55).

Female elk generally selected similar resources during the neonatal and summer seasons, although the magnitude of selection varied (Table 7, Figure 20, Figure 21). Among continuous covariates, predator detection frequency had the strongest negative association with elk probability of use during summer, but there was only a small negative association during the neonatal season. The relationship between frequency of predator detections and elk use could have been confounded with elk preference for high-elevation, burned areas in summer, where there were fewer predators detected. Thus, we caution interpretation of this finding as it relates to the effect of predators on elk habitat use. The next most-important continuous covariate was distance to road, which had strong negative associations with elk use during both seasons. DE, distance to canopy cover >40%, and distance to stream all had similar positive associations with elk use, except for distance to stream in summer, in which there was a small negative association (Figure 20).

For categorical landcover variables, elk generally had higher probability of use in burned, open landcover types, but the magnitude of use varied by season. Female elk were 55% more likely to use low and high severity burns compared to unburned forests in the neonatal season, but only 48% and 32% more likely to use low and high severity burns in summer, respectively. Elk preference for landcover types from high to low, based on probabilities of use, was: high severity burns, low severity burns, open, unburned forest, closed forest, and other during the neonatal season, and was: low severity burns, open, high severity burns, closed, unburned forest, and other during summer (Figure 20). Overall, elk were generally more likely to occur in burned, open areas during both neonatal and summer seasons (Figure 21).

Table 7. Parameter estimates, 95% credible intervals (LCrI = 2.5% and UCrI = 97.5% quantiles), and \hat{R} values from a neonatal/summer resource selection probability function for female elk in the Blackfoot-Clearwater region of west-central Montana, USA from 2019-2021. “Predator” = frequency of predator detections, “DE” = digestible energy, “Ruggedness” = vector ruggedness measure, “Dist. To Canopy” = distance to canopy >40%, “Dist. To Road” = distance to road, “Dist to Stream” = distance to hydrologic feature, “Land:Unburned” = unburned forest, “Land:Low Severity” = low severity burned forest, “Land:High Severity” = high severity burned forest, “Land:Open” = open landcover, and “Land:Closed” = closed landcover. Each variable is interacted with season (“*Neonate”), with the summer season and the “Land:Other” landcover types used as the reference (i.e., intercept).

Parameter	Estimate	LCrI	UCrI	\hat{R}
Intercept (Population)	-0.97	-2.61	0.66	1
Predator	-1.85	-1.96	-1.75	1
Predator*Neonate	1.73	1.6	1.87	1
DE	0.28	0.22	0.34	1
DE*Neonate	-0.04	-0.13	0.06	1
Ruggedness	0.06	0.03	0.09	1
Ruggedness*Neonate	0.25	0.19	0.32	1
Dist. to Canopy	0.30	0.25	0.41	1.01
Dist. to Canopy*Neonate	0.29	0.17	0.38	1.01
Dist. to Road	-0.72	-0.80	-0.65	1.01
Dist. to Road*Neonate	-1.12	-1.25	-0.98	1.01
Dist. to Stream	-0.24	-0.28	-0.21	1
Dist. to Stream*Neonate	0.46	0.4	0.52	1
Land:Unburned	0.20	0.00	0.41	1
Land:Unburned*Neonate	0.77	0.48	1.06	1
Land:Low Severity	2.34	2.12	2.56	1
Land:Low Severity*Neonate	3.59	3.19	3.98	1
Land:High Severity	1.52	1.30	1.74	1
Land:High Severity*Neonate	4.71	4.29	5.12	1
Land:Open	1.75	1.50	2.01	1
Land:Open*Neonate	0.29	-0.06	0.64	1
Land:Closed	0.61	0.34	0.89	1
Land:Closed*Neonate	0.36	0.01	0.72	1
Neonate	-0.23	-2.49	2.05	1

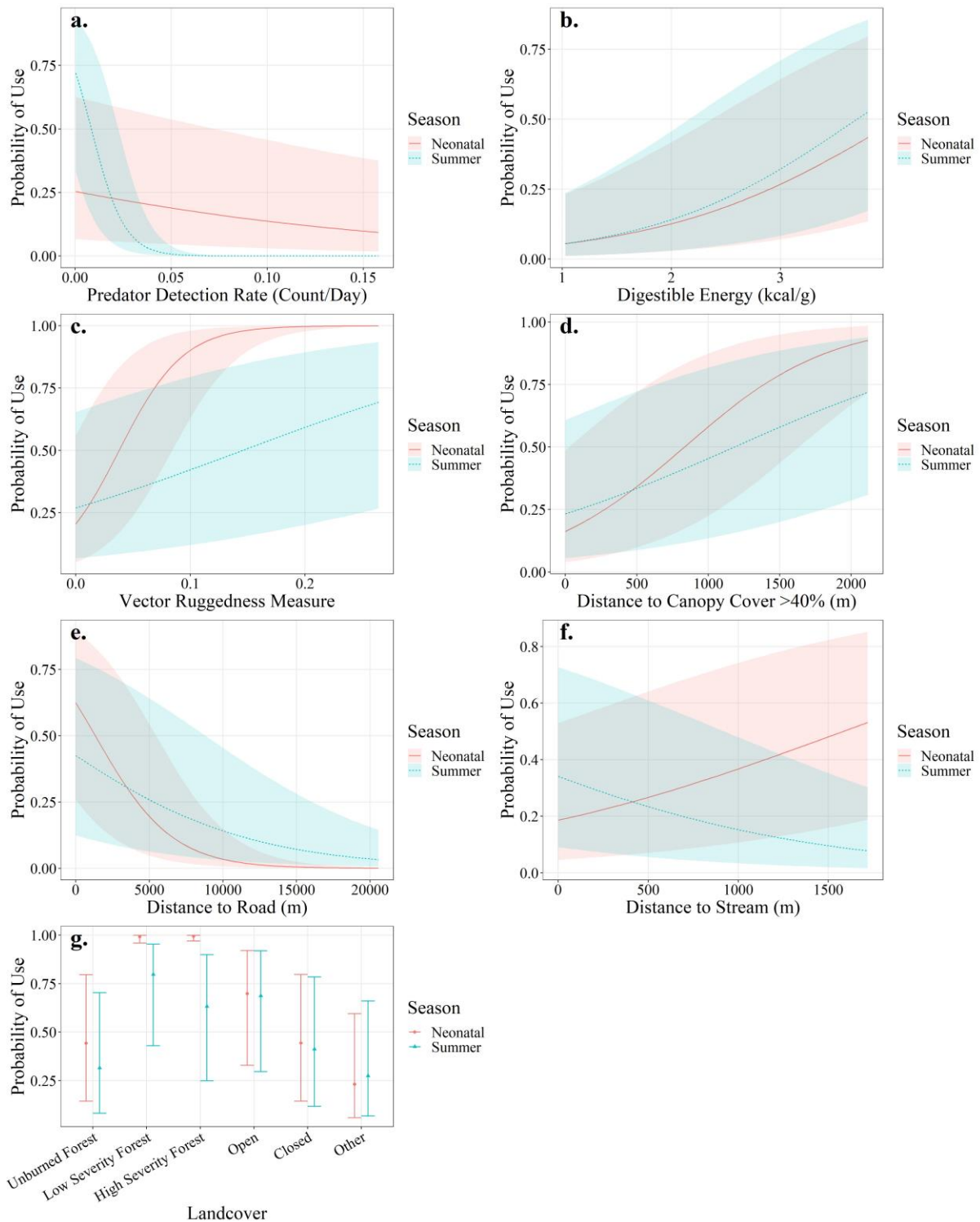
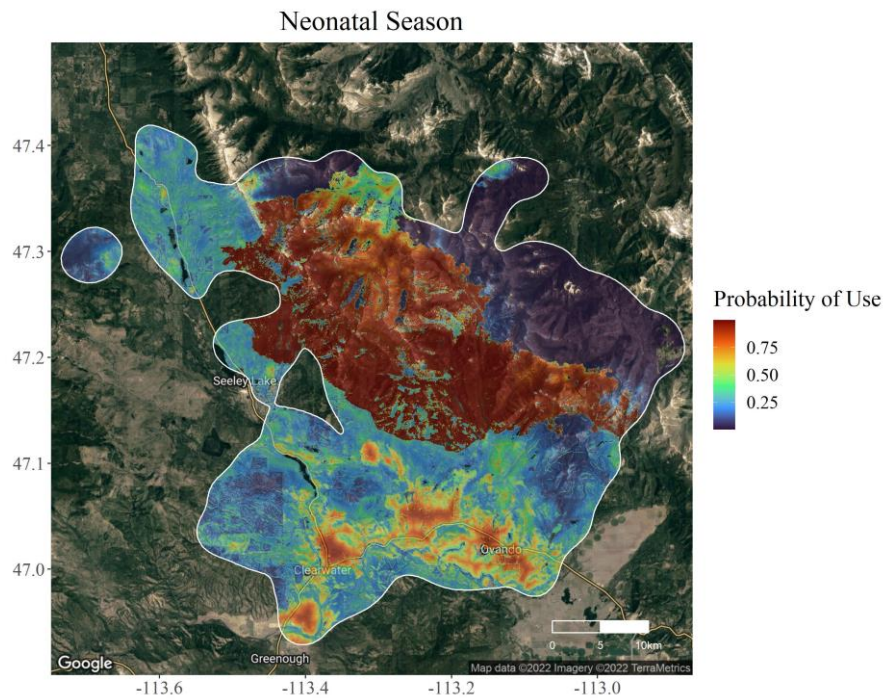


Figure 20. Estimated probability of use during the neonatal (May 31 – July 10; red) and summer (July 11 – August 23; blue, dashed) seasons as a function of a.) elk predator (gray wolf, mountain lion, grizzly bear, black bear, coyote) frequency of detections, b.) digestible energy (kcal/g), c.) terrain ruggedness, d.) distance to canopy cover >40%, e.) distance to road, f.) distance to stream, and g.) landcover category for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2021. The mean posterior distribution is represented by solid lines and the 95% credible intervals are represented by the ribbons/error bars. The reference landcover type used in figures a. through f. is “Other”.

a.



b.

