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Received: 22 May 2025 | Revised: 21 November 2025 | Accepted: 29 December 2025

DOI: 10.1002/jwmg.70170

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Evaluating the impact of hunter access and harvest regulations on elk movement and resource selection

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Funding information
Federal Aid in Wildlife Restoration Grant, Grant/Award Number: W-179-R; Department of Interior Secretarial Order #3362, Grant/Award Number: F19AP00849

Abstract

Wildlife managers in many parts of the western United States are tasked with managing elk (*Cervus canadensis*) populations that exceed population goals and strain public and landowner tolerance with problematic distributions. Reducing these populations through hunter harvest and achieving desirable distributions can be challenging in mixed landscapes of public and private lands where decisions to allow hunter access vary among landowners. We used global positioning system (GPS) data from 58 female elk in the Devil's Kitchen elk population in central Montana, USA, to evaluate how hunter access, harvest regulation, and other landscape factors influence elk movements and resource selection during a multi-phase hunting season. We fit Bayesian multistate models to evaluate factors influencing the daily probability of an elk transitioning between areas with different hunter access strategies, then constructed resource selection functions describing female elk resource selection in relation to hunter access, harvest regulation, and other landscape factors in 4 distinct periods during the hunting season. Our results indicate that elk were likely to transition between hunter access strategies during each hunting period, and the direction of their transitions appeared to be influenced by both hunter access and harvest regulations. Elk responded dynamically to harvest risk throughout the hunting season, generally selecting for less accessible hunter access strategies and more restrictive harvest regulations. Although elk moved to less accessible private lands in the early shoulder and archery seasons, restrictive regulations on open access public lands during the general season appeared to drive elk movements towards those public lands. A combination of restricted hunter access and harvest regulations maintained elk on those public lands through the late shoulder season, reducing conflict with private landowners in the area.

KEYWORDS

Cervus canadensis, distribution, harvest regulations, hunter access, management, resource selection, transition matrix

In many parts of the western United States, elk (*Cervus canadensis*) populations exceed numeric population objectives managed by wildlife management agencies, causing conflict with landowners and straining public tolerance (Krausman and Bleich 2013). This management challenge is most pressing where elk distributions overlap with private agricultural lands because of concerns over crop depredation, competition with livestock, disease transmission, and other property damage (Haggerty and Travis 2006, Walter et al. 2011). The primary tool available to reduce survival rates and decrease overabundant populations is the liberalization of adult female harvest regulations (Sinclair et al. 2006, Loe et al. 2016, Gruntorad and Chizinski 2020), as the population dynamics of elk and other large ungulate species are largely driven by adult female survival rates (Gaillard et al. 2000, Eacker et al. 2017). Wildlife managers may also develop harvest regulations and other management tools to create more desirable elk distributions that reduce conflict with private landowners (Cromsigt et al. 2013, Jones et al. 2021). Although the wildlife on private lands in the United States is a public resource managed in the public trust by wildlife agencies (Mahoney and Geist 2019), public access to private lands for hunting is provided at the discretion of individual landowners. Therefore, when elk distributions overlap private lands, manipulating elk distributions or reducing elk abundance through hunter harvest can be challenging because of the varying decisions to allow hunter access made by individual landowners (Haggerty and Travis 2006, Proffitt et al. 2016).

In the western United States, hunting access differs across the landscape and throughout the hunting season. Private landowner decisions around the level of hunting access they allow may be tied to personal values surrounding hunting, wildlife management, and the role of elk on the landscape, and economic realities and incentives (Haggerty and Travis 2006). Landowners may choose to allow hunting access only for friends and family, in exchange for a trespass or access fee, or to members of the public who inquire. Some may participate in state-managed partnerships that incentivize free public hunting access on private lands, and some may not allow hunting of any kind. It follows that such a matrix of hunter access can create a gradient of harvest risk on the landscape even if hunting regulations are the same across the landscape. Ample evidence suggests that elk respond to this gradient of risk with shifts in behavior (Burcham et al. 1999, Cleveland et al. 2012, Proffitt et al. 2013, Sergeyev et al. 2022). Public lands that are freely accessible to the public may be relatively high-risk areas for elk during hunting season, whereas private lands with varying degrees of hunting access restrictions may be relatively lower risk areas. Although many studies have shown that elk preferentially select for areas that restrict hunting access where available (Burcham et al. 1999; Conner et al. 2001; Proffitt et al. 2010, 2013; Sergeyev et al. 2020), our understanding of the factors that influence elk movement between areas with different strategies of hunter access remains limited.

Managers seeking to alleviate conflict with landowners by reducing overabundant elk populations may adjust harvest regulations to increase the number of female elk hunting licenses available, change permitted weapons, institute alternative season structures, or extend the period of legal harvest. However, changes in harvest regulation structure alone may not result in population reductions. Variable human hunting pressure can alter the way elk move across the landscape and use resources during the hunting season (Vieira et al. 2003, Proffitt et al. 2009, Cromsigt et al. 2013, DeVoe et al. 2019, Mikle et al. 2019). Lands with limited hunter access may serve as refuges where elk may aggregate to escape harvest risk during the hunting season (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013). Therefore, an increase in license availability or season length alone may not result in population reductions if elk can respond to these measures with movements to areas where hunting access is restricted (Conner et al. 2001; Proffitt et al. 2010, 2016). Alternatively, wildlife managers may use elk avoidance of harvest risk to manipulate elk distributions to meet management objectives (Cromsigt et al. 2013). For example, managers may reduce harvest risk on public lands by restricting harvest or hunter access to encourage elk to remain on public lands and reduce conflict with agricultural producers. In such situations, managers may encounter a trade-off between producing elk distributions that are favorable for private agricultural landowners and increasing the number of female elk harvested.

As state agencies seek to reduce overabundant elk populations and manipulate elk distributions through hunter access and harvest regulations, managers may encounter unintended consequences. For example, migratory and resident elk may be exposed to differential harvest risk, as seasonal movements may involve transitions between lands of different hunter access strategies or harvest regulations (Cole et al. 2015). Under these conditions, a management decision to increase elk harvest by liberalizing regulations may unevenly impact migratory and resident segments of the population. Alternatively, migratory elk may respond to increased harvest risk by shifting the timing of migratory behaviors, particularly if refuge areas are present (Mikle et al. 2019). A shift in the timing of seasonal movements such that they occur outside of hunting season could reduce the opportunity for hunter harvest along migratory corridors (Smith 2007), particularly if movements involve a transition from one refuge area to another. Although preserving variation in migratory behaviors is an important conservation objective across the globe (Berger 2004, Bolger et al. 2008), relationships between migratory behavior and hunting have received comparatively little attention.

The objectives of this observational study were to 1) evaluate factors influencing female elk transitions between areas of different hunter access strategies during the multi-phase hunting season and 2) evaluate the effects of hunter access, harvest regulations, and other landscape features on female elk resource selection during the multi-phase hunting season. We hypothesized that increased hunting pressure during the general season, more liberal harvest regulations, migratory behavior, and increasing levels of snow would increase elk transitions between hunter access strategies. We also hypothesized that elk would generally avoid the increased harvest risk associated with more hunter access and less restrictive harvest regulations.

