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Research Article

Hunter Access Affects Elk Resource Selection in the Missouri Breaks, Montana

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ABSTRACT Elk (*Cervus canadensis*) populations that exceed socially tolerable population levels create problems with private landowners over property damage and competition with livestock. Increasing harvest of adult female elk is the primary management tool for curtailing elk population growth and reducing elk populations. However, this tool is not effective when elk are not accessible to hunters during hunting seasons. The purpose of this project was to evaluate the effects of hunter access and other landscape factors on second-order and third-order elk resource selection during the archery and rifle hunting seasons in 2 populations: the Missouri River Breaks (MRB) and Larb Hills, Montana, USA. In our resource selection models, we first treated the individual elk-year as the sampling unit to estimate individual-level selection coefficients and second, we pooled data from all individuals to estimate population-level selection coefficients. Second-order population-level selection coefficients indicated that elk in MRB and Larb Hills selected home ranges in areas with no hunter access, and hunter access was the strongest predictor of second-order selection. Similarly, third-order population-level selection coefficients indicated elk in both populations selected locations within their seasonal home range with no hunter access, and the strength of selection for locations with no hunter access was stronger in the archery season than the rifle season. However, individual models revealed that although third-order population-level selection for locations with no hunter access was strong, only 46% of elk in the MRB selected for no hunter access during the archery season and 24% of elk selected for no hunter access during the rifle season. Additionally, the majority of all elk locations in the MRB (i.e., 68% of archery locations, 91% of rifle locations) occurred in areas accessible to hunters. These results highlight that population-level selection coefficients may not always represent individual selection patterns, and we recommend employing a combination of population-level and individual animal models as the basis of developing biological inferences. Even if hunter access is restricted in a relatively small geographic area within an elk population range, those areas may have a disproportionate effect on elk distributions and prevent effective harvest of female elk to maintain populations at objective levels (i.e., 1,700–2,000 elk). Working cooperatively with stakeholders to minimize elk harboring is necessary for curtailing further elk population increases and maintaining a distribution of elk across public and private lands.

KEY WORDS *Cervus canadensis*, elk security, hunting season, northern Great Plains, refuge areas, resource selection.

Elk (*Cervus canadensis*) populations across the western United States have increased over the last half century as elk management has focused on limited antlerless harvest and increased habitat security for males during fall hunting seasons as a means of conserving elk populations while maintaining high levels of hunter opportunity (Lonner and Cada 1982, Hillis et al. 1991, Picton 1991, O'Gara and Dundas 2002). More recently, elk populations in some areas exceeded socially tolerable population levels, resulting in increased conflicts with private landowners over crop damage and competition with livestock (Bunnell et al. 2002, Haggerty and Travis 2006). In many of these areas where growing elk populations are becoming increasingly problematic, wildlife managers are faced with the challenge of reducing elk populations. The primary management tool for reducing elk populations is increasing the number of adult female elk hunting licenses and the adult female harvest. However, for harvest to be an effective tool in reducing adult female survival and limiting population growth, sufficient numbers of female elk must be accessible to hunters for harvest. With many of these elk populations exhibiting increased use of lands that restrict hunter access to elk during hunting seasons, wildlife managers face a difficult challenge

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as they attempt to maintain elk populations at socially acceptable levels (Haggerty and Travis 2006).

In areas that include a matrix of lands with varying levels of hunter access, elk may alter their behavior by increasing use of areas that restrict hunter access instead of using traditional security areas on public lands during the hunting season (Burcham et al. 1999; Conner et al. 2001; Proffitt et al. 2010, 2013). Because the current geographic range of elk and problems associated with increasing elk populations have been concentrated around the montane and forested regions of the western United States, the majority of research has taken place in these environments (O'Gara and Dundas 2002, Skovlin et al. 2002). Relatively less is known about how elk use the landscape in plains or prairie environments (McCorquodale and Eberhardt 1990, Strohmeyer and Peek 1996), and the effects of hunting pressure on elk in these environments (Millspaugh et al. 2000, Sawyer et al. 2007). In contrast to elk in montane environments, elk in the prairie environments have access to less hiding cover and are more visible from greater distances to hunters. Information on habitat security (Hillis et al. 1991), how elk respond to hunting pressure (Burcham et al. 1999, Proffitt et al. 2010), and factors that contribute to elk vulnerability (Hurley and Sargeant 1991, Gratson and Whitman 2000, Hayes et al. 2002) in montane and coniferous forest habitats may or may not be applicable in plains prairie habitats. For example, management of elk habitat in fall has traditionally focused on maintaining blocks of timbered hiding cover or roadless areas; however, hiding cover is sparse in prairie environments and the size of roadless areas that may provide security for elk in the open prairie environment is unknown. Therefore, additional information regarding elk habitat selection during the hunting seasons in prairie environments is needed.