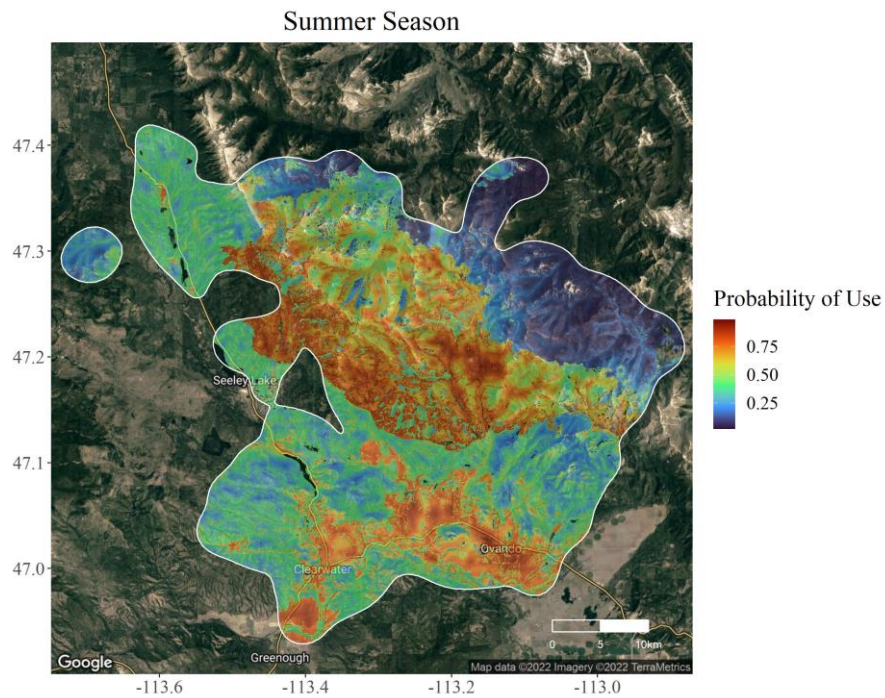


Figure 21. Probability of female elk use throughout the Blackfoot-Clearwater region of west-central Montana, USA from 2019-2021 during neonatal (May 31 – July 10; panel a) and summer (July 11 – August 23; panel b) seasons. Lighter colors represent higher probabilities of use, while darker colors represent lower probabilities of use. The white outline represents the annual home range of elk in the region.

RSPF: Prehunt.—We modeled female elk resource selection for the prehunt season based on 3,258 used locations and 16,583 available locations using 55 animal years from 46 animals. All parameters in the model adequately converged ($\hat{R} < 1.1$) and the model estimated mean prevalence was 0.46 (SD = 0.23).

During the prehunt season, female elk selected burned forests, and there was no difference in selection based on fire severity category. Female elk were 23%, 97%, 83%, and 83% more likely to select both low and high severity burned forests compared to the unburned forest, open, closed, and other landcover types, respectively (Figure 22). In order of estimated effect size on selection, female elk selected for areas further away from motorized routes, areas with greater digestible energy, areas further from dense canopy, and more rugged terrain (Figure 22, Table 8).

Table 8. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the prehunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized, distance to road was included in its pseudothreshold form, and the intercept term is the low severity burned forest.

Variable	Mean	SD	Lower 95% CrI	Upper 95% CrI
Dist. to dense canopy	0.21	0.08	0.06	0.37
Ruggedness	0.18	0.08	0.02	0.33
Digestible energy	0.91	0.15	0.64	1.21
Dist. to road	2.05	0.17	1.72	2.36
Unburned	-3.52	0.36	-4.20	-2.83
High severity	2.10	0.44	1.31	3.04
Open	-8.86	0.50	-9.95	-7.92
Closed	-6.40	0.35	-7.11	-5.74
Other	-6.44	0.39	-7.18	-5.67
Intercept	4.70	0.31	3.91	4.99

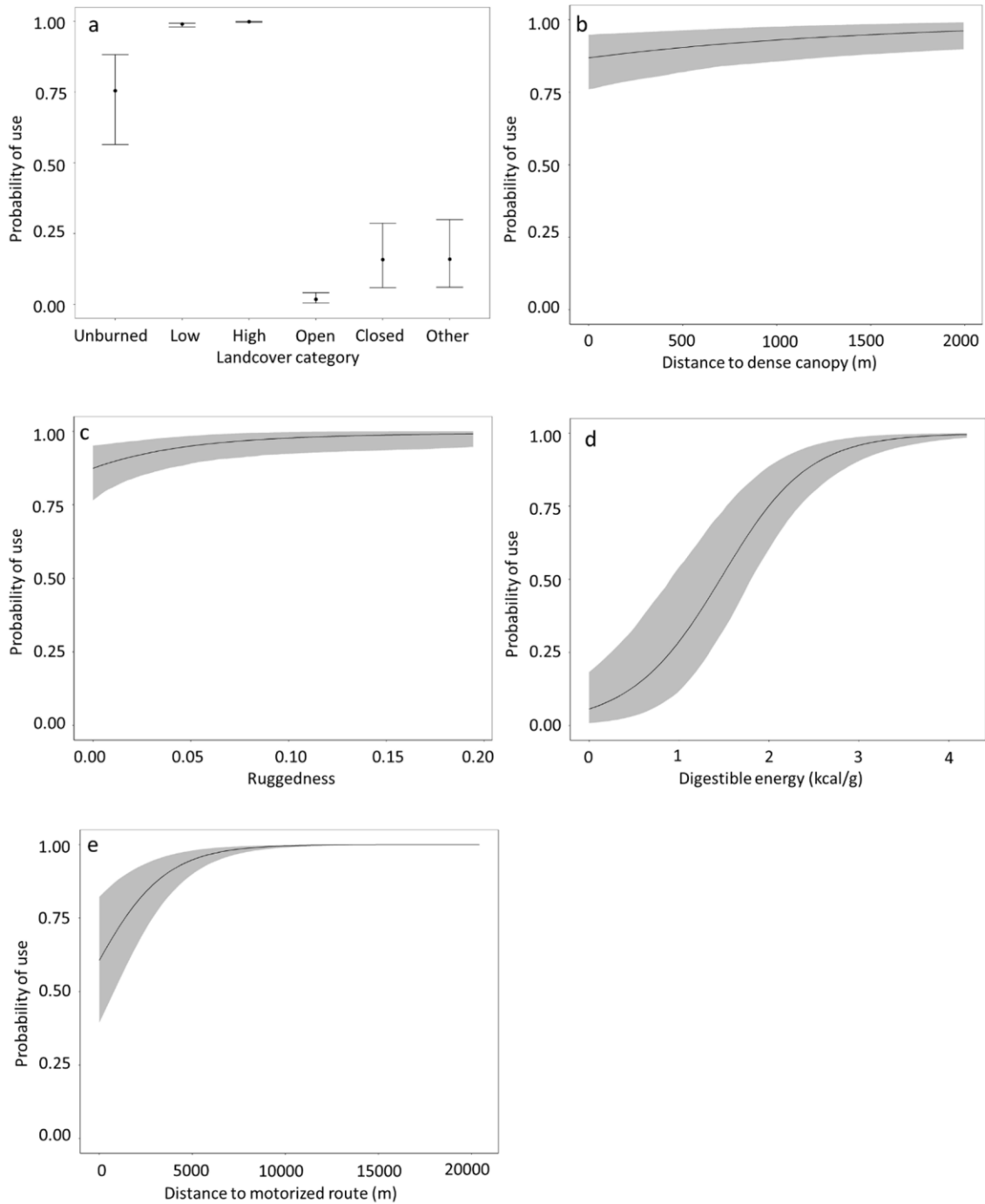


Figure 22. Estimated probability of use during the prehunt season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, and e) distance to open road, for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panels b - e assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons.

RSPF: Archery-Only.—We modeled female elk resource selection for the archery-only hunt season using 1,639 used locations and 8,302 available locations using 55 animal years from 46 animals. All parameters in the model adequately converged and the model estimated mean prevalence was 0.45 (SD = 0.24).

Similar to the prehunt season, female elk during the archery-only season selected for burned forests, and there was no difference in selection based on fire severity category. Female elk were 40%, 92%, 77%, and 67% more likely to select low and high severity burned forests over the unburned forest, open, closed, and other landcover types, respectively (Figure 23). In order of estimated effect size on selection, female elk selected for hunting districts with greater hunter pressure, and areas further from motorized routes, further from dense canopy, with greater digestible energy, and more rugged terrain (Figure 23, Table 9).

Table 9. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the archery-only hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized and the intercept term is low severity burned forest.

Variable	Mean	SD	Lower 95% CrI	Upper 95% CrI
Dist. to dense canopy	1.17	0.19	0.81	1.56
Ruggedness	0.23	0.10	0.04	0.43
Digestible energy	0.77	0.20	0.42	1.20
Dist. to road	1.32	0.36	0.59	2.03
Hunter pressure	3.12	0.32	3.84	4.99
Unburned	-4.31	0.47	-5.25	-3.40
High severity	1.76	0.34	1.13	2.44
Open	-7.52	0.75	-9.15	-6.20
Closed	-6.02	0.49	-7.00	-5.07
Other	-5.52	0.51	-6.55	-4.54
Intercept	4.68	0.32	3.84	4.99

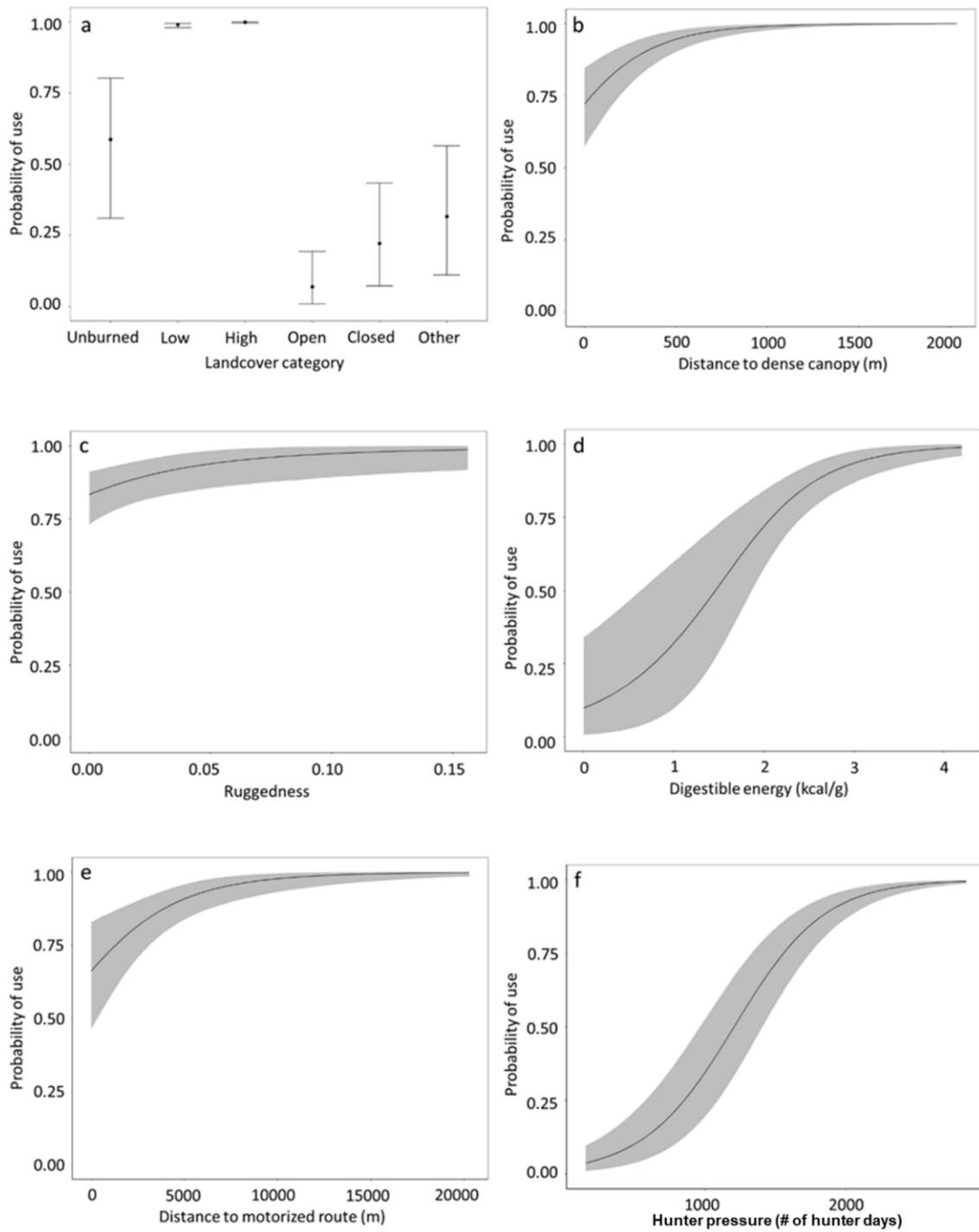


Figure 23. Estimated probability of use during the archery-only season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, e) distance to open road, and f) hunter pressure, for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panels b – f assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons.