STUDY AREA

Our study area encompassed the fall-winter range of the Devil's Kitchen elk population in hunting districts (HD) 445, 455, and 446 in central Montana, USA (Figure 1). This population was overabundant according to numerical population goals set by the state of Montana, and high densities of elk on private ranchlands were a management concern. The Montana Fish, Wildlife & Parks (FWP) 2023 Elk Management Plan outlined numerical objectives of 2,500–3,500 elk in HDs 445/455 and 1,500-2,000 elk in HD 446 (Montana Department of Fish, Wildlife and Parks 2023). During our study, elk population counts ranged from 3,460 elk to 5,989 elk in HDs 445/455 and 2,322 elk to 3,608 elk in HD 446. Cooperative efforts between state wildlife managers and private landowners produced a unique set of regulations intended to provide landowners and managers with a variety of harvest management tools (Table 1). The hunting season began on 15 August and ended on 15 February, composed of 4 distinct hunting periods: early shoulder season, archery season, general rifle season, and late shoulder season. There was a one-week break with no hunting in mid-October between the archery and rifle seasons. The majority of elk harvest occurred during the general rifle season, followed by the archery, late shoulder, and early shoulder seasons

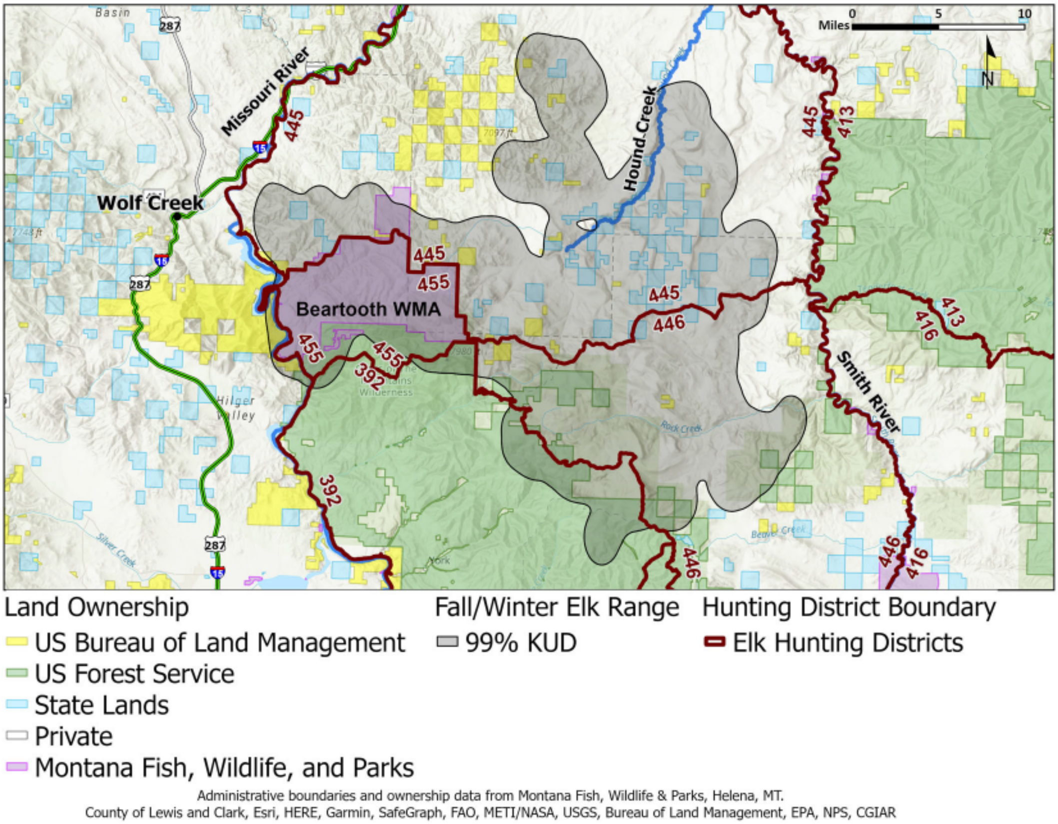

FIGURE 1 The Devil's Kitchen study area was located in central Montana, USA. The fall-winter elk range is represented by a 99% kernel utilization distribution (KUD) generated from elk locations occurring during hunting season (15 Aug–15 Feb) and legal hunting hours from 2020–2023.

(Table 2). Hunter effort varied between hunting districts (Table S1). Public hunting access on private lands varied throughout the hunting season and across the study area, though at least some hunting occurred on all properties at some point in the hunting season. The Beartooth Wildlife Management Area (BTWMA), owned and managed by FWP and located in the western portion of the study area, occupied 12.3% of the study area (Figure 1). The BTWMA was purchased in 1970 with primary objectives of providing critical winter range for elk, mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*), alleviating game damage conflict with local agricultural producers, and providing recreational use including hunting and wildlife viewing. The BTWMA is closed to recreational use (including hunting) from 1 December to 15 May.

Land ownership was predominately private agricultural (primarily pastureland grazed by cattle and hay production, 72.6%), though a matrix of FWP (12.3%), State of Montana (7.3%), United States Forest Service (5.7%), and Bureau of Land Management (1.9%) land occurred throughout the study area (Figure 1). Elevation ranged from 1,048 m in valley bottoms to 2,431 m on mountain slopes. The long-term annual precipitation average in the study area was 470 mm (range = 306–841 mm), and the average temperature was 16.8°C in July and −4.8°C in January (climate data downloaded at 800-m resolution with the prism package in R; Hart and Bell 2015). Over the last 6 years, precipitation during the fall hunting season averaged 29.1 mm, and the temperature averaged −2.1°C. Valley bottoms were primarily grasslands composed of native and introduced pasture grasses (49.8% total land cover) abutting irrigated or non-irrigated agricultural land in some areas (1.2% total land cover). Sagebrush-steppe (9.7% total land cover) and shrublands (4.6% total land cover) occupied low-mid elevation foothills, giving way to

TABLE 1 Harvest regulations effective in the Devil's Kitchen study area, central Montana, USA, 2020–2023. Hunting periods included early shoulder season (15 Aug–3 Sep), archery season (4 Sep–22 Oct), general rifle season (23 Oct–28 Nov), and late shoulder season (29 Nov–15 Feb). General licenses were valid across the state for the harvest of one elk depending on unit-specific regulations. Individuals could only purchase a single general license each year but there was no quota on the total number available for purchase by resident hunters. Elk B-licenses were only valid for the harvest of antlerless elk. An annual quota of 6,000 004-00 B-licenses (valid in 34 hunting districts in Montana Fish, Wildlife & Parks administrative Region 4) and 250 455-00 B-licenses were available during the study period. A hunter in possession of a general license could purchase 2 B-licenses each year. Elk permits were only valid with a general license and were allocated through a drawing. A quota of 30–40 445-20 permits, 50–60 455-20 permits, and 4,000 900-20 permits (valid in 22 hunting districts around the state) were available annually during the study period. The regulation class column indicates how regulations were classified for the harvest regulation covariate. Regulations were classified as liberal when an antlerless opportunity was available on the general license, and restricted when an antlerless opportunity was only available on a permit or B-license.

