

RESEARCH ARTICLE

Autumn resource selection by female elk in a recently burned landscape in western Montana

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Abstract

Wildfire activity across the western United States has increased in recent decades, with wildfires burning at a higher severity and larger scale. The effect of wildfires on forest structure and wildlife habitat is largely influenced by wildfire severity; however, few studies have evaluated the effects of wildfire severity on resource selection of ungulates, particularly during hunting seasons, when knowledge of resource selection is essential for making informed management decisions. To fill this knowledge gap, we fit resource selection probability functions for female elk (*Cervus canadensis*) in years 2 and 3 post-wildfire to evaluate the effects of wildfire severity and other environmental and anthropogenic factors on elk resource selection during 4 autumn periods with varying levels of hunter pressure (prehunt, archery-only, backcountry rifle, and rifle). The probability of female elk selecting low-severity burned forests during the prehunt, archery-only, backcountry rifle, and rifle periods was 0.99 (95% credible interval [CrI] = 0.98–1.00), 0.99 (CrI = 0.97–1.00), 0.99 (CrI = 0.99–1.00), and 0.0010 (CrI = 0.00067–0.0015), respectively, and did not strongly differ from the probability of selecting high-severity burned forests. During the prehunt period, elk also selected areas with greater forage quality and areas farther from open roads. Elk selected similar resources during the archery period, and selected areas with higher hunter pressure. Elk started leaving hunting districts that had higher snowpack (i.e., snow water equivalent; $\beta = -0.84$, CrI = -0.96 – -0.72) and allowed rifle hunting ($\beta = -5.39$, CrI = -5.80 – -4.97) but still selected areas with higher hunter pressure ($\beta = 0.92$, CrI = 0.78–1.07) during the backcountry rifle

period. During the rifle period, elk continued avoiding areas with high snowpack ($\beta = -3.96$, CrI = -4.22 – -3.71) and started selecting areas with lower hunter pressure ($\beta = -1.71$, CrI = -1.79 – -1.64) and lower canopy cover. Overall, wildfire affected elk distributions in early autumn 2 and 3 years after fire in our study area, with limited differences in resource selection between wildfire severity categories. By late autumn, hunter pressure and snowpack were the primary factors influencing elk distribution, and wildfire had little influence on selection. When estimating wildfire effects on elk movements during autumn and establishing appropriate hunting regulations, managers should consider the hunting season, hunter pressure, timing and amount of snowpack, location of traditional winter range, and the seasonal elk range burned, as all these factors may contribute to how elk use the landscape in autumn.

KEYWORDS

Cervus canadensis, elk, hunting pressure, hunting season, nutrition, resource selection probability function, snowpack, wildfire, wildfire severity

Wildfires in the western United States have been increasing in size and severity over the last several decades (Flannigan et al. 2013, Dennison et al. 2014, Westerling 2016, Parks and Abatzoglou 2020). Since 1985, there has been an 8-fold increase in the amount of annual area burned by high-severity fires, and climate forecasts suggest a continued increase in the future (Parks and Abatzoglou 2020). Fire severity influences the postfire forest structure by removing variable amounts of vegetation, which can set forest patches onto different successional trajectories (Kane et al. 2013). By changing vegetative structure, fire severity potentially alters the availability and distribution of key resources for wildlife such as food and cover, ultimately influencing habitat use (Buchalski et al. 2013, Galbraith et al. 2019, Stillman et al. 2019). Therefore, assessing wildlife responses to fire severity is needed to provide information to help wildlife and land managers meet habitat requirements, population objectives, and develop hunting regulations as wildfires continue to shape landscapes in western North America.

Wildfire can positively or negatively affect wildlife habitat, defined as the suite of resources and environmental conditions that determine the presence, survival, and reproduction of a population (Hall et al. 1997, Gaillard et al. 2010). For elk (*Cervus canadensis*), wildfire may positively affect nutritional resources. Wildfires move forests to early successional stages, frequently increasing the quality and quantity of forage available to ungulates shortly after a fire (Merrill et al. 1980, Cook et al. 1994, Tracy and McNaughton 1997, Proffitt et al. 2019, Snobl et al. 2022). In turn, elk typically select recently burned forests to increase foraging efficiency (Spitz et al. 2018). Adequate nutritional resources are particularly important during the late-summer and autumn, as female elk look to support physiological demands for both pregnancy and overwinter survival (Cook et al. 2004, Long et al. 2016). Thus, female elk body condition and pregnancy rates could be positively influenced if elk are able to access high quality forage in a recently burned landscape. Despite postfire nutritional benefits, the removal of vegetation by disturbances, such as fire, may negatively affect elk habitat by reducing security resources such as hiding cover (Lowrey et al. 2020), potentially increasing susceptibility, or risk, to predation and harvest. Therefore, elk may also avoid recently burned areas where risk is high (Hebblewhite et al. 2009).

One of the riskiest times for elk is during autumn hunting seasons. During autumn, elk typically select for areas with greater cover (Skovlin et al. 2002), less hunter pressure (Conner et al. 2001, Ranglack et al. 2017), and areas farther from open roads (Montgomery et al. 2013, Proffitt et al. 2013, Lowrey 2020) to reduce vulnerability to hunters. Thus, wildfires may present elk with a tradeoff in autumn between meeting physiological demands and minimizing risk of mortality, given recent wildfires generally increase nutritional resources yet reduce the availability of cover, dependent upon fire severity. Wildfires that burn on public lands could result in increased elk use of public lands during autumn because of the improved nutritional resources or could result in elk moving to sites with more security, including areas that limit hunter pressure (e.g., refuges or private lands; Proffitt et al. 2016, Sergeyev et al. 2022). One of the primary challenges of state wildlife agencies in the Intermountain West is managing elk populations that are increasingly using private lands (Haggerty and Travis 2006). Thus, understanding how wildfire influences elk distribution and resource selection during autumn could help managers develop tools to achieve more desirable elk distributions across public and private lands, thereby facilitating the accomplishment of management objectives.

Previous research on elk responses after wildfire have mainly focused on comparing resource selection between unburned and burned areas (Pearson et al. 1995, Biggs et al. 2010); however, fire severity adds another layer of complexity that warrants further research into the effects on elk habitat use. Fire severity plays a key role in developing the postfire structure and composition of forested ecosystems and, therefore, elk habitat. Within forested ecosystems, mixed-severity fires create a heterogenous landscape where some areas remain unburned (no recent fire history), are burned at a low or moderate severity (fire removes understory vegetation; some trees experience mortality, but many mature trees survive), or are burned at a high severity (fire removes understory vegetation and kills most trees; Ryan 2002, Keeley 2009). Although there may be limited differences in nutritional resources between fire severity classes in the years shortly after fire (Snobl et al. 2022), the differences in postfire forest structure between fire severity classes may create stark differences in security resources. Forests burned at a high severity experience the greatest amount of vegetation removal (Heinselman 1981, Turner et al. 1997), and therefore have less vertical vegetative structure for elk to use as security or thermal cover (Long et al. 2014, Lone et al. 2017). Shortly after a wildfire, the variability in vertical vegetative cover between fire severity classes may be most pronounced, as vegetation has not recovered, and horizontal visibility is high, thus leading to potential differences in susceptibility to predation and harvest (Greene et al. 2012). Thus, more information is needed to better understand how elk use recently burned forests as a function of fire severity and security resources, particularly during the autumn hunting seasons (Ciuti et al. 2012, Brodie et al. 2013, Thurjell et al. 2017).

Our objectives were to evaluate resource selection of female elk during autumn across fire severities in a recently burned landscape and determine whether selection varied across the autumn hunting seasons that represented differences in hunter pressure and method, and perceived risk to elk. We hypothesized that female elk resource selection would be related to wildfire severity throughout autumn because of increased forage resources and fire-induced reduction in vertical vegetative cover, which could lead to an increase in elk vulnerability to harvest through time. Therefore, we predicted that selection of burned conifer forests would be high in early autumn but decrease as hunter pressure increased. Further, we predicted that selection of low-severity burned forests would be greater than high-severity burned forests across all hunting seasons because of the limited cover in high-severity burned forests.