Recent expansions of elk populations in the prairie regions have created a need for more information on how elk are using the prairie landscape and how elk in these regions respond to hunting pressure. In the Missouri River Breaks, north-eastern Montana, USA, elk populations have increased in the last decade, and managers have struggled to achieve the level of adult female harvest necessary to maintain elk populations within objective levels set by the Montana Department of Fish, Wildlife, and Parks (MFWP). In response to increasing populations during 2004–2006, wildlife managers nearly doubled the number of antlerless hunting licenses in this area and were successful in increasing female harvest levels. However, in spite of maintaining adult female elk hunting opportunity, hunter success rates steadily decreased from 40% in 2007 to only 10% by 2014 (MFWP, unpublished data). This steady decline in the harvest rate of female elk has resulted in the population increasing to levels above population objective, and the declines in hunter success, in spite of growing elk population size, is difficult to understand. The area includes a matrix of public and private lands with varying levels of hunter access, and some stakeholders attribute declining hunter success to elk concentrating on areas without hunter access to elk. However, the degree to which elk use areas that restrict hunter access and the proportion of the herd that is available for harvest is unknown. The seasonal redistribution of elk to areas that restrict hunter access is documented in montane systems across the western United States where elk often move from higher elevation, accessible summer ranges to lower elevation, less accessible winter ranges. The situation in the Missouri River Breaks and other prairie areas differs in that elk are not distributed across distinct seasonal ranges and may use any portion of their annual range during the hunting seasons. Elk management in the Missouri River Breaks is highly scrutinized, highlighting the need for biological information to inform wildlife managers balancing a complex set of social, economic, and political influences. The goal of this project was to evaluate the effect of hunter access and other landscape factors on elk distribution during the archery and rifle hunting seasons.

STUDY AREA

We conducted this study in the Missouri River Breaks 100 km northeast of Lewistown, Montana, USA (Fig. 1). The study area included portions of hunting districts (HD) 621, 622, 631, 632, and 410. Land adjacent to the Missouri River was primarily owned by the United States Fish and Wildlife Service (USFWS), Charles M. Russell Wildlife Refuge. The study area was 4,963 km^2 and included upland sagebrush and mixed-grass prairies dominated by big sagebrush (*Artemisia tridentata*) and various species of wheatgrass (*Agropyrom* spp.); badlands composed of deep coulees with steep rocky slopes containing Rocky Mountain juniper (*Juniperus scopulorum*), ponderosa pine (*Pinus ponderosa*), Douglas fir (*Psuedotsuga menziesii*), choke cherry (*Prunus virginiana*), and western snowberry (*Symphoricarpos occidentalis*); and riparian areas along the Missouri River containing plains cottonwoods (*Populus sargentii*), various species of willow (*Salix* spp.), and western snowberry (Dood 1978, Watts et al. 1987). Irrigated croplands represented <1% of the study area. Elk are sympatric with mule deer (*Odocoileus hemionus*), whitetail deer (*O. virginianus*), and bighorn sheep (*Ovis canadensis*). Coyotes (C*anis latrans*) and mountain lions (*Puma concolor*) also occupy the study area. Elevations in the study area ranged from 630 m to 1,750 m.