District	Hunting period	License type	Harvest regulation	Regulation class
445	Early shoulder	General license	Antlerless	Liberal
		B-license: 004-00	Antlerless	
	Archery	General license	Either-sex	Liberal
		B-license: 004-00	Antlerless	
		Permit: 445-20	Either-sex	
	Early general	General license	Either-sex	Liberal
		B-license: 004-00	Antlerless	
		Permit: 445-20	Either-sex	
	Late general	General license	Antlerless	Liberal
		B-license: 004-00	Antlerless	
		Permit: 445-20	Either-sex	
	Late shoulder	General license	Antlerless	Liberal
		B-license: 004-00	Antlerless	
446	Early shoulder	General license	Antlerless	Liberal
		B-license: 004-00	Antlerless	
	Archery	General license	Brow-tined bull or antlerless	Liberal
		B-license: 004-00	Antlerless	
	Early general	General license	Brow-tined bull or antlerless	Liberal
		B-license: 004-00	Antlerless	
	Late general	General license	Brow-tined bull or antlerless	Liberal
		B-license: 004-00	Antlerless	
	Late shoulder	General license	Antlerless	Liberal
		B-license: 004-00	Antlerless	
455	Early shoulder		No harvest	No harvest
	Archery	Permit: 455-20	Either-sex	Restricted
		Permit: 900-20	Either-sex	
		B-license: 455-00	Antlerless	

(Continues)

TABLE 1 (Continued)

District	Hunting period	License type	Harvest regulation	Regulation class
	Early general	Permit: 455-20	Either-sex	Restricted
		B-license: 455-00	Antlerless	
	Late general	Permit: 455-20	Either-sex	Restricted
		B-license: 455-00	Antlerless	
	Late shoulder		No harvest	No harvest

TABLE 2 Mean elk hunter harvest estimates across license years 2020–2022 in the 3 focal hunting districts (HDs) in the Devil's Kitchen study area, central Montana, USA. Harvest estimates were gathered during Montana Fish, Wildlife & Parks annual hunter harvest survey, where a random sample of licensed hunters were called and asked about their effort and success while hunting. Harvest estimates include male and female elk. Estimates of hunter effort are displayed in Appendix A.

	Early shoulder		Archery		General		Late shoulder	
HD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
445	15.2	10.2	36.3	11.8	209.3	22.9	41.6	7.9
446	3.0	3.3	55.6	20.9	261.7	42.4	40.2	3.4
455	0	0	10.2	2.5	114.8	26.7	0	0
Total	18.2	10.7	102.1	24.1	585.8	55.1	81.8	8.6

coniferous forests (32.6% total land cover) at higher elevations. Riparian areas accounted for a modest portion of total land cover (1.9%). Mule deer, white-tailed deer (*O. virginianus*), and moose (*Alces alces*) were sympatric with elk in the study area. Limited amounts of game damage conflict occurred in the study area related to deer species, generally in different areas than the core elk range. Carnivores included black bear (*Ursus americanus*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and gray wolf (*C. lupus*).

METHODS

Elk location data

We used helicopter netgunning to capture 65 female elk in the study area in February 2020 and 2021. We outfitted captured individuals with remote upload global positioning system (GPS) collars (model LiteTrack Iridium 420; Lotek Wireless, New Market, Ontario, Canada) programmed to collect hourly locations for 2 years, after which drop-off devices released collars from animals. The collars were programmed to transmit a very high frequency (VHF) signal during daylight hours and switch to a mortality signal if stationary for >10 hours. We censored GPS fixes with low precision (i.e., dilution of precision >10) and only included GPS locations that occurred during legal hunting hours (30 minutes before sunrise to 30 minutes after sunset) in the hunting season (15 August–15 February) in HDs 445, 446, and 455. We associated elk locations with one of 4 hunting periods: early shoulder (15 August–3 September), archery (4 September–17

October), general rifle (23 October–28 November), and late shoulder (29 November–15 February). Elk locations occurring during the break in hunting in mid-October were included in the archery hunting period, as this period of no hunting pressure was more similar to the lower hunting pressure that occurred during archery season than the higher hunting pressure that occurred during the general rifle season (Table 2).

Covariate data

We developed covariates describing factors potentially influencing female elk transitions or resource selection during the hunting season, including hunter access, harvest regulation, migratory status, snow water equivalent (SWE), land cover type, slope, aspect, terrain ruggedness, and a security habitat metric. We defined hunter access by classifying individual land parcels into discrete hunter access strategies for each of the 4 hunting periods according to the strategy employed during each period (Figure S1). The hunter access strategies included open access, moderate access, and limited access, and were based on personal communication with local wildlife managers and private landowners. There were approximately 60 private landowners in the study area, and the mean private land parcel size was 21.8 km^2 (SD = 43.1 km^2, range = 0.16–226.7 km^2). We classified a parcel as open access if it was publicly owned and accessible or privately owned and enrolled in Montana's Block Management Access system (a program allowing public access on private lands) and not requiring a reservation to hunt. A parcel was categorized as moderate access if landowners allowed access to members of the public who inquired, or if it was enrolled in Montana's Block Management Access system but required a reservation, which limited the number of hunters. Parcels were classified as limited access if landowners allowed access only for friends and family or outfitted clients, or if no hunting opportunities were available. Publicly owned but landlocked parcels were classified using the most accessible of the access management strategies of surrounding private lands.

To define harvest regulation, we classified the antlerless (i.e., female) harvest regulation scenarios that elk could encounter in the study area as liberal harvest (if general license and elk B license valid), restricted harvest (antlerless harvest by permit only), or no harvest (no antlerless harvest allowed; Table 1; Figure S2). General elk licenses were available to all Montana resident hunters and to some nonresident hunters through a drawing. Elk B licenses were valid for antlerless harvest only and were available to residents through a drawing or over-the-counter, and to nonresidents through a drawing. Elk permits were available through a drawing only, could only be used in combination with the general elk license, and facilitated an enhanced hunting opportunity with fewer hunters on the landscape.

Migratory status was a binary variable indicating whether an individual was a migrant or not. To define migratory status of each animal-year, we used the Migration Mapper application (Merkle et al. 2022) to visually classify migratory behaviors using maps of GPS locations and associated net-squared displacement curves in spring and fall for each individual. Because missing data from harvest mortality limited our ability to classify fall migratory behaviors of harvested elk, we used spring classifications to assign migratory status for the following hunting season for all elk.