RSPF: Backcountry-Rifle.—We modeled female elk resource selection for the backcountry-rifle hunt season using 9,648 used locations and 49,829 available locations using 55 animal years from 46 animals. All parameters in the model adequately converged and the model estimated mean prevalence was 0.39 (SD = 0.29).

Similar to the prehunt and archery-only seasons, female elk during the backcountry rifle season selected burned forests, and there was no difference in selection between fire severity categories. Female elk were 28%, 16%, 20%, and 57% more likely to select low and high severity burned forests over the unburned forest, open, closed, and other landcover types, respectively (Figure 24). Female elk were 15% more likely to select hunting districts with only archery hunting compared to the two backcountry hunting districts with rifle hunting. Snowpack was the most important continuous covariate, with predicted elk probability of use dropping to near 0% at sites with SWE > 0.1 m. Digestible energy was not important as credible intervals overlapped zero (Table 10, Figure 24).

Table 10. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the backcountry-rifle hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. Continuous variables were standardized and the intercept term is low severity burned forest in archery only areas.

Variable	Mean	SD	Lower 95% CrI	Upper 95% CrI
Dist. to dense canopy	-0.15	0.03	-0.22	-0.09
Ruggedness	0.20	0.03	0.15	0.26
Digestible energy	0.02	0.03	-0.05	0.09
Dist. to road	-0.62	0.08	-0.78	-0.46
Hunter pressure	-0.62	0.03	-0.68	-0.57
Max SWE	-1.11	0.05	-1.22	-1.01
Unburned	-3.79	0.14	-4.06	-3.69
High severity	0.38	0.08	0.22	0.55
Open	-3.09	0.12	-3.34	-2.85
Closed	-3.32	0.13	-3.59	-3.23
Other	-5.03	0.18	-5.39	-4.69
Hunt Method - Rifle	-3.27	0.15	-3.56	-2.99
Intercept	4.67	0.32	3.81	4.99

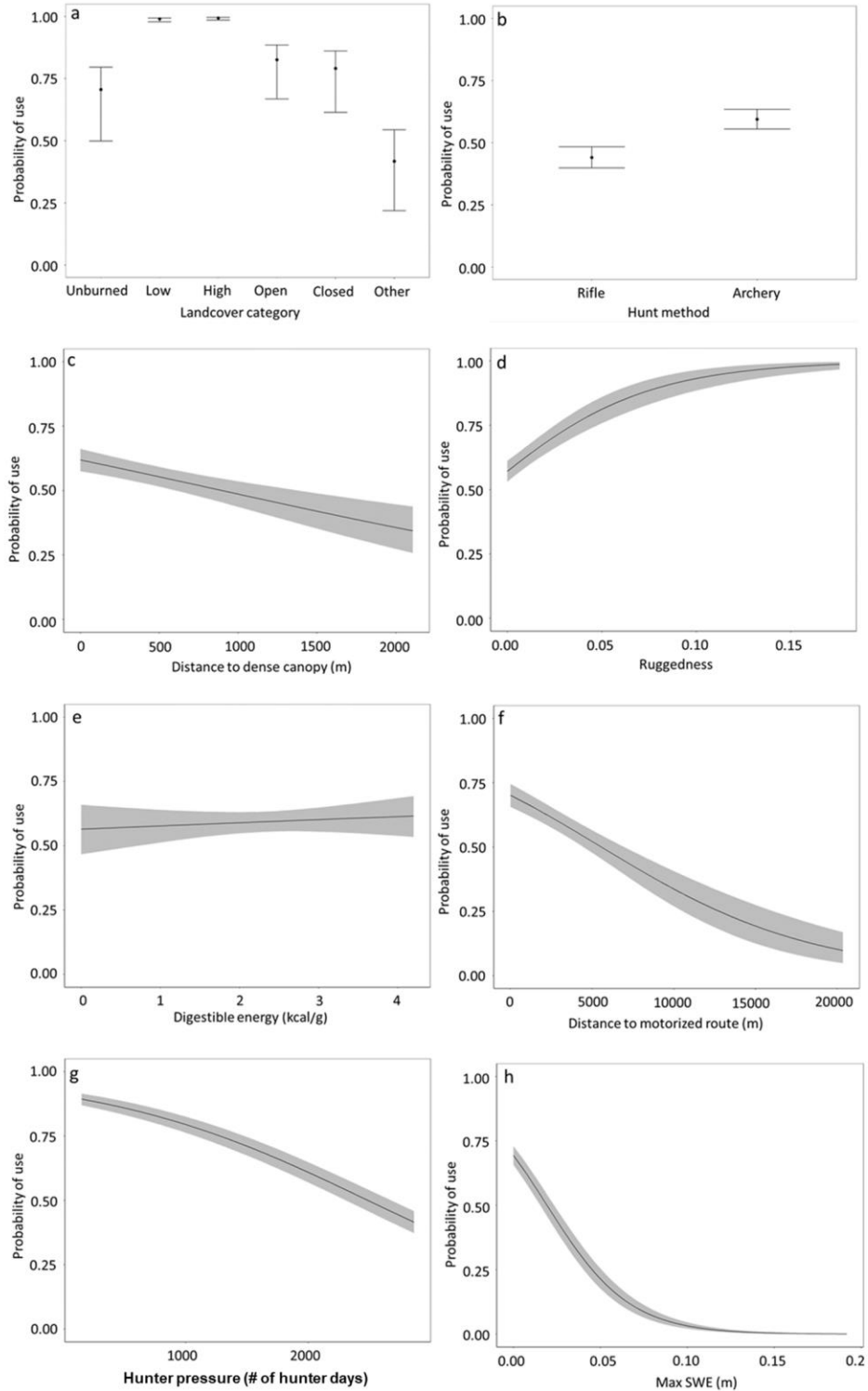


Figure 24. Estimated probability of use during the backcountry rifle season as a function of: a) landcover category, b) hunt method, c) distance to dense canopy, d) ruggedness, e) digestible energy, f) distance to motorized route, g) hunter pressure, and h) max snow water equivalent (SWE), for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. Panel a assumes that use occurs in archery only areas, panel b assumes that use occurs in high severity burned forests, and panels c - h assume all other continuous covariates are fixed at their mean observed value, and use occurs in high severity burned forests in archery-only areas. The 95% credible intervals are represented by the error bars in panels a and b, and gray ribbons in panels c - h.

RSPF: Rifle.—We modeled female elk resource selection for the rifle hunt season using 8,707 used locations and 40,310 available locations using 52 animal years from 43 animals. All parameters in the model adequately converged and the model estimated mean prevalence was 0.11 (SD = 0.15).

In contrast to the other three seasons, elk avoided burned and unburned conifer forests during the rifle season. Elk were 14-18% more likely to select the open landcover type compared to the remaining five landcover types (Figure 25). Overall use of burned forests was low, and elk were 3% more likely to use low severity burned forests compared to high severity burned forests. In order of estimated effect size on selection, female elk selected for areas with less snowpack, hunting districts with less hunter pressure, areas closer to motorized routes, and areas further from dense canopy. In contrast to the prehunt and archery-only seasons, elk selected for areas with lower digestible energy. Ruggedness was not important as credible intervals overlapped zero (Figure 25, Table 11).

Table 11. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the resource selection model for female elk during the general rifle hunt season for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019-2020. The continuous variables are standardized and the intercept term is low severity burned forest.

Variable	Mean	SD	Lower 95% CrI	Upper 95% CrI
Dist. to dense canopy	0.35	0.04	0.27	0.43
Ruggedness	0.04	0.04	-0.04	0.11
Digestible energy	-0.22	0.05	-0.32	-0.12
Dist. to road	-1.22	0.10	-1.42	-1.04
Hunter pressure	-2.18	0.05	-2.27	-2.09
Max SWE	-3.48	0.46	-3.98	-2.29
Unburned	-0.59	0.14	-0.87	-0.33
High severity	-3.32	0.27	-3.86	-3.13
Open	1.91	0.13	1.66	2.15
Closed	0.13	0.12	-0.11	0.36
Other	-0.39	0.13	-0.67	-0.15
Intercept	-3.48	0.46	-3.98	-2.29

From the prehunt to the rifle hunt seasons, elk transitioned from their summer range to their winter range, mostly within hunting district 282 (Figure 26, Figure 27). These movements were concurrent with both an increase in SWE at higher elevations and initiation of hunting seasons (Figure 28).