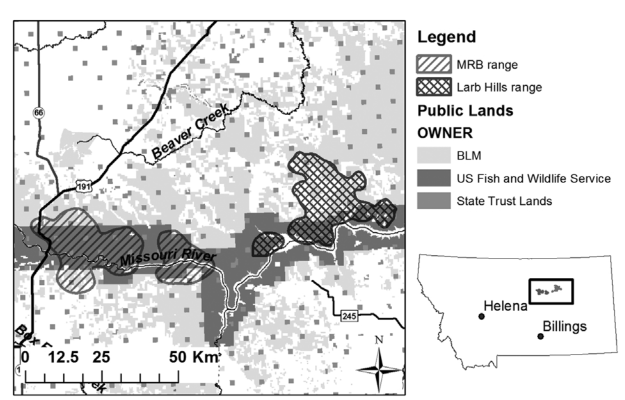

Figure 1. Missouri River Breaks (MRB) and Larb Hills elk population ranges in the Missouri River Breaks area of northeastern Montana, USA. Public land ownership includes the Bureau of Land Management (BLM), United States Fish and Wildlife Service, and State of Montana trust lands.

Seasonal temperatures range from lows of -10 to $-15°C$ in winter to highs of 25–29°C in summer. Average annual precipitation was 25–36 cm, 20–30% of which occurred as snowfall. During the September–November hunting seasons, average high temperature was $-1.1°C$ and average precipitation was 6.4 cm.

The study area included 2 adjacent elk populations, the MRB population in the western portion of the study area and the Larb Hills population in the eastern portion of the study area (Fig. 1). Elk population trend is measured by biennial winter aerial surveys conducted by MFWP. The elk population count decreased to 2,596 elk in 2014 from a high of 4,226 in 2006 but is still 30% above the desired population level of 1,700–2,000 elk (MFWP 2005). Elk hunting is by permit or special license through a drawing only. In the study area, the primary elk management tool for moving the population up or down toward objective levels has been an antlerless elk hunting license or permit valid during the 5-week rifle hunting season. During this study, approximately 2,000 either-sex and antlerless elk licenses or permits were issued annually for hunting during the archery season and 1,175 were issued annually for hunting during the rifle season. Annually, hunter pressure was approximately 9,679 hunter-days during the archery season and 5,324 hunter-days during the rifle season.

METHODS

We captured 25 adult (i.e, ≥1.5 years old) female elk in the MRB and 25 adult female elk in the Larb Hills population by helicopter netgunning on their winter ranges during February 2013. All animals were captured and handled according to the MFWP biomedical protocols for free-ranging cervidae in Montana. We fitted elk with store-on-board global positioning system (GPS) radiocollars (Lotek Wireless, model 3300L, New Market, Ontario, Canada) that were built with a timed release mechanism set to release the collar after 2 years. We programmed collars to record hourly locations 24 hours a day from February 2013 to February 2015 and to emit a distinct mortality signal if the collar was stationary for >6 hours. We monitored elk survival and locations monthly for 2 years using aerial and ground telemetry. After collars released, we retrieved collars and downloaded the location data. We used these locations in our resource selection analyses.

We evaluated potential effects of 5 covariates on elk resource selection: distance to dense cover, distance to roads, terrain roughness, hunter access, and land cover type. We defined dense cover based on the canopy cover land cover product from LANDFIRE (www.landfire.gov) and considered areas with ≥40% canopy cover as dense cover. We used Montana Department of Transportation data to define roads on private and state lands, and a local Bureau of Land Management (BLM) and USFWS roads layer to define motorized routes on BLM and USFWS lands, respectively. We defined terrain roughness based on a 30-m digital elevation model (DEM). We estimated terrain roughness as the amount of elevation difference between a given pixel of the DEM and all of its neighbors (Riley et al. 1999). We classified hunter access into 3 categories: accessible to public hunting, no public hunting, and limited or restricted public hunting. Accessible areas included public lands that allowed hunting and all privately owned lands either enrolled in a State of Montana's Block Management program (http://fwp.mt.gov/hunting/hunterAccess) or that did not restrict public hunter use. Areas without public hunting included a public land wildlife viewing area that prohibited hunting and privately owned lands that prohibited access to the public through lease agreements with paying clients. Areas with limited or restricted public hunting included private lands that charged a trespass fee or allowed for hunting without a fee to only family and friends. We defined land cover type based on the Montana Spatial Data Inventory land cover model. We broadly classified land cover into 4 categories: grasslands and shrublands, badlands, forest, and riparian. All non-habitat (i.e., developed areas, rivers, lakes) were clipped from land cover data and clipped from population and individual home ranges so no used or available points were generated or located in non-habitat areas.