We used snow water equivalent (SWE) data from the Snow Data Assimilation System (National Hydrological Remote Sensing Center) to calculate daily SWE values at 30-m resolution across time. We used land cover data from the Montana Land cover Framework (Montana Spatial Data Infrastructure [MSDI] Land Use/Land Cover Data, 30-m resolution) and reclassified land cover categories into 5 final categories: grassland, conifer forest, sagebrush steppe, shrubland, and nonhabitat (included open water and human development like highways and towns). We derived the slope, aspect, and terrain ruggedness covariates from the National Elevation Dataset downloaded with the FedData package in R at 1 arc-second resolution (R Core Team 2022). We calculated vector ruggedness measure (VRM; Sappington et al. 2007) with the spatialEco package in R using the default 3 × 3 neighborhood on 1 arc-second elevation data (Evans and Murphy 2023). We transformed aspect with a cosine function so that positive values represent northerly aspects and negative values represent southerly aspects.

We defined the security habitat metric covariate as secure or not secure according to elk security habitat recommendations for archery and rifle hunting periods outlined by Ranglack et al. (2017). These recommendations combine thresholds for distance from motorized routes, canopy cover, and minimum patch size. Patch size refers to the size of contiguous area meeting the threshold criteria for distance from motorized routes and canopy cover. We sourced canopy cover data from LANDFIRE 2019, and compiled motorized routes data from MSDI, United States Forest Service, and Montana Department of Natural Resources and Conservation roads layers. Areas defined as secure were required to have ≥13% canopy cover in archery season and ≥9% canopy cover in rifle season, be ≥2,760 m away from motorized routes in archery season and ≥1,535 m away in rifle season, and to have a minimum patch size of 20.23 km^2 during rifle season (no minimum patch size during archery season).

Elk transitions between hunter access strategies

We fit a series of Bayesian multistate models to evaluate factors associated with the daily probability that an elk transitioned between areas of different hunter access strategies during the hunting season. We evaluated the influence of 4 covariates (hunting period, harvest regulation, migratory status, and SWE) on the daily probability of transitioning between hunter access strategies. We included movement data from individuals whose annual 99% kernel utilization distribution (KUD) home range overlapped with each hunter access strategy during each hunting period to ensure that all strategies were available to each animal. We used animal-years as the sampling unit and randomly sampled one location for each animal-year on each day of the hunting season. We pooled locations from all years and developed competing univariate models evaluating the effect of each covariate and a null model.

We used each candidate model to evaluate an alternative hypothesis regarding the drivers of elk transitions between access strategies. We used the hunting period model to evaluate the hypothesis that the type of hunting season and associated conditions of the period best explained elk transitions between access strategies. We predicted transition probabilities across all hunter access strategies would be highest during the general rifle period, as elk are navigating the highest levels of harvest risk in that period. We used the harvest regulation model to evaluate the hypothesis that the availability of hunting opportunity best explained elk transitions between access strategies. We predicted that the daily probability of an elk transitioning into a less accessible strategy would increase under liberal regulations, as harvest risk would be higher, producing a stronger gradient of risk between open access and less accessible lands. We used the migratory status model to evaluate the hypothesis that the classification of individuals as either migrants or residents best explained elk transitions between access strategies. We predicted that migratory individuals would transition more frequently than resident individuals as they move longer distances and likely cross a larger number of land parcels. We used the SWE model to test the hypothesis that the presence of snow on the landscape best explained elk transitions between access strategies. We predicted that a threshold might exist where the daily probability of transitioning would increase as snowpack accumulated and animals moved towards winter ranges, but that at the highest SWE values, transition probabilities would stabilize as elk settled into wintering grounds. Finally, we used the constant model to evaluate the null hypothesis that transitions between access strategies were best explained by the intercept alone.

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

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

where $l\psi^{Open/Open} = \beta_0{}^{Open/Open} + \beta_1{}^{Open/Open} \times x$.

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

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

where $l\psi^{Open/Moderate} = \beta_0{}^{Open/Moderate} + \beta_1{}^{Open/Moderate} \times x$.

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

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

We repeated this process for each access strategy transition (e.g., moderate to moderate, moderate to open, moderate to limited) such that we estimated 9 intercept and slope terms. We centered and scaled data for models with continuous covariates and used normal priors for intercepts (0, 2). We ran 3 parallel chains for each model with 40,000 samples per chain. We discarded the first 10,000 samples as burn-in and did not thin chains. This process produced a posterior distribution of 90,000 samples from each model to inform inference. We assessed posterior convergence using graphical (trace and density plots) and numeric outputs (Rhat values < 1.1) from the MCMCvis package in R (Youngflesh 2018). We then ranked models according to Watanabe-Akaike Information Criterion (WAIC) score to determine which candidate model had the highest support and used this top model for inference (Watanabe 2010).

Elk resource selection

We evaluated elk resource selection between Johnson's (1980) second and third orders of selection in response to hunter access, harvest regulation, land cover, SWE, security habitat, terrain ruggedness, slope, and aspect. We constructed resource selection functions (RSFs) in a used-available framework (Manly et al. 2002) and sampled 4 locations per day for each individual to create our sample of used locations. We randomly generated available locations at an approximately 1:10 used to available ratio within the population fall-winter elk range defined by the 99% KUD of daylight hunting season locations. We additionally constrained the available range to HDs 445, 446, and 455 where it overlapped outside of these districts. We excluded elk locations and available locations designated as nonhabitat land cover because it was extremely rare in the study area (nonhabitat composed 0.3% of the study area). We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation to facilitate coefficient comparison. We screened for collinearity and excluded variables with correlation coefficients of $|r| > 0.6$.

We predicted that elk would select for less hunter access and more restrictive harvest regulations to avoid harvest risk. We predicted that elk selection for land cover categories and northern aspects would vary between hunting periods as seasonal habitat preferences shifted. We predicted that elk would select for security habitat, terrain ruggedness, and slope to avoid harvest risk. We predicted that elk would avoid higher SWE values to avoid difficulty moving through deep snow.

We constructed generalized mixed-effects models using the lme4 and MuMIn packages in R (Hebblewhite and Merrill 2008; Bates et al. 2015, 2018; Bartoń 2025). We considered individual elk as the sampling unit and incorporated random intercepts to account for variations among individual elk (Gillies et al. 2006). We first carried out model selection on the complete hunting season dataset pooled across hunting periods, then fit the top-performing model to each hunting period separately to evaluate similarities and differences in elk resource selection between periods. We used a 3-step process to develop and identify the top-performing models. In step 1, we evaluated univariate models to test linear and pseudothreshold (natural log) functional forms for each continuous covariate (excluding aspect because of negative values). In step 2, we evaluated all possible additive combinations of the landscape covariates (land cover, terrain ruggedness, aspect, slope, security habitat, and SWE) to establish the most supported model to generally explain elk resource selection. In step 3, we combined the most supported landscape covariate combination with the 4 possible additive and interactive combinations of hunter access and harvest regulation covariates (regulation, access, regulation + access, regulation × access). Because only 6 of 9 possible combinations of hunter access and harvest regulation categories existed, we coded the interaction as a new categorical covariate representing the 6 levels of existing combinations of access and regulation, referred to hereafter as regulation-access. At each step, we selected the top model based on the lowest Akaike's Information Criterion adjusted for small sample size (AIC_c) value, or if multiple models were within 2 ΔAIC_c of each other, we chose the model with the fewest variables (Burnham and Anderson 2002). We evaluated resource selection models using one repetition of 5-fold cross-validation based on correlation between 10 equal-area RSF bins and area-adjusted frequencies for each withheld sub-sample of the data (Boyce et al. 2002), where a strong positive correlation suggested strong model predictive performance.