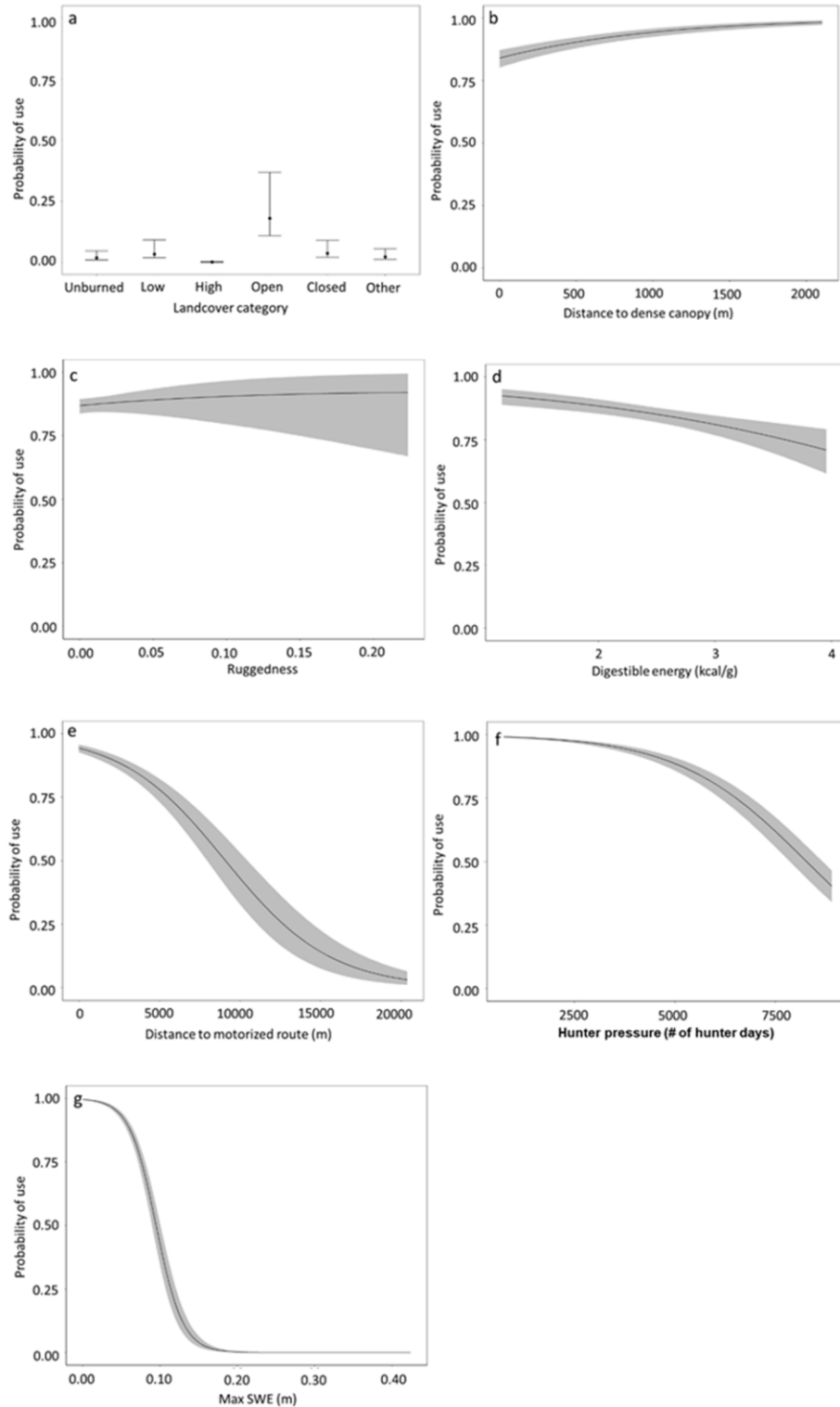


Figure 25. Estimated probability of use during the rifle season as a function of: a) landcover category, b) distance to dense canopy, c) terrain ruggedness, d) digestible energy, e) distance to open road, f) hunter pressure, and g) snow water equivalent (SWE), for the Blackfoot Clearwater elk population in west-central Montana, USA, 2019-2020. All panels assume all other continuous covariates are fixed at their mean observed value, and use occurs in the open landcover type. The mean posterior distribution is represented by the black line and the 95% credible intervals are represented by the gray ribbons.

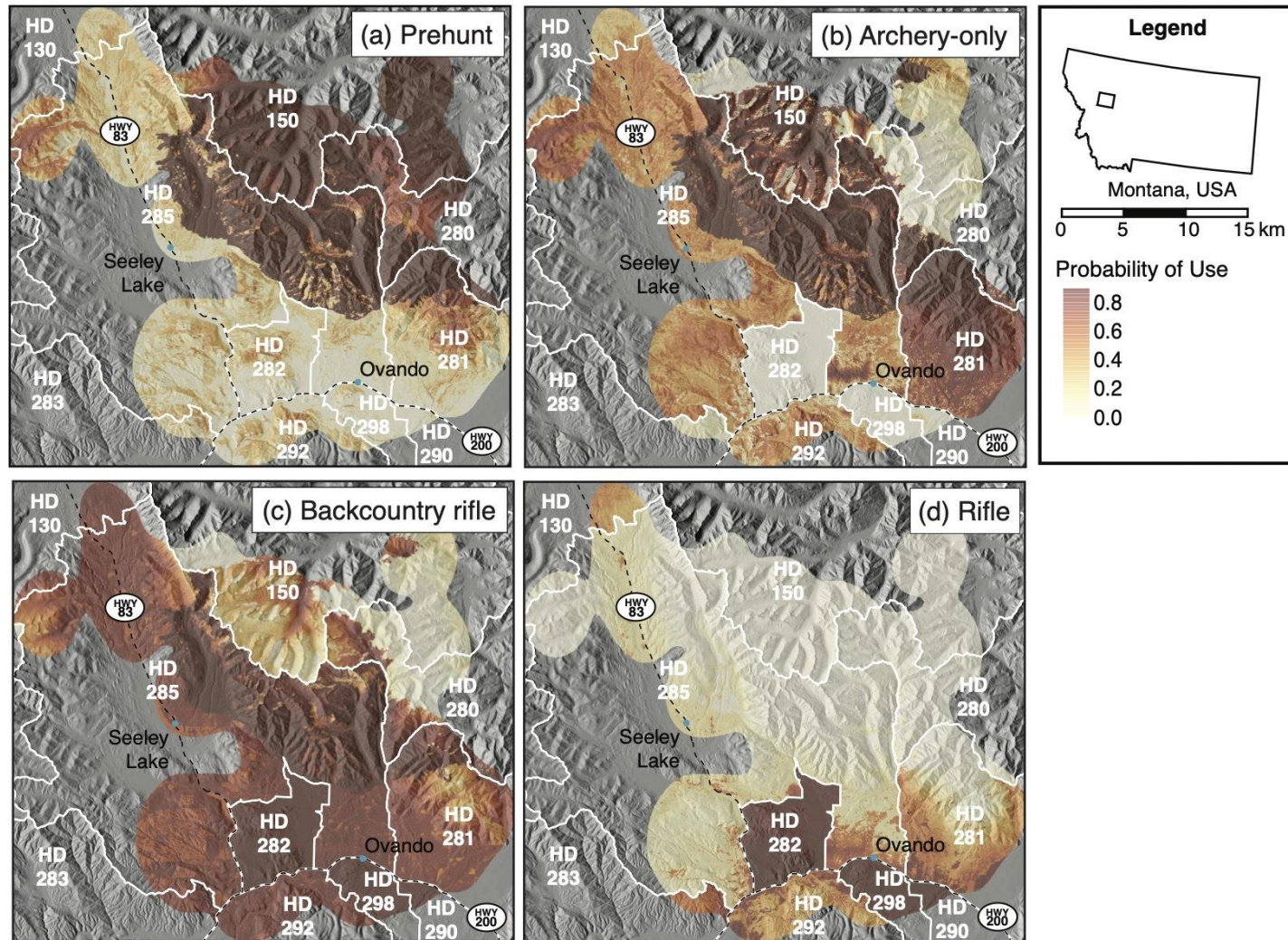


Figure 26. Probability of use predicted for the prehunt (panel a), archery-only (panel b), backcountry rifle (panel c), and rifle (panel d) hunt seasons for the Blackfoot-Clearwater elk population fall range in west-central Montana, USA using the RSPF model for each hunt season. Backcountry rifle hunting takes place in hunting districts 150 and 280 and hunting district 282 is by permit only for the rifle season. From the prehunt to the rifle season, female elk transitioned from their backcountry summer range to their front country winter range.

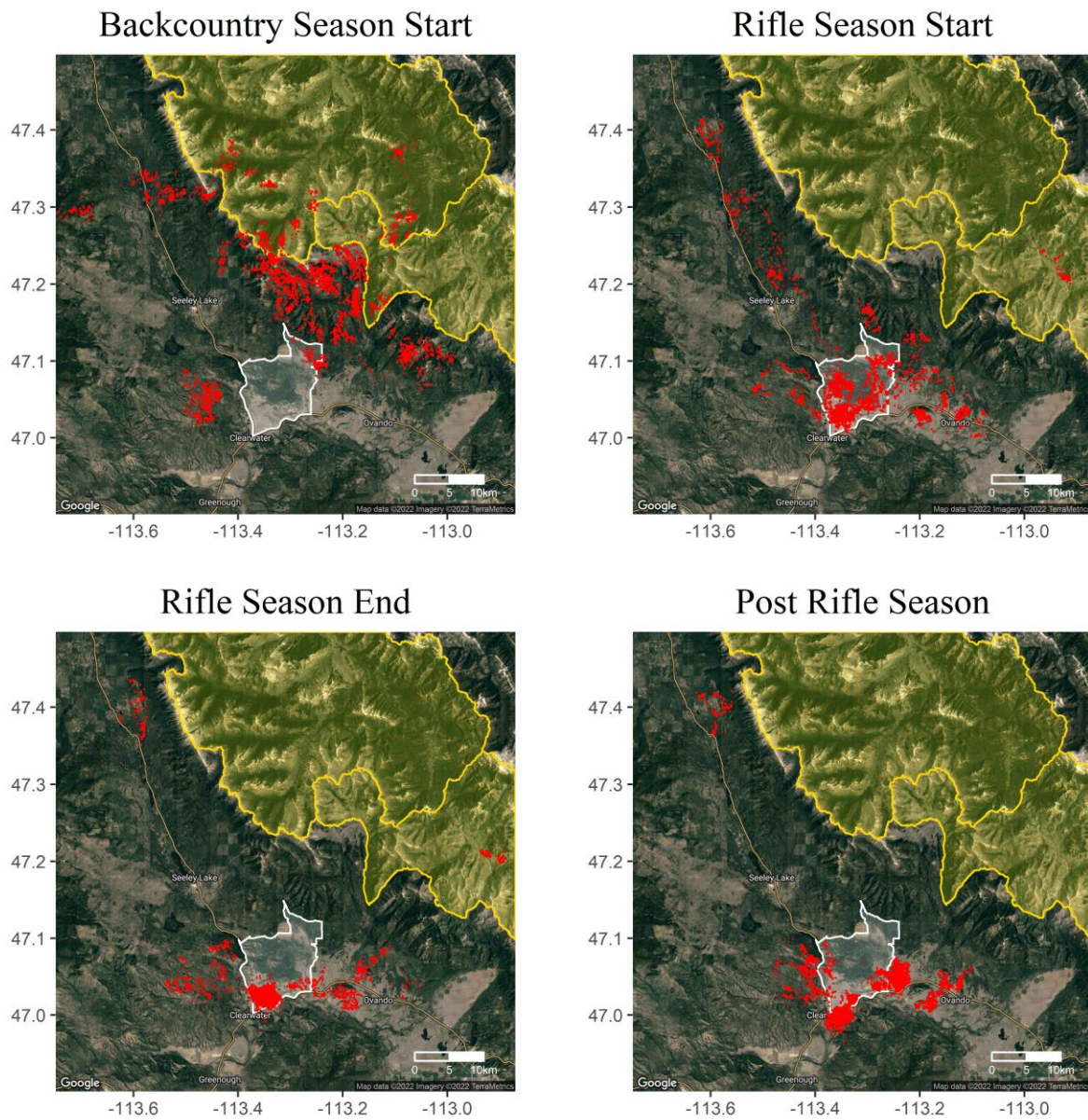


Figure 27. Female elk locations (red dots) during the first week of the backcountry rifle season (September 15 – 21), the first week of rifle season (October 25 – 31), the last week of rifle season (November 24 – 30), and post rifle season (December 25 – 31) in the Blackfoot-Clearwater region of west-central Montana in 2019 and 2020. Yellow regions on the map represent the backcountry hunting districts (150 and 280) and the white region represents district 282, which houses the Blackfoot-Clearwater Wildlife Management Area.