STUDY AREA

This study took place in west-central Montana, USA, in the Ovando-Seeley Lake area and focused on the 1,838-km² autumn range (24 Aug–1 Dec) of the Blackfoot-Clearwater (BC) elk population (Figure 1). The BC elk population was estimated at approximately 1,000 animals from 2018–2020 based upon aerial surveys (Montana Department of Fish, Wildlife and Parks 2023). Landownership within the autumn range consisted of privately owned property (20%) that

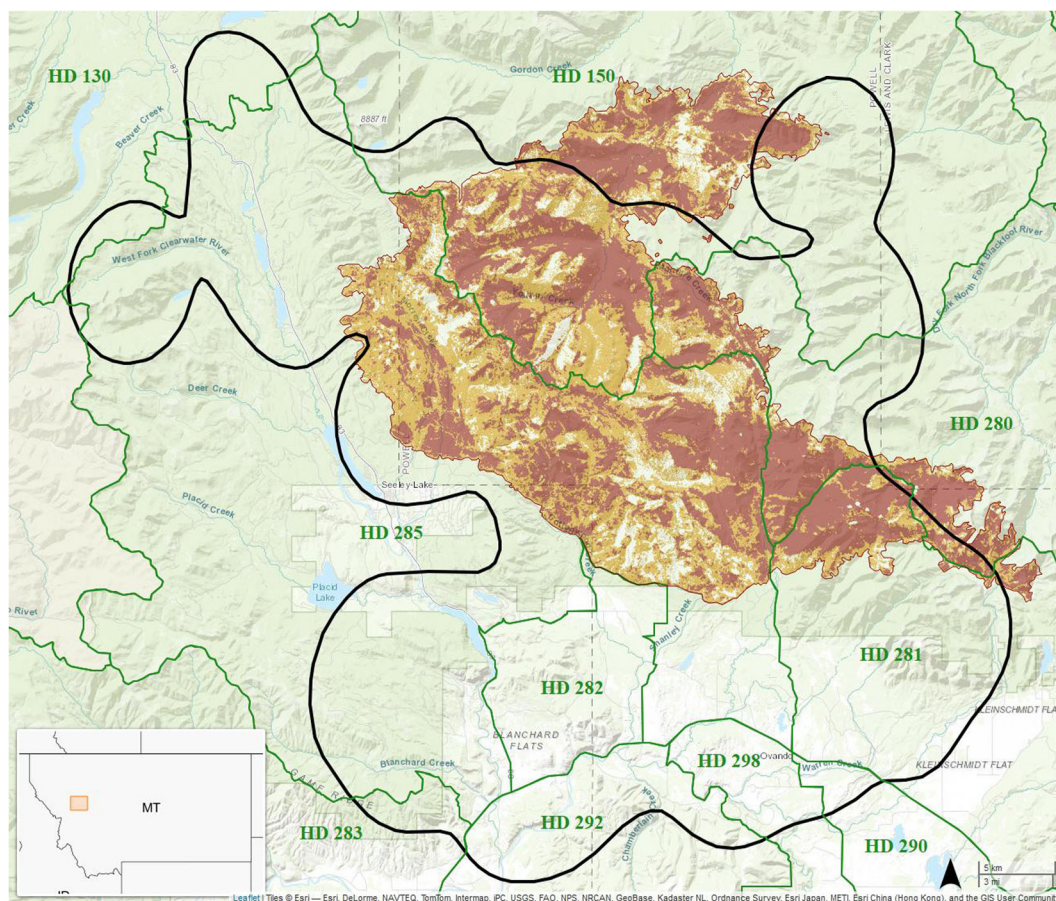


FIGURE 1 The Blackfoot-Clearwater elk population autumn range (22 Aug–1 Dec 2019–2020; black boundary), Rice Ridge Wildfire (dark red = high-severity burn, orange = low-severity burn), and hunting districts (HD; green boundaries) located in the Ovando–Seeley Lake area of west-central Montana, USA. Backcountry rifle hunting takes place in HDs 150 and 280, and HD 282 is by permit only for the rifle season.

primarily dominated the lower elevation areas, and publicly accessible federal lands (65%) and state lands (14%) found primarily in higher elevation areas. Elevations ranged from 1,132 m to 2,694 m with varied topography including flat bottomland, foothills, and steep and rugged mountain slopes. Mean autumn precipitation ranged from 35 mm in the valley to 153 mm on mountain summits, and mean temperature for the autumn was 4°C (PRISM Climate Group 2023).

Fire historically influenced 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 208 km² burning before 2010. From July through September 2017, approximately 29% of the elk population's autumn range was burned by the Rice Ridge Fire, which started because of a lightning strike. The approximately 623-km² mixed-severity fire included 46% low-severity and 54% high-severity burns and predominantly burned higher elevation public lands. 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*). Within the autumn elk range, 37% was classified as unburned conifer forest, and 14% and 16% were classified as low- and high-severity burned conifer forests, respectively. The main lower

elevation land cover types 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*). 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 BC elk population's autumn range spanned 10 hunting districts (HDs) with variable regulations influencing hunting timing, methods, and pressure (Table S1, available in Supporting Information). For the 8 front country HDs, archery hunting took place during a 6-week season in September and early October, followed by a 5-week general rifle hunting season during late October and November. For the 2 backcountry HDs (150 and 280), an approximately 1-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 (hunter days/km²), varied by HD and ranged from 0.051 to 6.60 hunter days/km² annually. For rifle season, hunter pressure ranged from 0.74 to 10.71 hunter days/km² annually (Table S1). Hunter pressure could not be parsed by elk sex; thus, these values represent the total hunter pressure for males and females combined.

METHODS

In December 2018 and February 2019, we captured and collared 19 adult female (≥ 1.5 years old) elk using helicopter net gunning or chemical immobilization. In December 2019, we captured and collared an additional 40 adult female elk. We outfitted elk with Iridium global positioning system (GPS) radio-collars (Lotek Wireless, model LiteTrack Iridium 420, New Market, ON, Canada) programmed to record a location every hour, transmit a mortality notification 6 hours post-mortality, and drop off after 2 years.

To understand elk resource selection throughout autumn, we divided elk location data into 4 periods based on hunting seasons: prehunt (no elk hunting in all HDs; 24 Aug–6 Sep 2019 and 22 Aug–4 Sep 2020), archery-only (only archery hunting allowed in all HDs; 7–14 Sep 2019 and 5–14 Sep 2020), backcountry rifle (both rifle and archery hunting in the backcountry [HDs 150 and 280], archery-only in other HDs; 15 Sep–25 Oct 2019 and 15 Sep–23 Oct 2020), and rifle (rifle hunting allowed in all HDs; 26 Oct–1 Dec 2019 and 24 Oct–29 Nov 2020). Front country districts had a 5-day break from all hunting activities (21–25 Oct 2019 and 19–23 Oct 2020), while backcountry districts still allowed hunting during these dates. We removed these dates from analysis to remain consistent regarding hunting method in districts during the backcountry rifle period.

We evaluated 10 covariates to describe the influences of nutritional, landscape, hunting, and environmental variables on elk resource selection during the 4 autumn periods for the BC elk population. For nutritional resources, we evaluated forage quality (digestible energy/g of forage; kcal/g) that we extracted from landscape models developed from elk diet and vegetation sampling conducted during the late summer and autumn (Snobl et al. 2022; S2, available in Supporting Information).

We evaluated 5 landscape variables that elk could use to reduce their vulnerability to harvest. We used the Rangeland Analysis Platform (Jones et al. 2018, Allred et al. 2021) to identify canopy cover of sites and designate areas of dense cover ($>40\%$ tree cover). We then calculated distance (m) to dense cover to identify how both canopy cover and distance from security cover influenced elk selection (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 for each hunt period (Hillis et al. 1991, Ranglack et al. 2017, Spitz et al. 2018, Lowrey et al. 2020). We log-transformed the distance to road measure because preliminary analyses suggested this variable form resulted in better model fit. To understand the influence of vertical vegetative structure on elk security, we used land cover type using the 2016 Montana Spatial Data Infrastructure land cover dataset (https://msl.mt.gov/geoinfo/msdi/land_use_land_cover/, accessed 1 Apr 2021) and the rapid assessment of vegetation condition after

wildfire product (<https://burnseverity.cr.usgs.gov/ravg/>, accessed 3 June 2021). We classified land cover 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 effect of terrain on elk resource selection, we used the vector ruggedness measure (i.e., ruggedness), which incorporates variation in aspect and slope to provide a unitless measure of terrain ruggedness (Sappington et al. 2007, Lowrey et al. 2020).