RESULTS

Elk transitions between hunter access strategies

We included movement data from 58 female elk in our transition analysis. The top-performing model in our candidate suite included hunting period as the explanatory variable (Table 3). At this daily scale, elk were generally more likely to remain within the same access strategy than to transition into a different strategy. This pattern was consistent across all hunting periods other than the late shoulder season, where elk were more likely to transition from open access to limited access than to remain in open access (Figure 2).

Elk appeared to behave in similar ways during the early shoulder and archery hunting periods, with moderate daily probabilities of moving from open access to moderate access and high daily probabilities of remaining in moderate and limited access (Figure 2). Elk in open access had a 0.285 daily probability (95% CI = 0.242, 0.330) of transitioning to moderate access in the early shoulder season and a 0.266 daily probability (95% CI = 0.236, 0.297) in the archery season.

During the general rifle season, elk had a high daily probability of remaining in open access and higher daily probabilities of transitions towards open access from moderate and limited access as compared to other hunting periods. Elk already present in open access had a daily probability of 0.841 (95% CI = 0.825, 0.855) of remaining in open access, which is the highest daily probability of remaining in open access found in any hunting period. The estimated daily probability of an elk transitioning from limited access to moderate access was estimated as 0.233 (95% CI = 0.209, 0.257), and the daily probability of an elk transitioning from moderate to limited access was

TABLE 3 Results of Watanabe-Akaike Information Criterion (WAIC) comparison of candidate multi-state models predicting the daily probability of elk transitioning between hunter access strategies during hunting season (15 Aug–15 Feb) in the Devil's Kitchen study area in central Montana, USA, 2020–2023. The ΔWAIC values indicate the difference between each candidate model's WAIC score and that of the top performing model.

Model	WAIC	ΔWAIC
Hunting period	19,242.73	0.00
Harvest regulation	19,564.93	322.20
Snow water equivalent	20,144.38	901.66
Migratory status	20,338.41	1,095.68
Constant or null	20,371.53	1,128.81

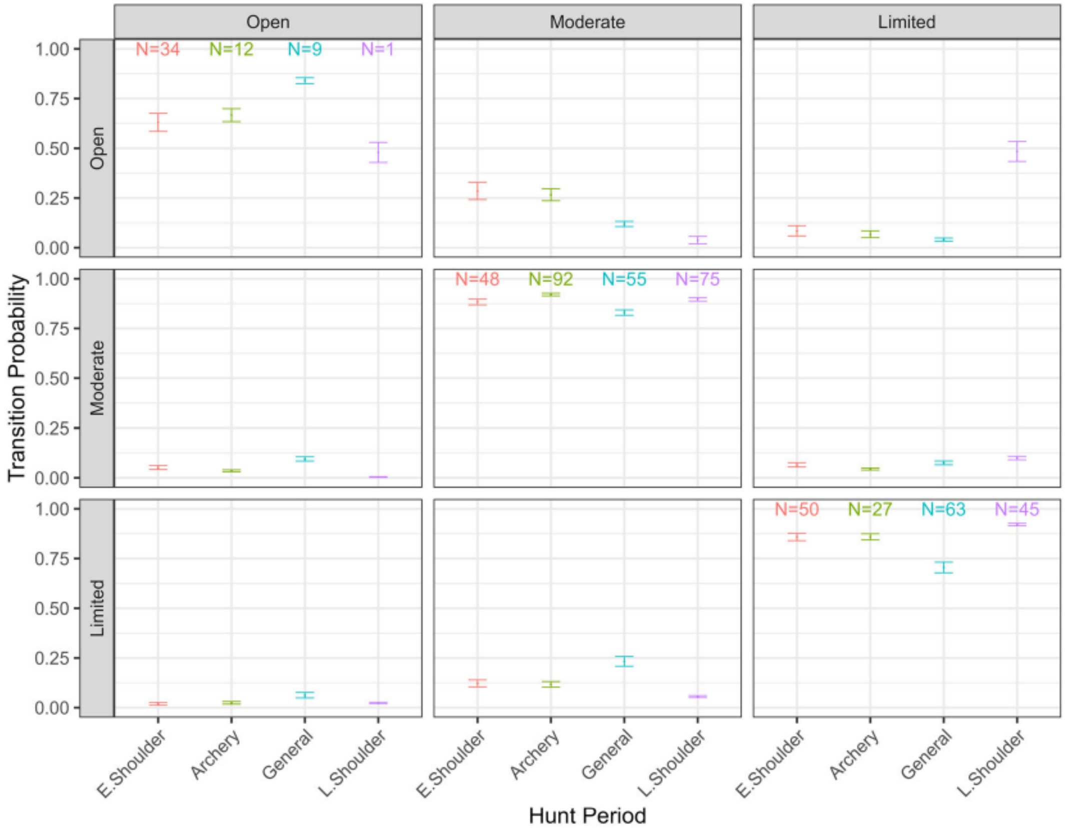

FIGURE 2 Estimated daily transition probabilities from the top-performing model investigating the daily probability of elk transitioning between hunter access strategies during the fall hunting season (15 Aug–15 Feb) in the Devil's Kitchen study area in central Montana, USA, 2020–2023. The plotted posterior means with 95% credible intervals show the estimated daily probability of transitioning from an access strategy on day *t* (rows) to an access strategy on day *t* + 1 (columns) in each of the 4 hunting periods of interest. Hunting periods included early shoulder season (E.Shoulder; 15 Aug–3 Sep), archery season (4 Sep–22 Oct), general rifle season (23 Oct–28 Nov), and late shoulder season (L.Shoulder; 29 Nov–15 Feb). Numbers (*N* = *j*) listed above within-category transition probabilities represent the number of individual-years in that access strategy on the first day of the hunting period.

estimated as 0.075 (95% CI = 0.066, 0.085). During the general rifle season, elk were more likely to transition from limited to open access (0.0621 daily probability, 95% CI = 0.049, 0.076) and from moderate to open access (0.095 daily probability, 95% CI = 0.085, 0.106) as compared to other hunting periods. The general rifle period had the lowest estimated daily probability of remaining in limited access of any hunting period (0.706 daily probability, 95% CI = 0.679, 0.732).

During the late shoulder season, elk had high daily probabilities of transitioning towards limited access and remaining in limited access. The daily probability that an elk transitioned from open access to limited access was 0.484 (95% CI = 0.434, 0.534), the highest estimated daily probability of transitioning across access strategies found in this study (Figure 2). Correspondingly, the daily probability that elk already present in limited access remained in limited access was 0.921 (95% CI = 0.915, 0.927), the highest estimated daily probability of remaining in limited access across all hunting periods. Finally, the daily probability that an elk remained in open access was 0.479 (95% CI 0.429, 0.530), the lowest of any hunting period.