Resource Selection Model Development

To evaluate factors affecting elk distributions during the hunting seasons, we evaluated the second-order selection of hunting season home ranges within population home ranges (S_2), and the third-order selection of hunting season locations within individual home ranges (S_3; DeCesare et al. 2012) using a use-available sampling design (Manly et al. 2002, Johnson et al. 2006). We separated the hunting season into archery and rifle seasons. We evaluated second-order selection by comparing individual archery and rifle season home ranges within the available population-level archery or rifle season range. We estimated individual and population-level ranges using 95% fixed-kernel isopleths calculated using the bivariate normal kernel (Worton 1989). We sampled the individual home range by generating 1,000 random points within each home range. This sample represented the used home range locations. We did not consider the actual elk locations within the home range as the used sample because contrasting the individual locations with population-level availability would represent selection somewhere between the second- and third-order, rather than the second-order. We randomly generated 5 available locations per used location for 5,000 available locations per individual within the population-level hunting season range to represent the available choice set. We identified a set of 5 biologically plausible hypotheses about how elk may position their archery and rifle season home ranges, and expressed various combinations of these hypotheses as 32 competing models. These competing models included all combinations of the 5 covariates and the null model.

We evaluated third-order selection by comparing individual hunting season locations within the available individual hunting season home range. We estimated individual archery season and rifle season home ranges using 95% fixed-kernel isopleths calculated using the bivariate normal kernel (Worton 1989). We randomly generated 5 available locations per used location within the individual home range to represent the available choice set. In the third-order analysis, we evaluated the same set of 32 competing models as described previously.

We used generalized linear models with a binomial distribution to compare attributes of used and available locations. After identifying a set of biologically plausible covariates for second-order and third-order selection, we evaluated all potential model combinations. We screened covariates for collinearity and eliminated models containing covariates with $|r| > 0.7$ (Dormann et al. 2013). We standardized all continuous covariates. We fit models in Program R and selected the best model for each individual based on the lowest Akaike's Information Criterion (AIC) score. First, we treated the individual animal-year as the sampling unit. This approach allowed us to evaluate individual animals' patterns of selection and assess individual and annual variations in selection. However, because some individuals rarely used areas with no hunter access and other individuals almost always used areas with no hunter access, we were unable to estimate the hunter access selection coefficient properly (i.e., there was complete or quasi-complete separation in the used locations dataset). Therefore, we were unable to use the coefficients and standard errors from models with animal-year as the sampling unit to estimate population-level selection coefficients. Instead, to estimate the population-level resource selection coefficients, we conducted a second model selection process using a dataset that included pooled data from all individuals and years. We selected the best model for each individual based on the lowest AIC score and used Akaike model weights (w_i) to quantify the support from the data for each of our hypothesized models. In this analysis, the variance of the selection coefficients was underestimated because it accounted for only the location-level variance but not the variance among individual animals, and individuals that died during the sampling period were underrepresented in estimation of selection coefficients. We chose not to use a mixed-effects modeling approach with individual as the random effect, which would have accounted for the different number of locations per individual, because this approach would not have correctly estimated effects of hunter access for the individuals that always or never used areas with hunter access. The second analysis with population as the sampling unit allowed us to estimate the overall population's patterns of selection.

Last, to evaluate the effects of hunter access on elk behavioral responses, we investigated whether third-order selection patterns varied across individual elk-years exposed to different levels of hunter access. For each animal-year, we estimated the proportion of the archery or rifle season home range accessible to hunters and selection coefficients from the individual animal global models representing the effects of all covariates on selection. We then tested for a relationship between selection coefficients and the proportion of the home range accessible to hunters using a linear model. We expected to find a negative relationship between the selection coefficient for distance to cover and proportion of hunter access, indicating that elk exposed to higher levels of hunter access showed stronger selection for locations near dense cover. We expected to find a positive relationship between the selection coefficient for distance to roads and proportion hunter access, and the selection coefficient for terrain roughness and proportion hunter access, indicating that elk exposed to higher levels of hunter access showed stronger selection for locations farther from roads and in rough terrain.

RESULTS

We retrieved radio-collar location data from 46 elk within the study area. Fifteen elk died during the 2-year monitoring period. Hunter harvest was the primary source of elk mortality. Of the 9 elk legally harvested, 8 were harvested in areas accessible to hunters and 1 was harvested on private land that did not allow public hunter access.