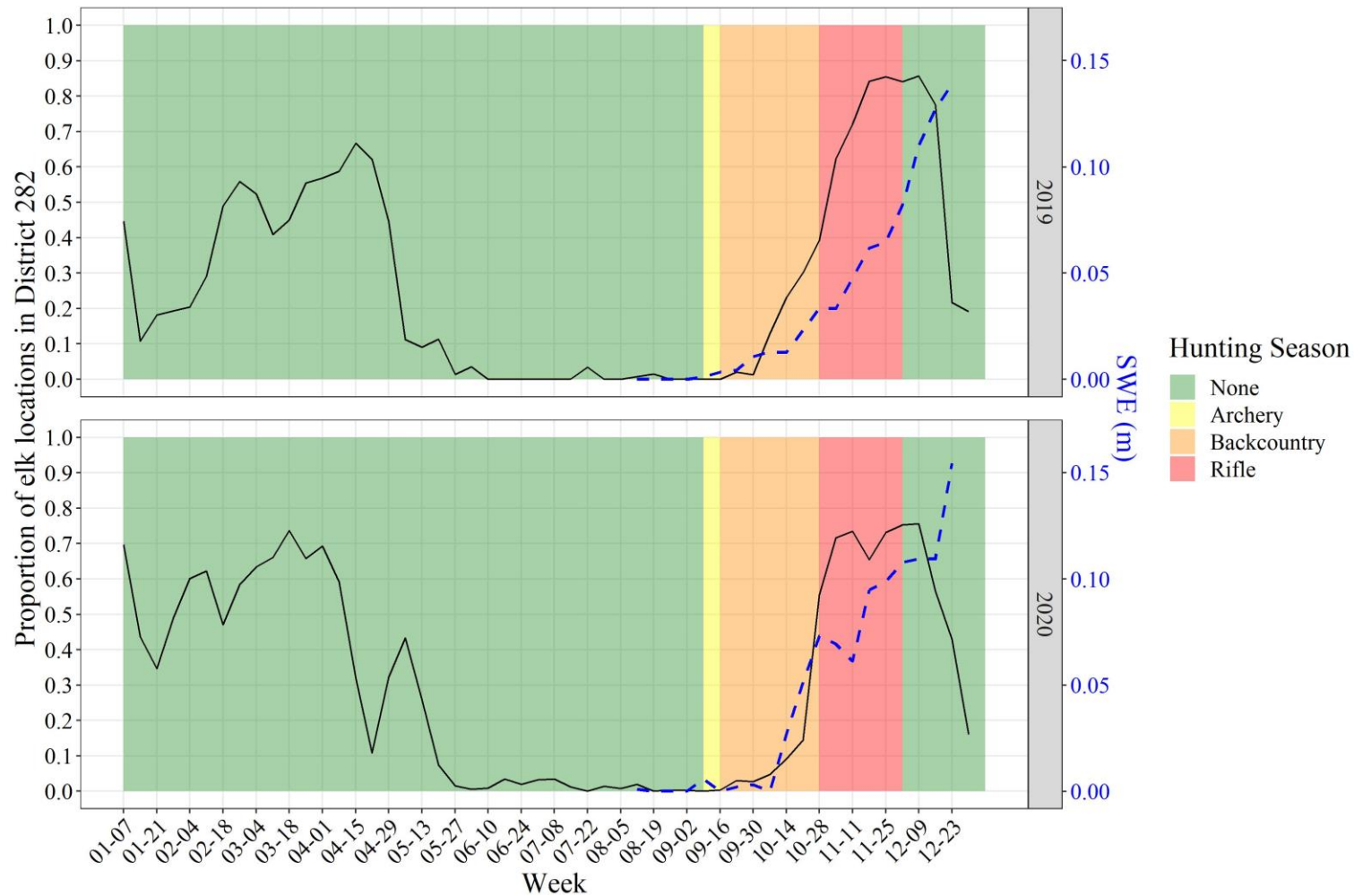


Figure 28. Proportion of elk locations within district 282 by week in 2019 and 2020 in the Blackfoot-Clearwater region of west-central Montana (black lines). Blue, dashed lines on the secondary axis represent mean snow water equivalent (m) by week (only shown from mid-August to late December). Background colors represent the type of general hunting season occurring during the week, with green, yellow, orange, and red representing no general hunting season, archery-only season, backcountry rifle season (rifle in backcountry districts and archery in front country districts), and general rifle season, respectively.

ADDITIONAL ANALYSIS: MAMMAL COMMUNITY USE OF AREAS THAT BURNED AT DIFFERENT LEVELS OF FIRE SEVERITY

Methods

We used mammal detection data from camera traps deployed in the Blackfoot-Clearwater region (see Objective 5) to identify the effects of fire severity on the broader mammal community.

Field Methods.—We classified each trail camera site as unburned, low, moderate, or high severity burn by making an ocular estimate of the percentage of live (green) tree canopy within a 20-meter radius of the camera location, in addition to visual assessment of other habitat characteristics (Table 13). Because moderately burned sites were not identified in the field, we reviewed pictures from each burned site to create a moderate severity burn category.

Table 12. Burn severity descriptions adapted from the protocol of the Blackfoot Clearwater Elk project in west-central Montana. Moderate severity fire classification was not part of the Blackfoot Clearwater Elk Project but was created based on criteria for low and high burn severities.

Fire Severity Class	Description
Unburned	<ul style="list-style-type: none"> • No sign of fire effects from the last 15 years. • Plant parts green and unaltered.
Low severity	<ul style="list-style-type: none"> • Canopy trees almost entirely alive and have green needles; although, the stems are scorched. • Surface litter and understory vegetation mildly charred. • Organic soil layer largely intact, though burned in small patches.
Moderate Severity	<ul style="list-style-type: none"> • Some canopy trees alive and needles partially consumed. • Some surface litter intact and vegetation mostly charred or consumed.
High severity	<ul style="list-style-type: none"> • Canopy trees killed, and needles are consumed. • Surface litter, understory vegetation, and the organic soil layer consumed.

Analytical Methods.—We counted the total number of species and number of unique individuals detected (number of unique individuals in photos taken at least 1 minute apart) in trail camera photos at each site. We did not account for imperfect detection in these analyses; thus, it is possible species detections were missed across all burn severities. However, we used similar protocols when setting trail cameras (camera model, height, angle, etc.), so we assume any

imperfection in detecting animals was consistent across burn severities. We also used an incidence-frequency data format within the iNEXT package in R (Hsieh et al. 2020) to create sample-based rarefaction curves and 95% confidence intervals for species richness and the exponential of Shannon’s diversity index (Hsieh et al. 2020) for each burn severity. We used sample-based rarefaction (Chao et al. 2014) because interpolating and extrapolating rarefaction curves allowed us to account for differences in sampling effort and assess the impact of sample size on species richness and diversity. Further, we used Shannon’s diversity index to estimate mammal species diversity because it measures entropy, or the amount of uncertainty in predicting the species of a random individual at a site (Spellerberg and Fedor 2003, Tuomisto 2010), and it provides a holistic measure of both species richness and evenness.

Results

We used camera data from a total of 62, 25, 34, and 55 cameras in unburned areas, low severity burns, moderate severity burns, and high severity burns, respectively, to identify the effects of burn severity on the mammal community. In total, we detected 26 species throughout the study area between May 2019 and October 2020 (excluding winter), with cervids being the most-detected species (Table 13). Combined detection frequency (count/100 days) of potential predators of elk (wolves, mountain lions, grizzly bears, black bears, coyotes) was higher in unburned sites (2.46) compared to low (1.23), moderate (0.55), and high (0.46) severity sites.

Table 13. Detection frequency (count/100 days) of mammal species detected on trail cameras within each burn severity (unburned, low, moderate, high) of the Rice Ridge Wildfire in west-central Montana, USA between May 2019 and October 2020 (excluding winter).

Species	Unburned	Low severity	Moderate severity	High severity	Total
White-tailed Deer (<i>Odocoileus virginianus</i>)	20.89	15.34	2.62	7.17	46.02
Elk (<i>Cervus canadensis</i>)	5.84	6.68	2.30	5.62	20.44
Mule Deer (<i>Odocoileus hemionus</i>)	2.54	3.14	5.53	3.85	15.06
Black Bear (<i>Ursus americanus</i>)	1.03	1.02	0.21	0.23	2.49
Lagomorph sp. (<i>Lagomorpha</i>)	0.16	0.07	1.07	0.10	1.40
Squirrel sp.	0.09	0.89	0.13	0.05	1.16
Mountain Lion (<i>Puma concolor</i>)	0.69	0.14	0.05	0.00	0.88
Chipmunk sp. (<i>Tamias</i> sp.)	0.56	0.07	0.08	0.15	0.86
Grizzly Bear (<i>Ursus arctos</i>)	0.14	0.07	0.16	0.18	0.55
Coyote (<i>Canis Latrans</i>)	0.51	0.00	0.00	0.03	0.54
Moose (<i>Alces alces</i>)	0.08	0.34	0.03	0.05	0.50

Red Fox (<i>Vulpes vulpes</i>)	0.16	0.07	0.13	0.13	0.49
American Marten (<i>Martes americana</i>)	0.02	0.00	0.11	0.29	0.42
Colombian Ground Squirrel (<i>Urocyon columbianus</i>)	0.12	0.00	0.03	0.26	0.41
Golden-Mantled Ground Squirrel (<i>Callospermophilus lateralis</i>)	0.00	0.00	0.11	0.18	0.29
Gray Wolf (<i>Canis lupus</i>)	0.09	0.00	0.13	0.02	0.24
Mountain Goat (<i>Oreamnos americanus</i>)	0.00	0.00	0.03	0.08	0.11
Badger (<i>Taxidea taxus</i>)	0.00	0.07	0.00	0.02	0.09
Lynx (<i>Lynx canadensis</i>)	0.02	0.00	0.03	0.00	0.05
Striped Skunk (<i>Mephitis mephitis</i>)	0.05	0.00	0.00	0.00	0.05
Wolverine (<i>Gulo gulo</i>)	0.00	0.00	0.03	0.02	0.05
Bobcat (<i>Lynx rufus</i>)	0.00	0.00	0.03	0.00	0.03
Fisher (<i>Pekania pennanti</i>)	0.00	0.00	0.03	0.00	0.03
Hoary marmot (<i>Marmota caligata</i>)	0.00	0.00	0.03	0.00	0.03
Porcupine (<i>Erethizon dorsatum</i>)	0.03	0.00	0.00	0.00	0.03
Weasel Sp. (<i>Mustela sp.</i>)	0.02	0.00	0.00	0.00	0.02
Total Rate	33.04	27.9	12.87	18.43	92.24
Total Species	19	12	21	18	26

Sample-based rarefaction using incidence-frequency data did not produce an asymptote for low and moderate severity burned sites (Figure 29), indicating that greater sample effort may produce more species. The 95% confidence intervals for observed species richness overlapped for all burn severities. A total of 12 species were detected in low severity burns, 21 species in moderate severity burns, 18 species in high severity burns, and 19 species in unburned areas. If species accumulation curves were extrapolated to 50 camera sites, low severity burns would have an estimated 17.0 species (95% confidence interval [CI] = 9.0 – 25.1), moderate severity burns would have 25.5 species (CI = 17.4 – 33.5), high severity burns would have 17.7 species (CI = 15.0 – 20.3), and unburned areas would have 17.8 species (CI = 13.8 – 21.8).