Elk resource selection

We included 88,089 GPS locations from 58 female elk in our resource selection analysis. The mean number of locations per individual was 1,519 (range = 24–2,218). Across the hunting season, 12% of elk used locations and 14% of available locations occurred within open access, 52% of elk used locations and 53% of available locations occurred within moderate access, and 36% of elk used locations and 33% of available locations occurred within limited access. Across the hunting season, 71% of elk used locations and 86% of available locations occurred within liberal harvest, 9% of elk used locations and 7% of available locations occurred within restricted harvest, and 20% of elk used locations and 7% of available locations occurred within no harvest.

Collinearity screening yielded no correlation coefficients of $|r| > 0.6$. In step 1 of model selection, the pseudothreshold functional form of slope was selected and all other functional forms selected were linear (Table S2). In step 2 of model selection, the top landscape model included all 6 landscape covariates (land cover, terrain ruggedness, aspect, slope, security habitat, SWE; Table S3). In step 3 of model selection, the final top model included the interactive combination of hunter access and harvest regulation (Tables 4 and 5; Figure 3). The final top model demonstrated strong predictive performance with Spearman rank correlations ranging from 0.93 to 0.99 amongst the 5 iterations and a correlation coefficient of 0.99 for the average frequencies. Predictive performance remained strong when the final top model was fit to each hunting period: correlation coefficients for the average frequencies were 1.0 for the early shoulder season, 0.95 for the archery season, 0.98 for the general season, and 0.96 for the late shoulder season.

During the early shoulder season, elk selected for all other regulation-access categories in comparison to liberal harvest-open access, with the strongest selection for liberal harvest-moderate access (Figure 3). Based on coefficient estimates from the early shoulder season model, the odds of elk selecting liberal harvest-moderate access were 216% higher (95% CI = 177%, 260%) in comparison to the reference category of liberal harvest-open access. Elk weakly avoided security habitat and terrain ruggedness and weakly selected for slope and northerly aspect. Elk strongly avoided grassland, sagebrush steppe, and shrubland land cover in comparison to conifer forest.

During the archery season, elk selected for all other regulation-access categories in comparison to liberal harvest-open access, with the strongest selection for liberal harvest-moderate access (Figure 3; Table 5). Based on coefficient estimates from the archery season model, the odds of elk selecting liberal harvest-moderate access were 496% higher (95% CI = 432%, 568%) in comparison to the reference category of liberal harvest-open access. Elk selected for security habitat, SWE, slope, and northerly aspect during the archery season. In reference to the conifer forest land cover category, elk weakly avoided grassland and shrubland land cover and weakly selected for sagebrush steppe.

TABLE 4 Model selection results from the third step of model selection where we added combinations of hunter access and harvest regulation to the top-performing landscape model evaluating female elk resource selection during hunting season (15 Aug–15 Feb) in the Devil's Kitchen study area in central Montana, USA, 2020–2023. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to select the most-supported model. We also present the number of parameters (K); SWE represents snow water equivalent.

Model structure	K	ΔAIC_c	AIC_c weight
Land cover + terrain ruggedness + aspect + slope + security + SWE + regulation-access	15	0	1
Land cover + terrain ruggedness + aspect + slope + security + SWE + access + regulation	14	908	0
Land cover + terrain ruggedness + aspect + slope + security + SWE + regulation	12	10,848	0
Land cover + terrain ruggedness + aspect + slope + security + SWE + access	12	31,494	0
Land cover + terrain ruggedness + aspect + slope + security + SWE	10	33,131	0

TABLE 5 Standardized selection coefficients and 95% confidence intervals from the top-performing pooled hunting season model fit to 4 hunting periods examining female elk resource selection during the hunting season (15 Aug–15 Feb) in the Devil's Kitchen study area in central Montana, USA, 2020-2023. Hunting periods included early shoulder season (15 Aug–3 Sep), archery season (4 Sep–22 Oct), general rifle season (23 Oct–28 Nov), and late shoulder season (29 Nov–15 Feb). Covariates labeled RA are categorical levels of regulation-access and covariates labeled LC are categorical levels of land cover; SWE represents snow water equivalent. Coefficients for categorical variables are relative to the reference category of conifer for land cover and liberal-open for regulation-access.

Covariate	Pooled	Early shoulder	Archery	General	Late shoulder
Terrain ruggedness	−0.258 (−0.269, −0.248)	−0.254 (−0.287, −0.222)	−0.200 (−0.219, −0.181)	−0.244 (−0.266, −0.222)	−0.306 (−0.324, −0.289)
Slope	0.0958 (0.0874, 0.104)	0.156 (0.130, 0.182)	0.190 (0.173, 0.207)	0.207 (0.187, 0.227)	−0.0683 (−0.0815, −0.0552)
Aspect	0.112 (0.104, 0.120)	0.287 (0.264, 0.311)	0.204 (0.189, 0.219)	0.0534 (0.0367, 0.0702)	0.0400 (0.0274, 0.0526)
SWE	−0.152 (−0.161, −0.144)		0.194 (0.0951, 0.293)	0.140 (0.111, 0.169)	0.0327 (0.0215, 0.0439)
Security habitat	0.128 (0.104, 0.151)	−0.120 (−0.178, −0.0619)	0.652 (0.611, 0.693)	−0.0321 (−0.0812, 0.0170)	−1.270 (−1.336, −1.203)
LC grassland	−0.113 (−0.135, −0.0907)	−0.692 (−0.750, −0.634)	−0.296 (−0.340, −0.252)	−0.195 (−0.241, −0.149)	0.371 (0.330, 0.413)
LC sagebrush steppe	−0.00746 (−0.0363, 0.0213)	−0.713 (−0.806, −0.621)	0.130 (0.0732, 0.187)	−0.349 (−0.413, −0.285)	0.387 (0.338, 0.436)
LC shrubland	−0.285 (−0.324, −0.247)	−1.117 (−1.263, −0.971)	−0.471 (−0.560, −0.383)	−0.635 (−0.726, −0.544)	0.280 (0.221, 0.338)
RA liberal-moderate	1.08 (1.020, 1.141)	1.151 (1.020, 1.281)	1.785 (1.671, 1.900)	0.561 (0.460, 0.662)	1.296 (1.125, 1.466)
RA liberal-limited	0.662 (0.601, 0.723)	0.425 (0.294, 0.556)	1.163 (1.046, 1.279)	0.266 (0.162, 0.370)	0.925 (0.752, 1.099)
RA restricted-open	1.470 (1.406, 1.534)		0.833 (0.710, 0.957)	1.621 (1.518, 1.724)	
RA no harvest-open	0.929 (0.852, 1.007)	0.295 (0.148, 0.441)			2.269 (2.083, 2.455)
RA no harvest-limited	2.906 (2.843, 2.968)				3.623 (3.451, 3.794)