We considered 3 variables related to hunting that may affect elk resource selection: hunting method, hunter pressure, and hunter access. To evaluate the effects of 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 period model. 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 period, we used the number of hunter days/km² within each hunt district for each method to represent relative hunter pressure. For the backcountry rifle period, within the 8 front country hunting districts, we used the number of archery hunter days/km² and within the 2 backcountry rifle hunting districts we used the total number of rifle hunter days/km². We classified hunter access into accessible or inaccessible categories. We classified public lands that allowed hunting and any private lands enrolled in the State of Montana's Block Management Program as accessible. We classified privately owned lands with varying levels of restrictions on hunting access as inaccessible.

We evaluated 1 environmental covariate, snow water equivalent (SWE; m), to represent the influence of snowpack on elk selection. We calculated the maximum SWE value per pixel during each week using data from the Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center 2004). We screened all covariates for collinearity, and only included covariates with a Pearson's correlation coefficient <0.55 in resource selection models. For each hunt period model, we only included the covariates that were hypothesized to influence resource selection during that period.

For each hunt period, we fit a case control model with contaminated controls using use-availability data to estimate parameters of a resource selection probability function (RSPF; Lele 2009, Rota et al. 2013). An RSPF estimates the absolute probability of selection of a resource, which allows for a more meaningful interpretation of selection compared to relative probability, particularly when baseline probabilities are near 0 or 1 (Rota et al. 2013).

For use data, we retained GPS locations for elk that were alive and collared for at least half of the period 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 5-hour interval between relocations (Hansteen et al. 1997) and included a random intercept term by unique elk identification (Gillies et al. 2006). We used a 5-hour interval to stagger location times, resulting in approximately the same number of locations from each hour of the day throughout the sampling period.

We identified available points within the population-level autumn home range (24 Aug–1 Dec; second-order selection [Johnson 1980]) using a 95% kernel density estimator contour based on the combined individual locations using the *adehabitatHR* package (Calenge 2006) in Program R (R Core Team 2022). We randomly generated available points for individuals at a 1:5 (used:available) ratio for each hunt period (Northrup et al. 2013, Lula et al. 2020) and assigned a week value to each random location such that the number of available locations was equivalent to 5 times the number of used locations that week. We used the week value to assign appropriate time-varying covariates, such as maximum SWE, for each used and available location. Evaluating resource selection at the second-order scale allowed us to address our primary objective of identifying how the burn and burn severity affected elk resource selection in autumn.

We estimated the absolute probability that an elk selected location i (ψ_i) as:

$$\psi_i = \frac{\exp(\beta_0 + \ln\left(\frac{n_i}{n_{na}} + 1\right) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})}{1 + \exp(\beta_0 + \ln\left(\frac{n_i}{n_{na}} + 1\right) + \beta_1 x_{i1} + \dots + \beta_j x_{ij})} \quad (1)$$

where β_0 was the intercept parameter, n_1 was the number of used locations in the analysis, n_a was the number of available locations in the analysis, π was a prevalence term equivalent to the average probability of use by elk across sample units, and β_1, \dots, β_j were the parameter coefficients associated with the j covariates (Rota et al. 2013). We fit 1 global RSPF model for each hunt period within a Bayesian framework using the R2jags package (Su and Yajima 2015) in R. We included unique elk identification (elk year) as a random effect so that a separate model intercept was calculated for each elk (β_{0e}), drawn from a normal distribution with a population mean μ_{β_0} and standard deviation σ_{β_0} : $\beta_{0e} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2)$. We used slightly informative hyperpriors (e.g., $\mu_{\beta_0} \sim N[0, 1]$; $\sigma_{\beta_0} \sim \text{Unif}[0, 10]$) to allow adequate sampling of parameter space, while being constrained to reasonable values. This structure prevented the model from estimating extremely large or small coefficients for land cover categories that were almost exclusively selected or avoided, thereby improving model fit. We included centered and scaled covariates described above as fixed effects predictors in models using similar priors as the intercept ($\beta_j \sim N[0, 1]$) and included prevalence as a fixed term with a vague prior ($\pi \sim \text{Unif}[0.001, 1]$) to allow for broad sampling of parameter space.

We estimated posterior distributions of predictors by running 3 Markov chain Monte Carlo chains, each for 25,000–50,000 iterations, with a burn-in of 10,000, 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 and by visually inspecting posterior distributions for adequate mixing. We also used posterior predictive checks to calculate a Bayesian p -value (p_B) to assess model fit, assuming $0.1 < p_B < 0.9$ represented adequate fit (Gelman et al. 2014).

RESULTS

Canopy cover and distance to dense canopy cover covariates were highly correlated (Pearson's correlation coefficient >0.55) for all hunt period models so we included only canopy cover in final models, given preliminary analyses suggested this variable improved model fit. Hunter access and land cover type were also highly correlated; thus, we only retained land cover type for modeling, given our main question focused on the effects of fire severity on elk resource selection.

Prehunt period

We modeled female elk resource selection for the prehunt period based on 3,258 used locations and 16,290 available locations from 46 elk. All parameters in the model adequately converged ($\hat{R} \leq 1.1$) and the Bayesian p -value suggested adequate model fit ($p_B = 0.68$). The model-estimated mean prevalence was 0.45 (95% credible interval [CrI] = 0.43–0.47). The population-level mean intercept was -0.44 (95% CrI = -1.13 – 0.25) and the standard deviation across individuals was 2.50 (95% CrI = 2.01–3.11; Figure S3, available in Supporting Information).

During the prehunt period, female elk had a slightly higher log odds of selecting high-severity burns ($\beta = 6.13$; 95% CrI = 5.30–7.06) over low-severity burns ($\beta = 5.60$; 95% CrI = 4.75–6.56; Table 1); however, the resulting absolute probability of elk selecting high (1.00; 95% CrI = 0.99–1.00) and low-severity burns (0.99; 95% CrI = 0.98–1.00) did not differ (Figure 2). Comparatively, the probability of elk selecting unburned, open, closed, and other land cover types was 0.40 (95% CrI = 0.25–0.58), 0.0064 (95% CrI = 0.00023–0.014), 0.041 (95% CrI = 0.0020–0.075), and 0.045 (95% CrI = 0.023–0.085), respectively. Female elk also selected areas farther from roads with higher digestible energy (Table 1; Figure 2).

TABLE 1 Parameter estimates, 95% credible intervals (2.5–97.5%; LCL and UCL), and random effect standard deviation (σ) for covariates included in resource selection probability functions for female elk in the Blackfoot-Clearwater elk population in west-central Montana, USA, during 4 autumn hunt periods in 2019 and 2020. Hunt periods included prehunt (24 Aug–6 Sep 2019 and 22 Aug–4 Sep 2020), archery-only (7–14 Sep 2019 and 5–14 Sep 2020), backcountry rifle (15 Sep–25 Oct 2019 and 15 Sep–23 Oct 2020), and rifle (26 Oct–1 Dec 2019 and 24 Oct–29 Nov 2020). Continuous covariates were centered and scaled, and the intercept term represents unburned forest (prehunt, archery-only, and rifle periods) or unburned forest in hunting districts with only archery hunting methods (backcountry rifle period). Land cover types (land) include unburned conifer forest (unburned; reference category); low-severity burned conifer forest (low); high-severity burned conifer forest (high); grasslands, agriculture, and shrublands (open); deciduous forests and riparian areas (closed); and forests burned or harvested between 2002–2017 (other).