The 2013–2014 MRB population archery season range was 87% publicly owned and approximately 97% was accessible to hunters. Two percent of the archery season range allowed no hunter access and 1% restricted hunter access. A 5.1-km^2 wildlife viewing area in the southern part of the range was closed to all hunting, as were several small, private parcels scattered across the range. Land cover within the archery season range included 21% forests, 6% riparian, 16% badland, and the remainder grassland and shrubland. Irrigated croplands comprised 0.2% of the range, and 6% of these lands were located in areas allowed public access. Motorized roads were common and evenly distributed throughout the range, and the average distance to a motorized road was 11.0 ± 8.8 km (SD). Dense cover was distributed across the range primarily along riparian corridors, and average distance to cover was 5.6 ± 7.0 km. The 2013–2014 MRB population rifle season range had 90% overlap with the archery season range.

The 2013–2014 Larb Hills population archery season range was 69% publicly owned, and approximately 79% was accessible to hunters. Eleven percent of the archery range did not allowed public hunter access and 10% restricted hunter access. Several large, adjacent parcels at the core of the range allowed no hunter access or restricted hunter access. Land cover included 10% forests, 2% riparian, 36% badland, and the remainder grassland and shrublands. Irrigated croplands comprised 0.7% of the range, and 57% of these lands were located in areas allowed public access. Motorized roads were common and evenly distributed throughout the range, and the average distance to a motorized road was 11.4 ± 11.8 km. Dense cover was distributed across the range primarily along riparian corridors, and average distance to cover was 6.5 ± 6.6 km. The 2013–2014 Larb Hills rifle season range had 86% overlap with the archery season range.

Second-Order Selection

In the MRB, the best archery season resource selection model varied among individuals. Elk most commonly selected for home ranges near dense cover ($n = 27$) and in rough terrain ($n = 25$; Table 1). Of the 15 individual elk sampled in 2 years, 6 selected for areas with hunter access in both years, 8 selected for areas with restricted or no hunter access in both years, and 1 selected for areas with hunter

Table 1. The covariates and hypotheses evaluated in second-order resource selection models for elk in the Missouri River Breaks (MRB) and Larb Hills, Montana, USA, 2013–2014, during archery and rifle season and the number of occasions that each hypothesis was supported by a covariate with a confidence interval that did not include zero in individual animals' top-ranked models.

		MRB		Larb Hills	
Covariate	Hypothesis	Archery	Rifle	Archery	Rifle
Badlands	Animals select for badlands over grassland and shrublands	18	18	14	14
Riparian	Animals select for riparian areas over grassland and shrublands	14	12	1	1
Forest	Animals select for forested areas over grassland and shrublands	9	11	3	5
No access	Animals select areas that do not allow public hunter access	16	8	24	18
Restricted access	Animals select areas that restrict hunter access	5	4	17	13
Terrain roughness	Animals select for more rugged terrain that may limit hunter access	25	25	14	13
Distance to cover	Animals select areas closer to dense forest cover	27	27	17	19
Distance to road	Animals select areas away from roads	7	6	8	7
Total elk-years		37	33	43	38

Table 2. The standardized population-level coefficients and 95% confidence intervals (in parentheses) representing the effects of covariates on second-order elk resource selection during the archery and rifle hunting seasons in the Missouri River Breaks (MRB) and Larb Hills, northeastern Montana, USA, 2013–2014.

	MRB		Larb Hills	
Covariate	Archery	Rifle	Archery	Rifle
Badland	0.23 (0.19, 0.26)	0.42 (0.37, 0.46)	−0.07 (−0.11, −0.06)	−0.04 (−0.07, −0.01)
Riparian	0.62 (0.57, 0.67)	0.75 (0.69, 0.81)	−0.12 (−0.22, −0.04)	−0.25 (−0.35, −0.16)
Forest	0.10 (0.07, 0.13)	0.18 (0.15, 0.21)	−0.05 (−0.08, −0.01)	0.09 (0.05, 0.12)
No access	1.68 (1.63, 1.74)	0.14 (0.06, 0.22)	0.48 (0.45, 0.52)	0.31 (0.27, 0.34)
Restricted access	−0.29 (−0.46, −0.12)	−0.64 (−0.83, −0.45)	0.01 (−0.04, 0.04)	0.02 (−0.02, 0.06)
Terrain roughness	0.17 (0.16, 0.19)	0.20 (0.18, 0.21)	0.01 (−0.01, 0.02)	0.03 (0.01, 0.04)
Distance to cover	−0.29 (−0.31, −0.28)	−0.39 (−0.41, −0.37)	0.07 (0.06, 0.08)	−0.07 (−0.09, −0.06)
Distance to road	−0.26 (−0.27, −0.24)	−0.12 (−0.13, −0.11)	−0.07 (−0.08, −0.05)	−0.11 (−0.12, −0.09)