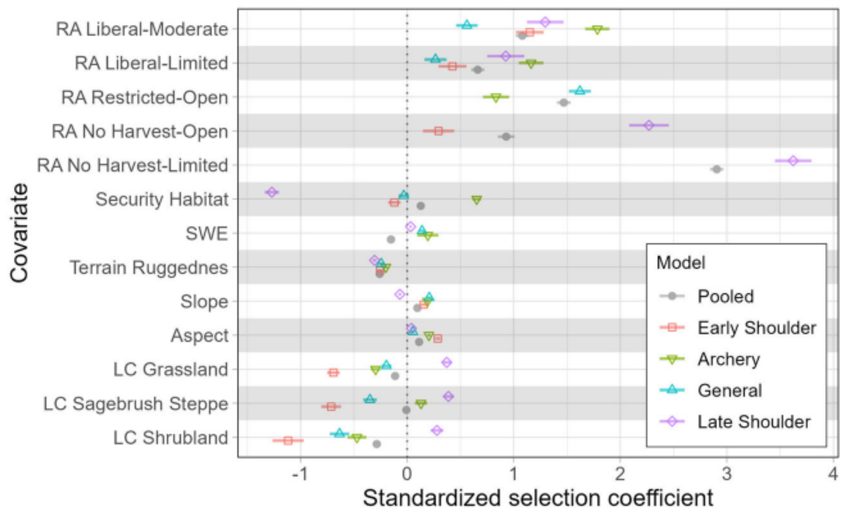

FIGURE 3 Standardized selection coefficients and 95% confidence intervals from the top-performing pooled hunting season model (gray estimates) fit to 4 hunting periods (colored estimates) examining female elk resource selection during the hunting season (15 Aug–15 Feb) in the Devil's Kitchen study area in central Montana, USA, 2020–2023. Hunting periods included early shoulder season (15 Aug–3 Sep), archery season (4 Sep–22 Oct), general rifle season (23 Oct–28 Nov), and late shoulder season (29 Nov–15 Feb). Covariates labeled RA are categorical levels of regulation-access and covariates labeled LC are categorical levels of land cover; SWE represents snow water equivalent. Coefficients for categorical variables are relative to the reference category of liberal-open for regulation-access and conifer for land cover.

During the general season, elk selected for all other regulation-access categories in comparison to liberal harvest-open access, with the strongest selection for restricted harvest-open access (Figure 3; Table 5). Based on coefficient estimates from the general season model, the odds of elk selecting restricted harvest-open access were 406% higher (95% CI = 356%, 461%) in comparison to the reference category of liberal harvest-open access. Elk had no significant response to security habitat during the general season. Elk selected for SWE, slope, and northerly aspect during the general season. Elk avoided grassland, sagebrush steppe, and shrubland in comparison to conifer forest.

During the late shoulder season, elk selected for all other regulation-access categories in comparison to liberal harvest-open access, with the strongest selection for no harvest-limited access (Figure 3; Table 5). Based on coefficient estimates from the late shoulder season model, the odds of elk selecting no harvest-limited access were 3,644% higher (95% CI = 3,054%, 4,344%) in comparison to the reference category of liberal harvest-open access. Elk avoided security habitat, terrain ruggedness, and slope and selected weakly for higher SWE and northerly aspects. Elk selected for grassland, sagebrush steppe, and shrubland in comparison to conifer forest.

DISCUSSION

Elk transitions between hunter access strategies

Our results demonstrate the dynamic nature of elk movements throughout the hunting season, aligning with other research showing an increase in elk movement rates in response to hunting pressure (Cleveland et al. 2012). To our knowledge, we are the first to estimate the daily probabilities of elk transitioning between lands of different hunter access strategies during the hunting season. Although the predicted daily probabilities of elk remaining in the same access strategy (range = 0.479–0.921) were almost entirely higher than the daily probabilities of elk moving between strategies (range = 0.004–0.484), the probability of an elk transitioning between access strategies at some point during each hunting period was high (range = 0.917–1.0; Table S4). For example, the 0.285 daily probability of transitioning from open to moderate access during the early shoulder season indicates that an elk would transition from open to moderate access after approximately 3.5 days, on average. Further, every elk we monitored transitioned between hunter access strategies at least once during the hunting season. Together these results suggest that elk moved readily between lands of different access strategies, responding flexibly to hunting pressure at a fine temporal scale throughout the duration of the hunting season.

Although elk were generally relatively likely to transition between access strategies, there was considerable individual variation in the number of transitions between hunter access strategies (Figure S3). Approximately 20% of elk stayed in one access strategy throughout at least 2 of the 4 hunting periods. These elk with low numbers of transitions between access strategies were generally individuals that remained on moderate or limited access lands the vast majority of the time, suggesting different strategies exist among elk to limit harvest risk across a landscape with diverse hunter access and regulations. In contrast to the overall trend of transitioning readily between access strategies, some elk may occupy areas of lower risk on less accessible lands that allow them to remain on those lands without transitioning between access strategies. Other research has demonstrated that elk with ingrained patterns of selection for less accessible lands may be difficult to influence with public land management strategies (Proffitt et al. 2026). While elk exhibiting these behavioral patterns seem to make up a relatively small proportion of this population, the potential management challenges that these patterns pose remain important to consider.

Female elk likely transitioned between lands of different hunter access strategies to avoid risk associated with hunting pressure, although not always in the direction expected based on hunter access alone. During the early shoulder and archery seasons, elk avoided harvest risk by leaving open access lands and transitioning to less accessible private lands. In accordance with our findings, hunting pressure during the onset of archery or early hunting seasons has been demonstrated to induce elk movement to private lands in other studies (Conner et al. 2001, Vieira et al. 2003). However, in opposition to our predictions, we found transitions towards less accessible lands were less likely and remaining in open access was more likely to occur during the general season than other periods, when hunting pressure was highest. This result, while seemingly unexpected, could be explained by the interaction between hunter access and harvest regulations in determining harvest risk as well as changing hunting pressure between hunting periods. A large portion of the available open access lands during the general season occurred on the BTWMA with restricted harvest regulations, resulting in decreased harvest risk and encouraging elk to remain on those open access lands. Hunters harvested over 5 times as many elk during the general season as compared to any other hunting period, and in the context of this increase in harvest risk, restricted harvest regulations on open access lands may render them less risky than less accessible lands. Elk transitions to limited access during the late shoulder season could also be influenced by harvest regulations on the BTWMA, which became limited access with no harvest during this hunting period. As such, it remains important to consider the interaction between hunter access and harvest regulations to understand elk movements during hunting seasons.