Hunt period	Covariate	Estimate	LCL	UCL	σ
Prehunt	Intercept	-0.44	-1.13	0.25	2.50
	Canopy cover	-0.11	-0.27	0.049	
	Ruggedness	0.11	-0.039	0.28	
	Digestible energy	0.77	0.57	0.98	
	Distance to road	0.38	0.18	0.58	
	Land: low	5.60	4.75	6.56	
	Land: high	6.13	5.30	7.06	
	Land: open	-4.69	-5.53	-3.90	
	Land: closed	-2.79	-3.34	-2.26	
	Land: other	-2.70	-3.29	-2.13	
Archery-only	Intercept	-1.28	-2.26	-0.26	3.98
	Canopy cover	0.070	-0.15	0.28	
	Ruggedness	0.087	-0.10	0.30	
	Digestible energy	0.47	0.24	0.72	
	Distance to road	2.73	2.36	3.12	
	Hunter pressure	0.60	0.17	1.01	
	Land: low	5.96	5.17	6.80	
	Land: high	7.37	6.56	8.20	
	Land: open	-2.47	-3.40	-1.61	
	Land: closed	-0.89	-1.57	-0.22	
Land: other	-0.87	-1.58	-0.16		
Backcountry rifle	Intercept	0.21	-0.53	0.94	2.94
	Canopy cover	-0.092	-0.18	-0.0066	
	Ruggedness	0.20	0.10	0.31	
	Digestible energy	0.23	0.11	0.36	
	Distance to road	0.81	0.67	0.95	
	Hunter pressure	0.92	0.78	1.07	
	Snow water equivalent	-0.84	-0.96	-0.72	

TABLE 1 (Continued)

Hunt period	Covariate	Estimate	LCL	UCL	σ
Rifle	Hunt method: rifle	-5.39	-5.80	-4.97	0.83
	Land: low	5.15	4.77	5.55	
	Land: high	5.28	4.90	5.67	
	Land: open	0.015	-0.27	0.30	
	Land: closed	0.0054	-0.26	0.26	
	Land: other	-1.47	-1.80	-1.15	
	Intercept	-6.61	-6.92	-6.28	
	Canopy cover	-0.49	-0.54	-0.44	
	Ruggedness	-0.0095	-0.069	0.047	
	Digestible energy	-0.29	-0.37	-0.22	
	Distance to road	-0.063	-0.12	-0.0031	
	Hunter pressure	-1.71	-1.79	-1.64	
	Snow water equivalent	-3.96	-4.22	-3.71	
	Land: low	-0.31	-0.61	-0.0076	
	Land: high	-2.54	-2.97	-2.13	
	Land: open	2.02	1.80	2.24	
	Land: closed	0.76	0.60	0.93	
	Land: other	0.53	0.36	0.69	

Archery-only period

We modeled female elk resource selection for the archery-only hunt period using 2,213 used locations and 11,065 available locations from 46 elk. All hyper-parameters in the model adequately converged and the Bayesian p -value suggested adequate model fit ($p_B = 0.76$). The model-estimated mean prevalence was 0.45 (95% CrI = 0.42–0.48). The population-level mean intercept was -1.28 (95% CrI = -2.26 – -0.26) and the standard deviation across individuals was 3.98 (95% CrI = 3.17–5.01; Figure S3).

Similar to the prehunt period, female elk during the archery-only period had higher log odds of selecting high-severity burned forests ($\beta = 7.37$; 95% CrI = 6.56–8.20) over low-severity burned forests ($\beta = 5.96$; 95% CrI = 5.17–6.80), but the absolute probability of selecting low-severity (0.99; 95% CrI = 0.97–1.00) or high-severity burned forests (1.00; 95% CrI = 0.99–1.00) was not different (Table 1; Figure 3). Comparatively, the probability of elk selecting unburned, open, closed, and other land cover types was 0.23 (95% CrI = 0.095–0.43), 0.027 (95% CrI = 0.0069–0.072), 0.11 (95% CrI = 0.037–0.25), and 0.12 (95% CrI = 0.037–0.25), respectively. Female elk also selected areas farther from roads with higher hunter pressure and higher digestible energy (Table 1; Figure 3).

Backcountry rifle period

We modeled female elk resource selection for the backcountry rifle hunt period using 7,933 used locations and 39,665 available locations from 46 animals. All hyper-parameters in the model adequately converged; although, the

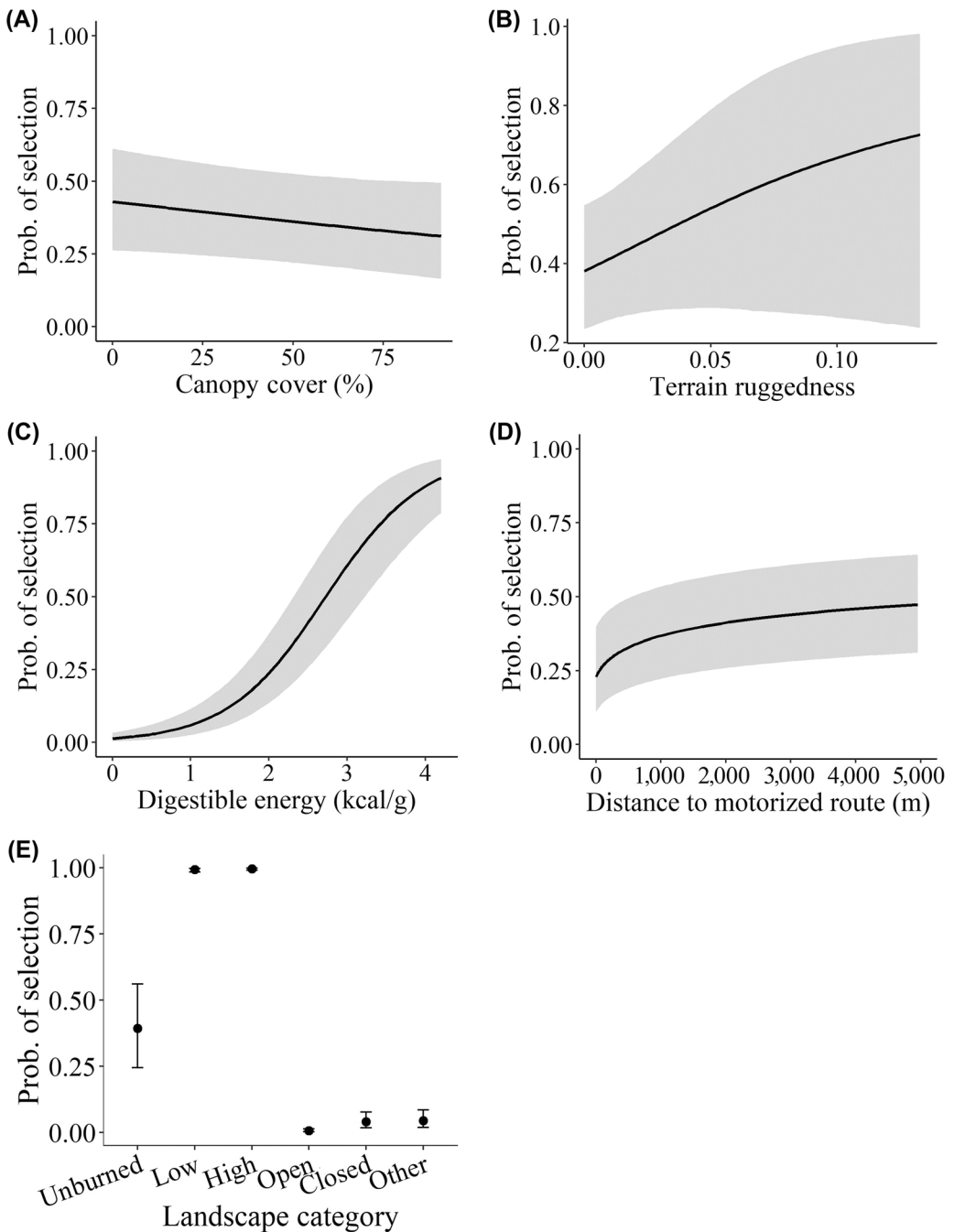


FIGURE 2 Estimated probability (prob.) of female elk selection during the prehunt period (24 Aug–6 Sep 2019 and 22 Aug–4 Sep 2020) as a function of A) canopy cover, B) terrain ruggedness, C) digestible energy, D) distance to open motorized route, and E) land cover category (unburned = unburned conifer forest; low = low-severity burned conifer forest; high = high-severity burned conifer forest; open = grasslands, agriculture, and shrublands; closed = deciduous forests and riparian areas; other = forests burned or harvested between 2002–2017) for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019–2020. Panels A–D assume all other continuous covariates are fixed at their mean observed value, and selection occurs in unburned forests. Mean estimates are represented by the black line or dots and the 95% credible intervals are represented by the gray ribbons or error bars.