Sample-based rarefaction for the exponential of Shannon's diversity index reached an asymptote, or very near an asymptote, for all burn severities. When extrapolated to 50 camera sites, moderate severity had the highest predicted diversity ($H = 12.5$, CI = 8.9 – 16.0), compared to low severity sites ($H = 7.8$, CI = 5.7 – 10.0), high severity sites ($H = 8.8$, CI = 7.4 – 10.1), and unburned sites ($H = 9.6$, CI = 8.1 – 11.1; Figure 29).

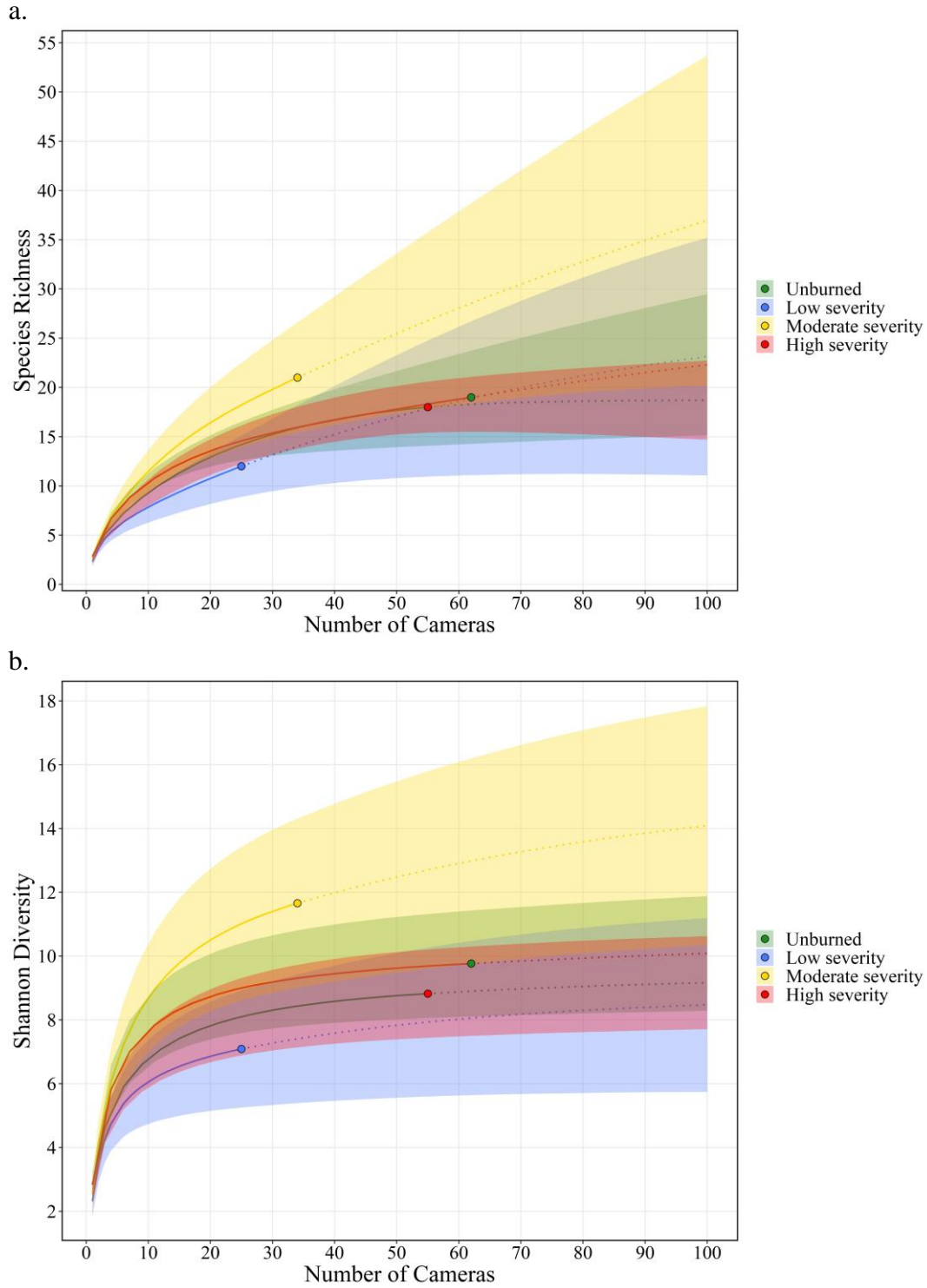


Figure 29. Rarefaction curves for species richness (a.) and Shannon Diversity (b.) of wild mammals as a function of sites sampled with trail cameras within the Rice Ridge Wildfire in west-central Montana, USA between May 2019 and October 2020 (excluding winter). Dots represent observed values, solid lines represent interpolated values, dotted lines represent extrapolated values, and ribbons represent 95% confidence intervals.

OBJECTIVE 6: RECOMMENDATIONS FOR FIRE MANAGEMENT TO IMPROVE ELK HABITAT

Conclusions.— As wildfire activity continues to increase throughout the western United States, understanding impacts of fire severity on wildlife habitat and resource selection will be key in managing populations in burned landscapes. Our results highlight that in years two and three after a large-scale wildfire, elk forage quality and quantity changed during the summer as a function of landscape characteristics and vegetation cover types. We found that fire improved forage quality regardless of fire severity, and that fire severity had variable effects on forage quantity dependent upon forage type and forest type. Fire altered the availability and distribution of forage to elk by extending the duration in which elk could access high quality forage throughout the summer. These results have strong implications for management, as changes in the nutritional landscape could potentially lead to changes in female elk body condition, demography, and distributions.

We found that fire improved forage quality and quantity of herbaceous biomass in both mesic and dry forests in years two and three postfire, with the largest increases in forage quality occurring in mesic forests. Higher forage quality and quantity within burned forests may be explained by the high ratio of highly palatable herbaceous forage to less palatable shrubs within low and high severity burned forests compared to unburned forest (Merrill et al. 1980, Cook, J. G. et al. 1994, Sachro et al. 2005). We did not find large differences in forage quality or quantity between low and high severity burned areas. This result was likely due to the overall high proportion of low and high severity burned vegetation sampling sites that contained fireweed, an important forage species with high forage quality through all phenological stages that rapidly establishes and spreads postfire due to its airborne seeds and rhizomatic nature. Thus, our results suggest that fire improved forage quality regardless of fire severity.

Although we found that wildfire improved forage availability in our study area, elk also seek security from top-down mortality risk (Hebblewhite et al. 2009, Middleton et al. 2013, DeVoe et al. 2019). Other studies have found that ungulate vulnerability to predation and human harvest may be higher in high severity burned forests, (Greene et al. 2012) and elk may alter their behavior to avoid high-risk areas (Hebblewhite et al. 2008, Spitz et al. 2018, DeVoe et al. 2019). Regardless of these potential risks, we found that female elk disproportionately used both low and high severity burned areas during neonatal, summer, and early fall seasons, compared to unburned areas, in years two through four postfire.

The highest energetic demands for female elk are incurred from late spring to mid-summer when lactation occurs, and when elk look to recoup body fat stores lost during the previous winter (Cook et al. 2004). Thus, female elk in our study were likely taking advantage of the increased and lengthened availability of high-quality forage in burned regions, regardless of potential risk from predation. However, we also found that elk predators, especially black bears, the most prevalent predator in our study, were detected less frequently in burned areas (e.g., Table 13, Figure 19). This is consistent with other research that found predators may avoid recently burned areas due to a lack of cover (e.g., Cunningham et al. 2003, Eby et al. 2013). As

a result, in our study area, elk may have been able to capitalize on both increased forage quality and a reduction in predation risk due to the decrease in predator activity in burned areas.

Elk selected for burned forests until mid-late October, when elk started moving toward winter range and selected areas with lower snowpack and hunter pressure. Hunter pressure and snowpack both increased throughout mid-late fall; thus, it is likely that both snowpack and hunting pressure affected elk movements and resource use during this season. Unfortunately, given the concurrent timing of high-pressure hunting seasons and snowfall (e.g., Figure 28), we could not fully disentangle the effects of snowpack vs. hunting pressure on large-scale elk movements. A dataset with more variability in annual snowpack and hunter pressure metrics is necessary to identify the unique contributions of each factor on landscape-scale elk resource use. Further, analyzing elk resource use at smaller scales (e.g., factors affecting daily resource use) may provide additional insight into the factors that drive elk movements during the late fall.

Fire has historically impacted our study area, with 23 fires occurring between 1985 and 2015 ranging in size of area burned from 0.05 km² to 96 km². Our study occurred two to four years postfire, where there were limited differences in use of low and high severity burned forests; however, greater differences might be seen in the future as the burned areas move through different successional stages (Turner et al. 1999, Kane et al. 2013). Forage quality could potentially differ between low and high severity burned forests in the future as vegetation regenerates at varying paces, altering the composition and phenology of vegetation communities. In turn, elk may alter their use of low and high severity burned forests to select for areas with the greatest nutritional return. Further, as time since fire increases, more fire killed snags will fall (Ritchie and Knapp 2014, Grayson et al. 2019), potentially negatively influencing locomotion for elk in burned areas in the future. High severity burned forests have more fire-killed trees (Ryan 2002, Keeley 2009), and therefore, may experience more downed logs in the future. Following this increase in downed logs, elk may avoid high severity burned forests in the future even if there is good forage available (Lamont et al. 2019).

Recommendations.—Below we provide recommendations for fire management to improve elk habitat based on our research findings.