Elk resource selection

Similar to our findings that elk transitions across access strategies were related to hunter access and harvest regulations, elk resource selection was largely influenced by the interaction of hunter access and harvest regulation. Female elk generally avoided hunting pressure and the associated harvest risk by selecting for areas with less hunter access and more restrictive harvest regulations, echoing elk avoidance of hunting pressure in other studies (Burcham et al. 1999; Proffitt et al. 2013, 2016; Ranglack et al. 2017). Elk responded differently to each of the 6 combinations of harvest regulation and hunter access, indicating that elk perceived varying amounts of harvest risk from each combination. Additionally, elk selection for each regulation-access category varied among hunting periods, suggesting that harvest risk varied beyond the categories we were able to represent.

Changing hunting pressure and permitted weapons (i.e., archery equipment vs. rifle) may explain the variation in harvest risk for each regulation-access category across hunting periods. However, a variety of land management practices that we were not able to account for may have also affected elk behavior. We classified harvest regulation based on harvest opportunity for female elk to align with our collared sample of females, but elk may perceive hunting pressure differently. For example, female elk may avoid hunters who are only permitted to hunt male elk, hunters targeting other species of game, or other recreators who are not hunting. Counter-intuitively, female elk selected more strongly for liberal harvest-moderate access than liberal harvest-limited access throughout all hunting periods. This unexpected result may indicate that landscape features not associated with hunting were important predictors of selection, or that our classifications of hunter access did not accurately represent actual hunting pressure. For example, differences in the availability of forage resources may have encouraged elk use of lands classified as moderate access. Lands classified as moderate hunter access contained more agricultural lands and slightly higher herbaceous biomass than open or limited access lands (Table S5). We classified hunter access strategies based on the groups of people allowed to hunt but were unable to collect more specific data regarding number of hunters, frequency of hunting events, or harvest success. This limitation means that within each hunter access strategy, there were variations in the number of hunters, intensity of hunting, and harvest risk. However, we believe our classification of hunter access generally correlated with differing levels of hunting pressure and allowed for inferences about elk responses to different hunter access strategies.

Although elk responded most strongly to the regulation-access covariate, elk also responded to landscape variables included in our analysis. The varying selection for and avoidance of security habitat did not align with our prediction (Ranglack et al. 2017), potentially reflecting varying seasonal habitat preferences for canopy cover between hunting periods (Snobl et al. 2023). The weak selection for SWE across hunting periods also did not align with our prediction and other research demonstrating avoidance (Ranglack et al. 2017, Snobl et al. 2023), potentially driven by elk use of higher elevations or other landscape features associated with snow. Contrary to our prediction and other research (Sergeyev et al. 2020), elk avoided terrain ruggedness across all hunting periods, suggesting that elk in this area do not use rugged terrain to avoid harvest risk from hunting. Aligning with our prediction and other research (Proffitt et al. 2013), elk did generally select for greater slopes. Elk selection for aspect and land cover varied between hunting periods, likely reflecting seasonal habitat preferences.

The harvest regulations and hunter access management implemented on the BTWMA concentrated elk over the course of the hunting seasons, maintaining elk on public land and achieving an elk distribution that reduced conflict with agricultural producers. The only portion of the study area where the no harvest and restricted harvest regulation occurred was HD 455, primarily composed of the BTWMA. Additionally, the BTWMA in the late shoulder season was the only parcel area classified as a limited access strategy that allowed no access. Elk selection for the BTWMA increased throughout the hunting season, notably increasing during the general season as hunting pressure increased. Other research has found that reducing hunter numbers by 50% did not reduce elk movement to inaccessible land (Vieira et al. 2003), but it appears the restricted harvest regulations in HD 455 effectively maintained elk on or attracted elk to public lands in the general season. The strongest selection for the BTWMA occurred when harvest risk was eliminated through both harvest regulation and access strategy during the late shoulder season.

Seasonal changes in habitat preferences may also contribute to elk movements to the BTWMA, where harvest regulations are more restrictive. Movements to the BTWMA are considered migratory movements and may be driven in part by pre-existing cultural knowledge of the migratory route and seasonal habitat preferences for winter range. However, this elk population is only partially migratory (56% migratory), with a high degree of switching between migratory and resident behaviors (44% of monitored elk switched at least once). The flexibility of these seasonal movement behaviors suggests that migratory movements could largely be considered a behavioral choice in this population. Additionally, historical data indicate that liberal harvest on the BTWMA in the 1990s was associated with much smaller wintering elk numbers, further supporting the idea that fall movements to the BTWMA are influenced by harvest risk. In this context, migratory behavior may influence elk responses to harvest risk, but harvest risk may also impact elk migratory behavior and seasonal movement patterns (Mikle et al. 2019).

The current consensus from managers and landowners in the area prioritizes the role of the BTWMA to reduce conflict with agricultural producers, so our results support that those objectives are being met. However, this elk population is currently over the population abundance objective outlined in the state elk management plan, and the use of the BTWMA by large numbers of elk may be hampering hunter harvest (Montana Department of Fish, Wildlife and Parks 2023). If priorities for elk management in the area change, access strategies and harvest regulations in the BTWMA may need to be reconsidered.

MANAGEMENT IMPLICATIONS

Our results demonstrate that both hunter access and harvest regulations are important drivers of elk movements and resource selection during the hunting season. Although hunter access may be challenging for wildlife managers to influence in many cases, our results suggest that restricted female harvest regulations reduced elk perceptions of risk. Applying restrictive harvest regulations in areas where elk are desired may encourage elk to maintain or increase their use of these areas, particularly during periods of heavy hunting pressure. Additionally, our findings suggest that the application of restrictive harvest regulations on public lands may reverse elk movements to less accessible private lands that occur early in the hunting season.

Although restricted harvest regulations or limited hunter access may successfully increase elk presence in desired areas, such intentional creation of refuges may have other consequences. Decreasing harvest risk in these areas may limit hunter harvest and make it more difficult to achieve population objectives. Priorities vary between areas, and this approach may not be acceptable in other contexts, highlighting the need to thoroughly understand stakeholder priorities and make decisions accordingly. In complex landscapes of public and private ownership, managers and stakeholders may have to prioritize between distribution and population size management objectives for elk populations and identify appropriate management actions.

ACKNOWLEDGEMENTS

We thank A. Kunkel, J. Kolbe, J. Jones, J. Doggett, and M. Evans for their assistance with this project. We thank C. Hansen, J. Gude, T. Verzuh, and 2 anonymous reviewers for their comments to improve this manuscript. Funding was provided by Montana Fish, Wildlife & Parks through Elk Habitat Management in Montana PR Grant W-179-R and DOI Secretarial Order 3362 Grant #F19AP00849.

DATA AVAILABILITY STATEMENT

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

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal capture efforts were performed in accordance with Montana Department of Fish, Wildlife & Parks animal welfare protocols (permit number FWP09-2019).

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Associate Editor: Tana Verzuh.

SUPPORTING INFORMATION

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

How to cite this article: Bealer, N. P., S. M. Petch, J. J. Rotella, J. D. DeVoe, C. Loecker, and K. M. Proffitt. 2026. Evaluating the impact of hunter access and harvest regulations on elk movement and resource selection. Journal of Wildlife Management 90:e70170. https://doi.org/10.1002/jwmg.70170