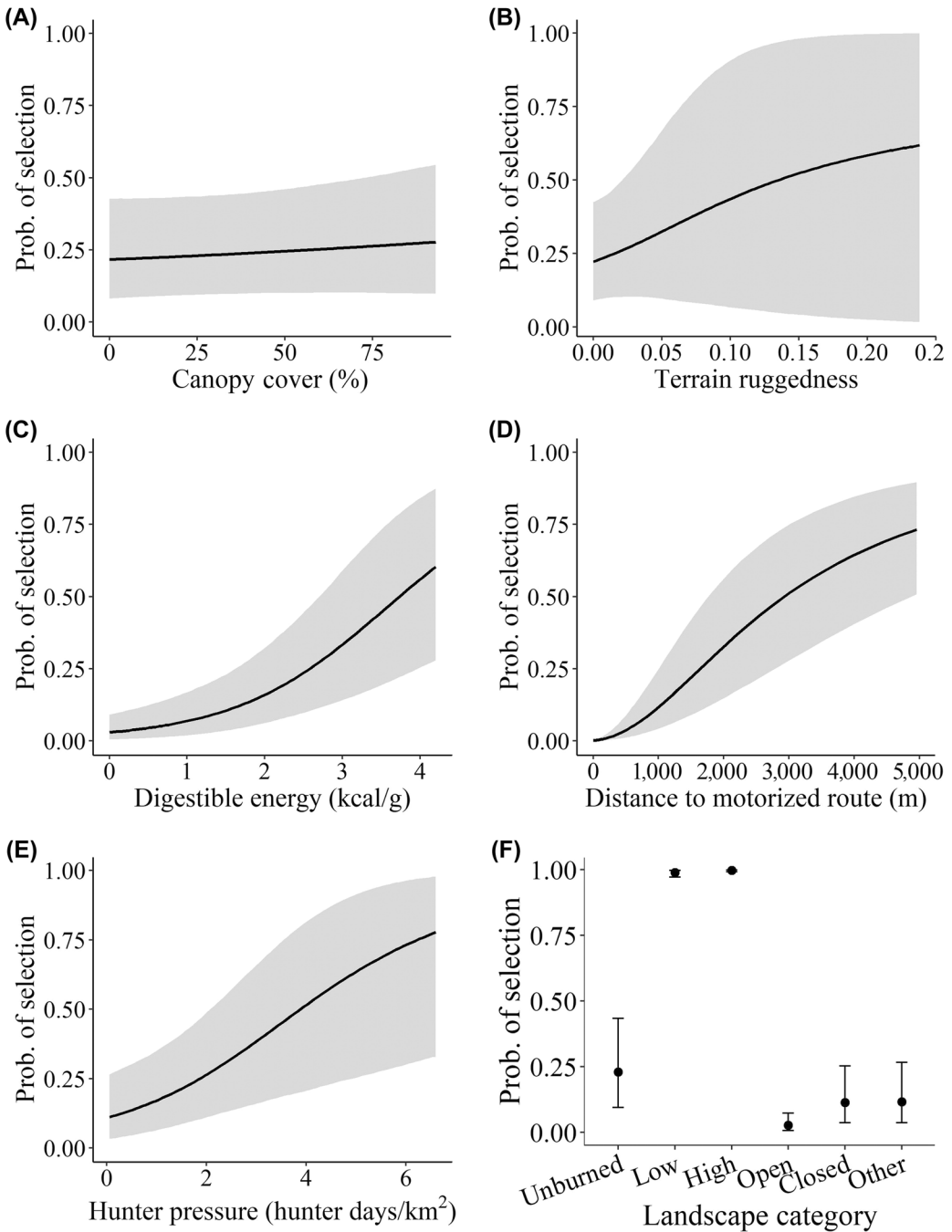


FIGURE 3 Estimated probability (prob.) of female elk selection during the archery period (7–14 Sep 2019 and 5–14 Sep 2020) as a function of A) canopy cover, B) terrain ruggedness, C) digestible energy, D) distance to open motorized route, E) hunter pressure, and F) land cover category (unburned = unburned conifer forest; low = low-severity burned conifer forest; high = high-severity burned conifer forest; open = grasslands, agriculture, and shrublands; closed = deciduous forests and riparian areas; other = forests burned or harvested between 2002–2017) for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019–2020. Panels A–E assume all other continuous covariates are fixed at their mean observed value, and selection occurs in unburned forests. Mean estimates are represented by the black line or dots and the 95% credible intervals are represented by the gray ribbons or error bars.

Bayesian p -value suggested inadequate model fit ($p_B = 0.999$). The model estimated mean prevalence was 0.48 (95% CrI = 0.46–0.49). The population-level mean intercept was 0.21 (95% CrI = -0.53–0.94) and the standard deviation across individuals was 2.94 (95% CrI = 2.39–3.63; Figure S3).

Similar to the prehunt and archery-only periods, female elk during the backcountry rifle period had the highest log odds of selecting high-severity ($\beta = 5.28$; 95% CrI = 4.90–5.67) and low-severity burned forests ($\beta = 5.15$; 95% CrI = 4.77–5.55) compared to other land cover types (Table 1; Figure 4). Further, female elk had lower log odds of selecting sites that allowed both archery and rifle hunting methods ($\beta = -5.39$; 95% CrI = -5.80–-4.97), compared to sites with only archery hunting methods. For example, the probability of female elk selecting low-severity burn forests in rifle hunting areas was 0.49 (95% CrI = 0.30–0.69), while the probability of selecting low-severity burn forests in archery-only areas was 0.99 (95% CrI = 0.99–1.00; Figure 4). Female elk also selected areas with lower SWE ($\beta = -0.84$; 95% CrI = -0.96–-0.72) and higher hunter pressure ($\beta = 0.92$; 95% CrI = 0.78–1.07), as well as areas farther from roads with higher digestible energy, lower canopy cover, and more rugged terrain (Table 1; Figure 4).

Rifle period

We modeled female elk resource selection for the rifle hunt period using 8,707 used locations and 43,535 available locations from 43 animals. All hyper-parameters in the model adequately converged ($\hat{R} \leq 1.1$; Gelman et al. 2014) and the Bayesian p -value suggested adequate model fit ($p_B = 0.79$). The model estimated mean prevalence was much lower than other periods, at 0.027 (95% CrI = 0.021–0.033). The population-level mean intercept was -6.61 (95% CrI = -6.92–-6.28) and the standard deviation across individuals was 0.83 (95% CrI = 0.67–1.04; Figure S3).

In contrast to the other 3 periods, elk had higher log odds of selecting open ($\beta = 2.02$; 95% CrI = 1.80–2.24) or closed ($\beta = 0.76$; 95% CrI = 0.60–0.93) land cover types, compared to low- ($\beta = -0.30$; 95% CrI = -0.61–-0.0076) or high-severity burned forests ($\beta = -2.54$; 95% CrI = -2.97–-2.13; Table 1). Low prevalence throughout the autumn range, due to elk congregating in HDs with lower hunter pressure during the rifle period (i.e., HD 282), resulted in low absolute probabilities of elk selecting any land cover category (Figures 5 and 6). Female elk selection during the rifle period was largely influenced by avoidance of areas with high SWE ($\beta = -3.96$; 95% CrI = -4.22–-3.71) and hunter pressure ($\beta = -1.71$; 95% CrI = -1.79–-1.64). Elk also selected areas closer to roads with lower canopy cover and lower digestible energy (Table 1; Figure 5).

DISCUSSION

In years 2 and 3 postfire, female elk shifted selection of both low- and high-severity burned forests during the prehunt, archery-only, and backcountry rifle hunt periods to open areas with less snowpack and less hunter pressure during the rifle hunt period (Figure 6). This pattern of selection was likely related to a variety of factors, including nutritional requirements during early autumn, traditional movements out of high-elevation areas to winter range with less snowpack, and avoidance of risk from human hunters.