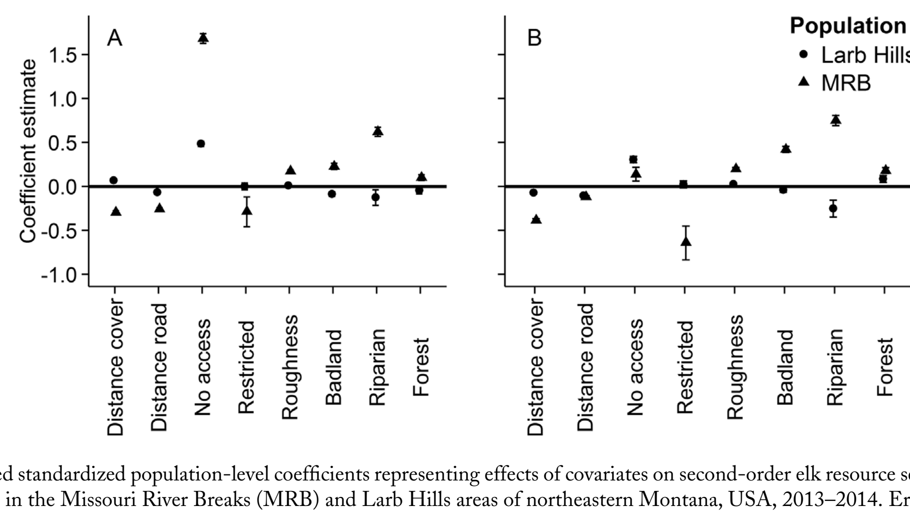

Figure 2. The estimated standardized population-level coefficients representing effects of covariates on second-order elk resource selection during the archery (A) and rifle (B) season in the Missouri River Breaks (MRB) and Larb Hills areas of northeastern Montana, USA, 2013–2014. Error bars represent the 95% confidence interval.

access in 1 year but not the second year. The best population-level archery season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk strongly selected for home ranges in areas with no hunter access over areas with hunter access ($\hat{\beta} = 1.68$, 95% CI = 1.63–1.74; Table 2 and Fig. 2).

In the MRB, the best rifle season resource selection model varied among individuals. Elk most commonly selected for home ranges near dense cover ($n = 27$; Table 1). Of the 13 individual elk sampled in 2 years, 5 elk selected for areas with hunter access in both years, 6 elk selected for areas with restricted or no hunter access in both years, and 2 elk selected for areas with hunter access in 1 year but not the second year. The best population-level rifle season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk strongly select home ranges in

Table 3. The covariates and hypotheses evaluated in third-order resource selection models for elk exposed to archery and rifle hunting risk in the Missouri River Breaks (MRB) and Larb Hills, Montana, USA, 2013–2014, and the number of occasions that the covariate was included with a confidence interval that did not include zero in individual animals' top-ranked models.

		MRB		Larb Hills	
Covariate	Hypothesis	Archery	Rifle	Archery	Rifle
Badlands	Animals select for badlands over grassland and shrublands	14	20	2	4
Riparian	Animals select for riparian areas over grassland and shrublands	22	11	10	3
Forest	Animals select for forested areas over grassland and shrublands	7	1	17	1
No access	Animals select areas that do not allow public hunter access	17	8	33	27
Restricted access	Animals select areas that restrict hunter access	27	17	29	12
Terrain roughness	Animals select for more rugged terrain that may limit hunter access	12	7	5	9
Distance to cover	Animals select areas closer to dense forest cover	22	22	22	20
Distance to road	Animals select areas away from roads	17	25	31	27
Total elk-years		37	33	43	38

riparian areas over grasslands and shrublands ($\hat{\beta} = 0.75$, 95% CI = 0.69–0.81; Table 2 and Fig. 2).