1. Undisturbed mesic and dry forests in this study area may not provide sufficient nutrition for elk. We found the biggest increase in forage quality between unburned and burned mesic forests; thus, where possible, managers should allow fires in mesic forests to burn.
 - a. Prescribed burn effects on forage for elk may differ from wildfires (Proffitt et al. 2019) due to reduced severity, smaller extent, and annual times of occurrence (Ryan et al. 2013). However, prescribed burn efficacy may be maximized by burning in mesic vs dry forest.
 - b. The effects of fire on elk resource use will largely depend on the elk seasonal range that is burned and the vegetation species that recolonize after the fire. Because elk have highest energetic demands during summer (Cook et al. 2004), prioritizing burns in elk summer range where fireweed is likely to recolonize may be an effective strategy for improving elk nutrition.

2. There were not large differences in elk forage resources or elk selection across fire severities. Thus, fires may not need to be managed based on severity to improve elk habitat, in the short-term following wildfires.
 - a. Effects of fire severity on elk movements and resource use could change over time as burned areas move through different successional stages (Turner et al. 1999, Kane et al. 2013). Long-term, post-fire changes in elk forage were beyond the scope of our study, so we cannot provide recommendations regarding long-term, post-fire elk habitat management.
3. Hunter pressure during the early fall (i.e., archery season and early backcountry rifle season) did not affect elk use of burned areas, as elk did not stop using burned sites until the rifle season. Thus, managers may not need to consider fire when making early-season hunting regulations at the levels of hunting pressure we observed.
4. Snowpack and hunter pressure were confounded and correlated with elk movements from burned areas to open grasslands in hunting district 282 in late fall (i.e., rifle season). Risk of human harvest can affect elk resource selection (Proffitt et al. 2009, Proffitt et al. 2010). However, we cannot conclude that elk movements out of burned areas were due solely to increased risk from human hunters, given timing of movements also coincided with increases in snowpack (Figure 28). Thus, we cannot provide recommendations on whether managers should consider the effects of fire in harvest management during rifle season.
 - a. Effects of fire on elk resource use and movements during high-pressure hunting periods may vary, depending on which elk seasonal range is burned. The contribution and interaction of burn severity and hunting pressure may become more apparent in locations where the elk late fall/winter range is burned, especially in areas with higher hunter pressure.

LITERATURE CITED

- Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60:255-265. doi:10.1093/biomet/60.2.255.
- Allred, B. W., B. T. Bestelmeyer, C. S. Boyd, C. 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. doi:10.1111/2041-210x.13564.
- Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecology and Evolution* 1:132-144. doi:10.1002/ece3.12.
- Ando, H., C. Fujii, M. Kawanabe, Y. Ao, T. Inoue, and A. Takenaka. 2018. Evaluation of plant contamination in metabarcoding diet analysis of a herbivore. *Scientific Reports* 8:15563-10. doi:10.1038/s41598-018-32845-w.
- Banchi, E., C. G. Ametrano, S. Greco, D. Stanković, L. Muggia, and A. Pallavicini. 2020. PLANiTS: a curated sequence reference dataset for plant ITS DNA metabarcoding. *Database* 2020:baz155. doi:10.1093/database/baz155.
- Barker, K. J., M. S. Mitchell, K. M. Proffitt, and J. D. DeVoe. 2019. Land management alters traditional nutritional benefits of migration for elk. *The Journal of Wildlife Management* 83:167-174. doi:10.1002/jwmg.21564.
- Barton, K. 2020. MuMIn: Multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>.
- Bell, K. L., V. M. Loeffler, and B. J. Brosi. 2017. An rbcL reference library to aid in the identification of plant species mixtures by DNA metabarcoding. *Applications in Plant Sciences* 5:1600110. doi:10.3732/apps.1600110.
- Berg, J. E., J. Reimer, P. Smolko, H. Bohm, M. Hebblewhite, and E. H. Merrill. 2021. Mothers' movements: shifts in calving area selection by partially migratory elk. *The Journal of Wildlife Management* 85:1476-1489. doi:10.1002/jwmg.22099.
- Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* 18:320-331. doi:10.1111/j.1523-1739.2004.00548.x.
- Boyce, M. S. 1991. Migratory behavior and management of elk (*Cervus elaphus*). *Applied Animal Behaviour Science* 29:239-250.

- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Écoscience* 10:421-431. doi:10.1080/11956860.2003.11682790.
- Brook, R. K. 2010. Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes. *Canadian Journal of Zoology* 88:968-976. doi:10.1139/Z10-061.
- Brown, T. J., B. L. Hall, and A. L. Westerling. 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: An applications perspective. *Climatic Change* 62:365-388. doi:10.1023/b:clim.0000013680.07783.de.
- Burcham, L. T. 1956. Historical backgrounds of range land use in California. *Journal of Range Management* 9:81-86. doi:10.2307/3894555.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516-519. doi:10.1016/j.ecolmodel.2006.03.017.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45-67. doi:10.1890/13-0133.1.
- Chen, S., H. Yao, J. Han, C. Liu, J. Song, L. Shi, Y. Zhu, X. Ma, T. Gao, X. Pang, K. Luo, Y. Li, X. Li, X. Jia, Y. Lin, and C. Leon. 2010. Validation of the ITS2 region as a novel DNA barcode for identifying medicinal plant species. *PLoS ONE* 5:e8613. doi:10.1371/journal.pone.0008613.
- 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.
- 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. doi:10.1002/wsb.182.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310. doi:10.1126/science.199.4335.1302.
- Cook, J. G., T. J. Hershey, and L. L. Irwin. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. *Journal of Range Management* 47:296-302.

- Cook, J. G., R. C. Cook, R. W. Davis, and L. L. Irwin. 2016. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. *Wildlife Monographs* 195:1-81. doi:10.1002/wmon.1020.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. *Wildlife Monographs* 155:1-61. doi:10.1002/wmon.1020.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. Mccorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenecker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *The Journal of Wildlife Management* 74:880-896. doi:10.2193/2009-031.
- 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. doi:10.1002/wmon.1008.
- Cunningham, S. C., W. B. Ballard, L. M. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, Central Arizona. *Wildlife Society Bulletin* 31:786-792.
- Deagle, B. E., A. C. Thomas, J. C. Mcinnes, L. J. Clarke, E. J. Vesterinen, E. L. Clare, T. R. Kartzinel, and J. P. Eveson. 2018. Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? *Molecular Ecology* 28:391-406. doi:10.1111/mec.14734.
- D'Eon, R., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *The Journal of Applied Ecology* 42:383-388. doi:10.1111/j.1365-2664.2005.01010.x.
- 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. doi:10.1002/jwmg.21638.
- Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9:113-122. doi:10.2307/3237229.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* 311:352. doi:10.1126/science.1122855.
- Dumelle, M., T. M. Kincaid, and A. R. Olsen. 2022. spsurvey: Spatial Sampling Design and Analysis. R package version 5.3.0.

- Eby, S., A. Mosser, A. Swanson, C. Packer, and M. Ritchie. 2013. The impact of burning on lion *Panthera leo* habitat choice in an African savanna. *Current Zoology* 59:335-339. doi:10.1093/czoolo/59.3.335.
- Eggeman, S. L., M. Hebblewhite, H. Bohm, J. Whittington, E. H. Merrill, and A. Loison. 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *The Journal of Animal Ecology* 85:785-797. doi:10.1111/1365-2656.12495.
- Erickson, D. L., E. Reed, P. Ramachandran, N. A. Bourg, W. J. McShea, and A. Ottesen. 2017. Reconstructing a herbivore's diet using a novel rbcL DNA mini-barcode for plants. *AoB Plants* 9:plx015. doi:10.1093/aobpla/plx015.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51-81. doi:10.1111/j.1365-2907.2005.00053.x.
- Fontaine, J. J., A. D. Fedele, L. S. Wszola, L. N. Messinger, C. J. Chizinski, J. J. Lusk, K. L. Decker, J. S. Taylor, and E. F. Stuber. 2019. Hunters and their perceptions of public access: A view from afield. *Journal of Fish and Wildlife Management* 10:589-601. doi:10.3996/082018-JFWM-077.
- Ford, M. J., J. Hempelmann, M. B. Hanson, K. L. Ayres, R. W. Baird, C. K. Emmons, J. I. Lundin, G. S. Schorr, S. K. Wasser, and L. K. Park. 2016. Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. *PLoS ONE* 11:e0144956. doi:10.1371/journal.pone.0144956.
- Found, R., and C. C. St. Clair. 2016. Behavioural syndromes predict loss of migration in wild elk. *Animal Behaviour* 115:35-46. doi:10.1016/j.anbehav.2016.02.007.
- Fryxell, J. M., and A. R. E. Sinclair. 1988. Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology* 26:17-31. doi:10.1111/j.1365-2028.1988.tb01125.x.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457-511.
- Grayson, L. M., D. R. Cluck, and S. M. Hood. 2019. Persistence of fire-killed conifer snags in California, USA. *Fire Ecology* 15 doi:10.1186/s42408-018-0007-7.
- Greenberg, S., T. Godin, and J. Whittington. 2019. Design patterns for wildlife-related camera trap image analysis. *Ecology and Evolution* 9:13706-13730. doi:10.1002/ece3.5767.
- Greene, L., M. Hebblewhite, and T. R. Stephenson. 2012. Short-term vegetation response to wildfire in the eastern Sierra Nevada: Implications for recovering an endangered ungulate. *Journal of Arid Environments* 87:118-128. doi:10.1016/j.jaridenv.2012.06.001.

- 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. doi:10.1016/j.geoforum.2005.12.004.
- Hansen, C. P. 2021. Sustainability in a changing landscape: the effect of land use on vegetation and mammal communities. Dissertation, University of Montana, Missoula, MT, USA.
- Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of Spatiotemporal Scale on Autocorrelation and Home Range Estimators. *The Journal of Wildlife Management* 61:280-290. doi:10.2307/3802583.
- Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141-166. doi:10.1890/06-1708.1.
- Hebblewhite, M., R. H. Munro, and E. H. Merrill. 2009. Trophic consequences of postfire logging in a wolf–ungulate system. *Forest Ecology and Management* 257:1053-1062. doi:10.1016/j.foreco.2008.11.009.
- Heinselman, M. L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374-405 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest Succession*. Springer Advanced Texts in Life Sciences. Springer, New York, NY, USA.
- Hillis, J. M., M. J. Thompson, J. E. Canfield, L. J. Lyon, C. L. Marcum, P. M. Dolan, and D. W. McCleerey. 1999. Defining elk security: the Hillis paradigm. Pages 38-43 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. *Proceedings of the elk vulnerability symposium*. Montana State University, Bozeman, Montana, USA.
- Hollingsworth, T. N., J. F. Johnstone, E. L. Bernhardt, and 3. Chapin F Stuart. 2013. Fire severity filters regeneration traits to shape community assembly in Alaska's Boreal Forest. *PLoS ONE* 8:e56033. doi:10.1371/journal.pone.0056033.
- Hsieh, T. C., K. H. Ma, and A. Chao. 2020. iNEXT: iNterpolation and EXTrapolation for species diversity. R Package Version 2.0.20
URL:<http://chao.stat.nthu.edu.tw/wordpress/software-download/>.
- Jones, M. O., B. W. Allred, D. E. Naugle, J. D. Maestas, P. Donnelly, L. J. Metz, J. Karl, R. Smith, B. Bestelmeyer, C. Boyd, J. D. Kerby, and J. D. McIver. 2018. Innovation in rangeland monitoring: annual, 30m, plant functional type percent cover maps for U.S. rangelands, 1984-2017. *Ecosphere* 9:e02430. 10.1002/ecs2.2430.
- Kane, V. R., J. A. Lutz, S. L. Roberts, D. F. Smith, R. J. McGaughey, N. A. Povak, and M. L. Brooks. 2013. Landscape-scale effects of fire severity on mixed-conifer and red fir forest structure in Yosemite National Park. *Forest Ecology and Management* 287:17-31. doi:10.1016/j.foreco.2012.08.044.

- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457-481. doi:10.1007/978-1-4612-4380-9_25.
- Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in the Rocky Mountain ecosystems: a literature review. General Technical Report. RMRS-GTR-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 24 p.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116-126. doi:10.1071/WF07049.
- Kerns, B. K., and M. A. Day. 2018. Prescribed fire regimes subtly alter ponderosa pine forest plant community structure. *Ecosphere* 9:e02529-n/a. doi:10.1002/ecs2.2529.
- Krausman, P. R., S. A. Christensen, J. E. McDonald, and B. D. Leopold. 2014. Dynamics and social issues of overpopulated deer ranges in the United States: a long term assessment. *California Fish and Game* 100:436-450.
- Krueger, W. C. 1972. Evaluating Animal Forage Preference. *Journal of Range Management* 25:471-475. doi:10.2307/3897012.
- Kuhn, M. 2021. Classification and Regression Training. R package version 6.0-90. <https://CRAN.R-project.org/package=caret>. .
- Lamont, B. G., K. L. Monteith, J. A. Merkle, T. W. Mong, S. E. Albeke, M. M. Hayes, and M. J. Kauffman. 2019. Multi-scale habitat selection of elk in response to beetle-killed forest. *The Journal of Wildlife Management* 83:679-693. doi:10.1002/jwmg.21631.
- Lande, U. S., L. E. Loe, O. J. Skjærli, E. L. Meisingset, and A. Mysterud. 2013. The effect of agricultural land use practice on habitat selection of red deer. *European Journal of Wildlife Research* 60:69-76. doi:10.1007/s10344-013-0751-6.
- Lindeløv, J. K. 2020. mcp: An R package for regression with multiple change points. doi:10.31219/osf.io/fzqxv.
- Long, R. A., J. L. Rachlow, J. G. Kie, and M. Vavra. 2008. Fuels Reduction in a Western Coniferous Forest: Effects on Quantity and Quality of Forage for Elk. *Rangeland Ecology & Management* 61:302-313. doi:10.2111/07-046.1.
- Lord, R., and K. Kielland. 2015. Effects of variable fire severity on forage production and foraging behavior of moose in winter. *Alces* 51:23.

- 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. doi:10.1002/jwmg.21781.
- Lula, E. S., B. Lowrey, K. M. Proffitt, A. R. Litt, J. A. Cunningham, C. J. Butler, and R. A. Garrott. 2020. Is habitat constraining bighorn sheep restoration? A case study. *The Journal of Wildlife Management* 84:588-600. doi:10.1002/jwmg.21823.
- Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry* 81:592-613.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. *Ecology* 83:2248. doi:10.2307/3072056.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2003. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Second Edition. Kluwer Academic Publishers, London.
- McCorquodale, S. M. 2003. Sex-specific movements and habitat use by elk in the Cascade Range of Washington. *The Journal of Wildlife Management* 67:729-741. doi:10.2307/3802679.
- McIver, J. D., and L. Starr. 2000. Environmental effects of postfire logging: literature review and annotated bibliography. Gen. Tech. Rep. PNW-GTR-486. Portland, OR:US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 72 p.
- Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society. B, Biological Sciences* 283:20160456. doi:10.1098/rspb.2016.0456.
- Merrill, E. H., H. F. Mayland, and J. M. Peek. 1980. Effects of a fall wildfire on herbaceous vegetation on xeric sites in the Selway-Bitterroot wilderness, Idaho. *Journal of Range Management* 33:363-367. doi:10.2307/3897884.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245-1256. doi:10.1890/11-2298.1.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs* 186:1-62. doi:10.1002/wmon.1011.

- Mould, E. D., and C. T. Robbins. 1982. Digestive Capabilities in Elk Compared to White-Tailed Deer. *The Journal of Wildlife Management* 46:22-29. doi:10.2307/3808404.
- Newton, M., S. Fitzgerald, R. R. Rose, P. W. Adams, S. D. Tesch, J. Sessions, T. Atzet, R. F. Powers, and C. Skinner. 2006. Comment on post-wildfire logging hinders regeneration and increases fire risk. *Science* 313:615a-615; author reply 615. doi:10.1126/science.1126478.
- Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology* 94:1456-1463. doi:10.1890/12-1688.1.
- Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Frontiers in Ecol Environ - 2006 - Noss - Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* 4:481-487.
- Noyes, J. H., R. G. Sasser, B. K. Johnson, L. D. Bryant, and B. Alexander. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. *Wildlife Society Bulletin* 25:695-698.
- Pearson, K. 1895. Notes on regression and inheritance in the case of two parents. *Proceedings of the Royal Society of London* 58:240-242.
- Peterson, D. W., and E. K. Dodson. 2016. Post-fire logging produces minimal persistent impacts on understory vegetation in northeastern Oregon, USA. *Forest Ecology and Management* 370:56-64. doi:10.1016/j.foreco.2016.04.004.
- Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. *Ecological Applications* 26:2156-2174.
- Proffitt, K. M., J. DeVoe, K. Barker, R. Durham, T. Hayes, M. Hebblewhite, C. Jourdonnais, P. Ramsey, and J. Shamhart. 2019. A century of changing fire management alters ungulate forage in a wildfire-dominated landscape. *Forestry* 92:523-537. doi:10.1093/forestry/cpz017.
- Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. *The Journal of Wildlife Management* 74:210-218. doi:10.2193/2008-593.
- 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. *The Journal of Wildlife Management* 73:345-356. doi:10.2193/2008-210.

- Ranglack, D. H., K. M. Proffitt, J. Gude, J. Canfield, J. Rotella, and R. A. Garrott. 2016. Evaluating elk summer resource selection and applications to summer range habitat management. *Intermountain Journal of Sciences* 22:114-115.
- 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. doi:10.1002/jwmg.21258.
- Ritchie, M. W., and E. E. Knapp. 2014. Establishment of a long-term fire salvage study in an interior ponderosa pine forest. *Journal of Forestry* 112:395-400. doi:10.5849/jof.13-093.
- Rota, C. T., J. J. Millsbaugh, D. C. Kesler, C. P. Lehman, M. A. Rumble, C. M. B. Jachowski, and F. Huettmann. 2013. A re-evaluation of a case-control model with contaminated controls for resource selection studies. *The Journal of Animal Ecology* 82:1165-1173. doi:10.1111/1365-2656.12092.
- Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *The Journal of Wildlife Management* 64:672-684. doi:10.2307/3802737.
- Ryan, K. C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* 36 doi:10.14214/sf.548.
- Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the Environment* 11:e15-e24. doi:10.1890/120329.
- Sachro, L. L., W. L. Strong, and C. C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. *Journal of Environmental Management* 77:183-193. doi:10.1016/j.jenvman.2005.04.003.
- Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave desert. *The Journal of Wildlife Management* 71:1419-1426. doi:10.2193/2005-723.
- Sittler, K. L., K. L. Parker, and M. P. Gillingham. 2015. Resource separation by mountain ungulates on a landscape modified by fire. *The Journal of Wildlife Management* 79:591-604. doi:10.1002/jwmg.869.
- Smith, J. K., L. J. Lyon, M. H. Huff, R. G. Hooper, E. S. Telfer, D. S. Schreiner, and J. K. Smith. 2000. Wildland fire in ecosystems. Effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-vol. 1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 83 p.

- Snobl, L. S., K. M. Proffitt, and J. J. Millsaugh. In press. Wildfire extends the shelf-life of elk nutritional resources regardless of fire severity. *Ecosphere*.
- Spellerberg, I. F., and P. J. Fedor. 2003. A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. *Global Ecology and Biogeography* 12:177-179. doi:10.1046/j.1466-822X.2003.00015.x.
- Spitz, D. B., D. A. Clark, M. J. Wisdom, M. M. Rowland, B. K. Johnson, R. A. Long, and T. Levi. 2018. Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales. *Ecological Applications* 28:2082-2091. doi:10.1002/eap.1797.
- Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. *Journal of the American Statistical Association* 99:262-278. doi:10.1198/016214504000000250.
- Su, Y., and M. Yajima. 2015. R2jags: Using R to Run 'JAGS'. R package version 0.5-7. <https://CRAN.R-project.org/package=R2jags>.
- Therneau, T. M. 2021. A package for survival analysis in R. R package version 3.2-13. <https://CRAN.R-project.org/package=survival>.
- Tracy, B., and S. McNaughton. 1991. The interaction of fire, vegetation and large mammalian herbivores, on ecosystem processes in Yellowstone National Park. The UW National Parks Service Research Station Annual Reports 15:260-262. doi:10.13001/uwnpsrc.1991.3043.
- Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2-22. doi:10.1111/j.1600-0587.2009.05880.x.
- Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9:21-36. doi:10.1071/WF99003.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411-433. doi:10.1890/0012-9615(1997)067[0411:eofsap]2.0.co;2.
- 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. doi:10.2307/3801989.
- Van Dyke, F., and J. A. Darragh. 2006. Short- and longer-term effects of fire and herbivory on sagebrush communities in south-central Montana. *Environmental Management* 38:365-376. doi:10.1007/s00267-005-0168-4.

- Van Dyne, G. M., and J. A. Darragh. 1963. An Artificial Rumen System for Range Nutrition Studies. *Journal of Range Management* 16:146-147. doi:10.2307/3895110.
- Van Soest, P. J. 1982. Nutritional ecology of the ruminant metabolism, nutritional strategies, the cellulolytic fermentation and the chemistry of forage and plant fibers. O and B Books, Corvallis, OR, USA.
- Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2004. Spatial partitioning by mule deer and elk in relation to traffic. *Transactions of the 69th North American Wildlife and Natural Resources Conference* :509-530.
- Wisdom, M. J., H. K. Preisler, L. M. Naylor, R. G. Anthony, B. K. Johnson, and M. M. Rowland. 2018. Elk responses to trail-based recreation on public forests. *Forest Ecology and Management* 411:223-233. doi:10.1016/j.foreco.2018.01.032.
- Yao, H., J. Song, C. Liu, K. Luo, J. Han, Y. Li, X. Pang, H. Xu, Y. Zhu, P. Xiao, and S. Chen. 2010. Use of ITS2 region as the universal DNA barcode for plants and animals. *PLoS ONE* 5:e13102. doi:10.1371/journal.pone.0013102.