Contrary to our predictions, there were not large differences in female elk selection of different fire severities during any hunt period. During the prehunt and archery-only periods, female elk may have been attracted to all burned areas because of the increase in foraging efficiency (Canon et al. 1987) that would support their nutritional demands for pregnancy, lactation, and overwinter survival (Cook et al. 2004). Overall, wildfire improved the forage quality in conifer forests in our study area, and there were not large differences in forage quality between low- and high-severity burned forests (Snobl et al. 2022). This result was likely due to the overall high proportion of burned sites that contained fireweed (*Chamerion angustifolium*), an important forage species with high forage quality that rapidly establishes and spreads postfire in both low- and high-severity burns. Forage quality could potentially differ

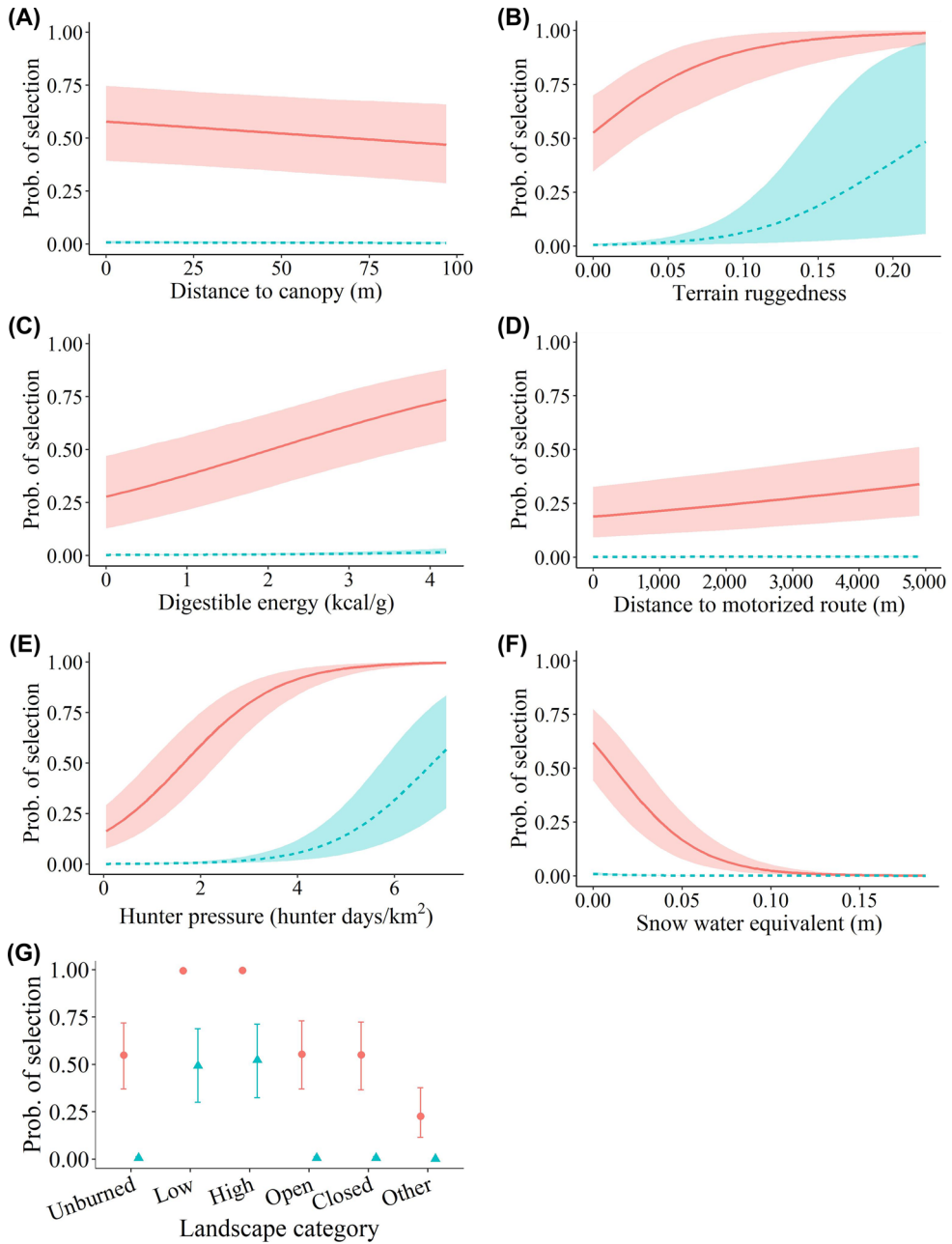


FIGURE 4 Estimated probability (prob.) of female elk selection during the backcountry rifle period (15 Sep–25 Oct 2019 and 15 Sep–23 Oct 2020) as a function of A) canopy cover, B) terrain ruggedness, C) digestible energy, D) distance to open motorized route, E) hunter pressure, F) snow water equivalent, and G) land cover category (unburned = unburned conifer forest; low = low-severity burned conifer forest; high = high-severity burned conifer forest; open = grasslands, agriculture, and shrublands; closed = deciduous forests and riparian areas; other = forests burned or harvested between 2002–2017) for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019–2020. Panels A–F assume all other continuous covariates are fixed at their mean observed value, and selection occurs in unburned forests in districts that either have archery-only hunting (red, solid lines or circles) or the option of rifle hunting (blue, dashed lines or triangles). Mean estimates are represented by lines, dots, or triangles and the 95% credible intervals are represented by ribbons or error bars.

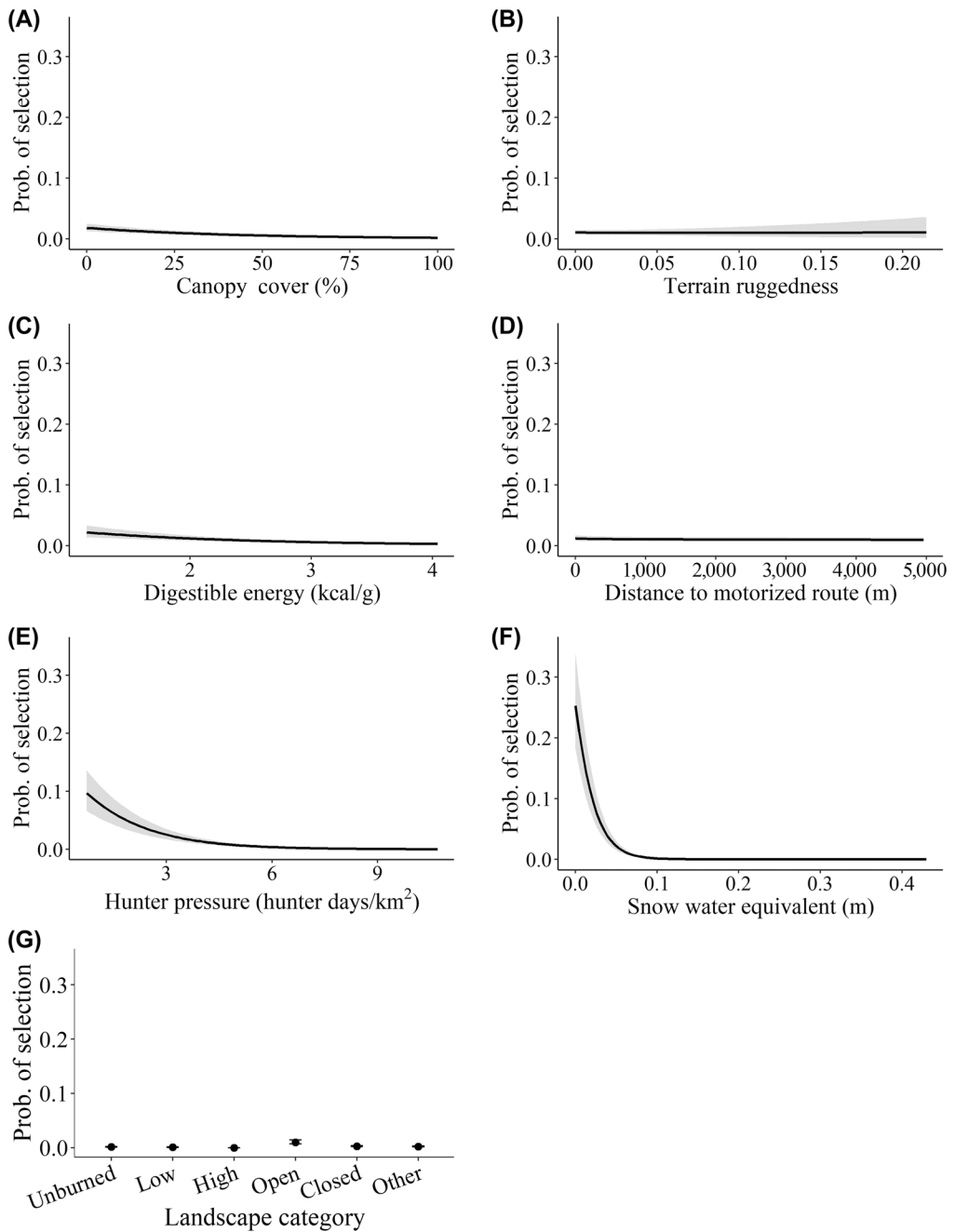


FIGURE 5 Estimated probability (prob.) of female elk selection during the rifle period (26 Oct–1 Dec 2019 and 24 Oct–29 Nov 2020) as a function of A) canopy cover, B) terrain ruggedness, C) digestible energy, D) distance to open motorized route, E) hunter pressure, F) snow water equivalent, and G) land cover category (unburned = unburned conifer forest; low = low-severity burned conifer forest; high = high-severity burned conifer forest; open = grasslands, agriculture, and shrublands; closed = deciduous forests and riparian areas; other = forests burned or harvested between 2002–2017) for the Blackfoot-Clearwater elk population in west-central Montana, USA, 2019–2020. Panels A–F assume all other continuous covariates are fixed at their mean observed value, and selection occurs in open land cover types. Mean estimates are represented by the black line or dots and the 95% credible intervals are represented by the gray ribbons or error bars.

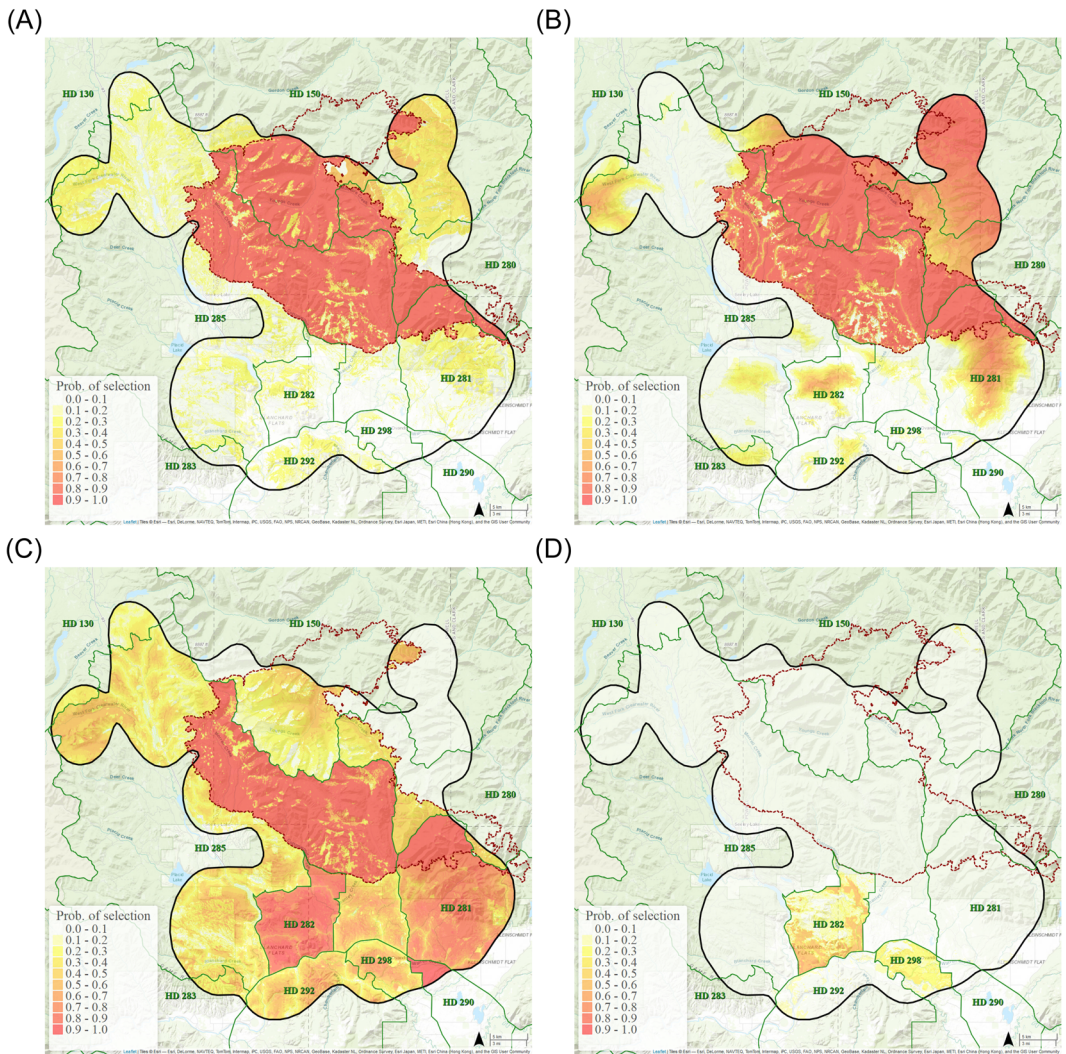


FIGURE 6 Predicted absolute probability (prob.) of female elk selection during the prehunt (panel A), archery-only (panel B), backcountry rifle (panel C), and rifle (panel D) hunt periods for the Blackfoot-Clearwater elk population from 2019–2020 in west-central Montana, USA. Black lines represent the boundary of elk autumn home range; green lines represent hunting district (HD) borders; red, dashed lines represent the border of the Rice Ridge wildfire; and color gradients represent low (white) to high (dark red) probability of elk selection.

between low- and high-severity burned forests in the future as vegetation regenerates at varying paces, altering the composition and phenology of vegetation communities (Turner et al. 1999, Kane et al. 2013). In turn, elk may alter their selection of low- and high-severity burned forests to select areas with the greatest nutritional return.

Female elk selected low- and high-severity burned conifer forests with higher hunter pressure during the archery-only period, which opposes our prediction that elk selection of burned forests would decrease as hunter pressure increased. During the prehunt period, elk did not experience any hunter pressure, so risk of elk mortality was relatively low. Thus, elk were able to select burned forests of either fire severity category, where higher forage quality occurred, regardless of the reduced cover (Spitz et al. 2018). Hunter pressure increased during the archery-only periods; however, this pressure may have been low enough, particularly in rugged, difficult to access areas, that elk did not perceive enough risk to leave these high forage quality sites, where hunter pressure was higher. Elk also

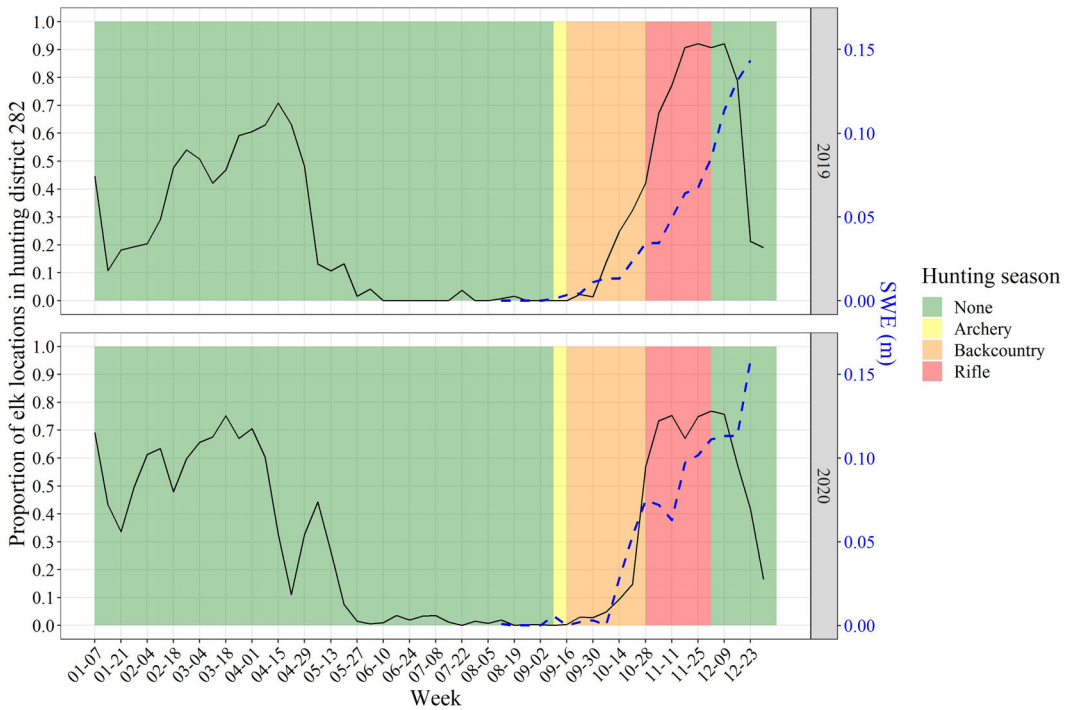


FIGURE 7 Proportion of female elk locations within hunting district 282 by week in 2019 and 2020 in the Blackfoot-Clearwater region of west-central Montana, USA (black lines). Blue, dashed lines on the secondary axis represent mean snow water equivalent (SWE; m) by week (only shown from mid-August to 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. Rifle season in HD 282 closed on 10 November, which was roughly 3 weeks earlier than other HDs. Decreases in proportion of elk locations in hunting district 282 in mid-December were likely due to elk capture efforts in the area at that time.

may have selected burned areas during archery-only hunt periods because the rugged terrain made it more difficult for hunters to access (Thurfjell et al. 2017, Lowrey et al. 2020); however, female elk selected rugged terrain before hunting seasons started, which suggests elk were selecting these sites for forage resources and not solely to avoid hunters.

Elk continued to select burned forests and areas with higher hunter pressure during the backcountry rifle period but also selected areas with archery-only hunting methods, which could be explained by multiple temporally confounded mechanisms. Similar to the archery period, hunter pressure during the backcountry rifle period may have been low enough to not have strong negative effects on elk selection in districts that only allowed archery methods. Elk may have avoided the backcountry HDs that allowed rifle hunting because of hunters; however, these districts had the lowest hunter pressure (<1 hunter days/km²) of all districts, and snow also began accumulating during the backcountry rifle period (Figure 7). The SWE covariate in our backcountry rifle model had a strong negative influence on elk selection, suggesting elk may have started avoiding the backcountry HDs because of snowpack, rather than solely hunter pressure. Snow cover can affect elk selection (Poole and Mowat 2005, Messer et al. 2009) because of the restricted availability of forage and increased energetic costs (Parker et al. 1984). Thus, elk movements out of areas with increasing snowpack was likely a traditional movement towards winter range, where forage resources were more available.

Backcountry rifle model diagnostics suggested a lack of fit, which we attribute to strong inter-individual variation in selection patterns (Paterson et al. 2022) and temporal variation in elk selection during that period. Elk began moving from summer and autumn range in the high-elevation mountains to winter range in the valley during the backcountry rifle period (Figure 7), so there was considerable intra-individual variation in selection patterns throughout the period. As such, we caution interpretation of model results during the backcountry rifle period and suggest analyses at finer temporal scales may better explain elk selection during this dynamic time.

During the rifle period, female elk changed selection patterns, moving out of burned areas into mostly open land cover types in HDs with low hunter pressure (primarily HD 282; Figure 6). Similar to the backcountry rifle period, there were likely multiple mechanisms causing this shift in selection. It is well-known that risk of human harvest can affect elk resource selection (Proffitt et al. 2009, 2010; Cleveland et al. 2012; Ranglack et al. 2017), with elk selecting lands with less hunter pressure or areas with more vertical vegetative cover to reduce their susceptibility to harvest (Conner et al. 2001, Skovlin et al. 2002, Proffitt et al. 2013, Long et al. 2014, Lone et al. 2017). Thus, elk selection of areas with less hunter pressure could be partially explained by avoidance of hunters as hunter pressure and susceptibility to harvest via rifle methods increased; however, the SWE covariate was the most influential continuous covariate on elk selection, with hunter pressure a close second, during the rifle period. Unfortunately, the concurrent timing of snowfall and rifle season make it challenging to disentangle the importance of these 2 variables on elk movements (Figure 7). Previous research on elk in the Blackfoot Valley reported that elk wintering within HD 282, a district with more restrictive harvest regulations than adjacent districts, moved to winter range toward the beginning of rifle season. In contrast, elk wintering within the adjacent HD 280, a district with more liberal harvest regulations than HD 282, moved away from winter range at the beginning of rifle season, toward areas inaccessible to hunters in dense timber (Hurley 1994). Further, Hurley (1994) reported that elk wintering in HD 282 moved out of the HD in years with higher hunting pressure (i.e., more permits allocated in that HD). Our findings and those of Hurley (1994) suggest hunter pressure plays an important role in elk movements during the rifle period and that a combination of snowpack and hunter pressure likely reduced the importance of burned forests to elk in our study area during this period.

Previous research reported that elk avoid areas close to roads (Ranglack et al. 2017, Spitz et al. 2018, Lowrey et al. 2020) and open areas (Thurfjell et al. 2017, Lowrey et al. 2020) during the rifle season, but we found the opposite. One potential explanation is that our road and land cover covariates were confounded with other covariates such as SWE and hunter pressure. Road density was lowest in high-elevation areas located partially within federally designated wilderness with greater snowpack, and highest in low-elevation areas with less snowpack. Additionally, open areas often occurred in areas with less hunter pressure (either private lands or lands with restricted permits). Thus, elk selection for open areas closer to roads during the rifle season may have been a result of elk transitioning out of their higher elevation, backcountry summer range (farther from roads) to their lower elevation, front country winter range (closer to roads) where there was less snow and refuge from hunters. By reducing their exposure to high hunter pressure, elk may have selected open areas, such as grasslands, to access forage without increasing their susceptibility to harvest (Proffitt et al. 2010, Sergeev et al. 2020).

We evaluated the effects of wildfire severity on female elk resource selection during the hunting season. Although elk demonstrated substantial variability in selection, there was strong evidence that elk selected for low- and high-severity burned conifer forests in years 2 and 3 postfire during prehunt, archery, and backcountry rifle hunt periods. Selection for all fire severities during these periods was likely due to the high forage quality in burned areas (Snobl et al. 2022); however, elk habitat and resource selection may differ in the future in our study area as low- and high-severity burned forests move through successional stages at varying paces (Proffitt et al. 2019). Elk became more predictable during the rifle period, primarily moving out of burned forests to areas with less snowpack and hunter pressure; thereby, resulting in lower elk prevalence across the autumn range. However, we could not fully disentangle the contribution of each of these covariates on elk resource selection, given their concurrent timing. Resource selection analyses at finer spatial and temporal scales (e.g., third-order selection; Johnson et al. 1980) that also consider timing of selection (e.g., day vs. night) could help elucidate the

relative importance of these variables and the importance of scale on elk resource selection during this period. Our findings are largely influenced by the location of the wildfire and hunting risk, in relation to elk seasonal ranges. The Rice Ridge fire burned primarily in higher elevation elk summer range, and there was low hunter pressure within the HD 282 portion of the winter range. Thus, it is unsurprising that elk selected burned areas during summer and early autumn, then moved from burned areas to HD 282 in late autumn. The importance and timing of elk selection of recently burned areas may differ in regions where other seasonal ranges are burned (e.g., winter range) or where hunter pressure differs. Thus, while our findings are an important first step in understanding elk selection of a variety of wildfire severities during hunting seasons, we recommend consideration of these factors before making elk management decisions in other areas of the Intermountain West.

MANAGEMENT IMPLICATIONS

In years 2 and 3 post wildfire, female elk selected low- and high-severity burned forests during early autumn, suggesting that the presence of recent wildfires has the potential to alter the distribution of elk. Elk disproportionately selected burned forests in early autumn and hunter pressure did not strongly affect elk selection of burned forests during this period. Thus, managers may not need to consider the effects of wildfire when making early-season (i.e., archery-only season) hunting regulations at the levels of hunting pressure we observed. By the onset of the rifle hunting period, when hunter pressure was relatively high in all districts except HD 282, elk selection of burned forests started to decrease, likely because the fire burned on high-elevation summer ranges and elk began transitioning out of the burn towards lower elevation winter ranges with less snowpack. Hunter pressure also contributed to these movements, highlighting the need for wildlife managers to carefully consider how different harvest management regulations may result in differences in hunter pressure across the landscape, and their consequences on elk distributions. Managers may also consider the use of prescribed fires within the autumn range of elk as a tool to influence the distribution of forage, and elk.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We captured elk by a combination of helicopter net gunning and chemical immobilization following approved Montana Fish, Wildlife & Parks animal capture protocols (FWP13-2018).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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