In Larb Hills, the best archery season resource selection model varied among individuals. Elk most commonly selected for home ranges in areas with no hunter access ($n = 24$; Table 1). Of the 20 individual elk sampled in 2 years, 6 selected for areas with hunter access in both years, 8 selected areas with restricted or no hunter access in both years, and 4 elk selected for areas with hunter access in 1 year but not the second year. The best population-level archery season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk strongly selected for areas with no hunter access over areas with hunter access ($\hat{\beta} = 0.48$, 95% CI = 0.45–0.52; Table 2 and Fig. 2).

In Larb Hills, the best rifle season resource selection model varied among individuals. Elk most commonly selected for home ranges in areas near dense cover ($n = 19$; Table 1). Of the 17 individual elk sampled in 2 years, 5 elk selected for areas with hunter access in both years, 9 selected areas with no hunter access in both years, and 3 selected for areas with hunter access in 1 year but not the second year. The best population-level rifle season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk strongly selected for areas with no hunter access over areas with hunter access ($\hat{\beta} = 0.31$, 95% CI = 0.27–0.34; Table 2 and Fig. 2).

Third-Order Selection

In MRB, 68% of all archery season locations occurred in areas accessible to hunters, 30% occurred in areas with no hunter access, and 2% occurred in areas with restricted hunter access. The best archery season resource selection model varied among individuals. Within their annual archery season home range, elk most commonly selected for locations with restricted hunter access ($n = 27$; Table 3). Of the 15 individual elk sampled in 2 years, 1 elk selected for areas with hunter access in both years, 11 selected for areas with restricted or no hunter access in both years, and 3 selected for areas with hunter access in 1 year but not the second year. The best population-level archery season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk selected strongly for locations that restricted ($\hat{\beta} = 1.73$, 95% CI = 1.63–1.83) or did not allow hunter access ($\hat{\beta} = 0.93$, 95% CI = 0.90–0.97) over areas with hunter access (Table 4 and Fig. 3)

In MRB, 91% of all rifle season locations occurred in areas accessible to hunters, 9% occurred in areas with no hunter access, and <1% occurred in areas with restricted hunter access. The best rifle season resource selection model varied among individuals. Elk most commonly selected for locations away from roads ($n = 25$; Table 3). Of the 13 individual elk sampled in 2 years, 4 elk selected for areas with hunter access in both years, 6 elk selected for restricted or no hunter access in both years, and 3 elk selected for areas with hunter access in 1 year but not the second year. The best population-level rifle season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk selected for locations in accessible areas over areas that restricted hunter access ($\hat{\beta} = -1.36$, 95% CI = −1.84–0.94), and selected for areas

Table 4. The standardized population-level coefficients and 95% confidence intervals (in parentheses) representing the effects of covariates on third-order elk resource selection during the archery and rifle hunting seasons in the Missouri River Breaks (MRB) and Larb Hills study areas in northeastern Montana during 2013–2014.

	MRB		Larb Hills	
Covariate	Archery	Rifle	Archery	Rifle
Badland	−0.08 (−0.13, −0.04)	0.30 (0.26, 0.34)	−0.24 (−0.27, −0.21)	−0.20 (−0.23, −0.17)
Riparian	0.76 (0.72, 0.80)	0.46 (0.40, 0.52)	0.01 (−0.08, 0.09)	−0.17 (−0.28, −0.06)
Forest	0.37 (0.34, 0.41)	−0.32 (−0.36, −0.28)	0.61 (0.57, 0.64)	−0.26 (−0.30, −0.22)
No access	0.93 (0.90, 0.97)	0.54 (0.47, 0.61)	1.39 (1.36, 1.42)	1.03 (1.00, 1.06)
Restricted access	1.73 (1.62, 1.83)	−1.36 (−1.84, −0.94)	0.64 (0.60, 0.67)	−0.41 (−0.46, −0.35)
Terrain roughness	−0.04 (−0.06, −0.02)	−0.06 (−0.08, −0.04)	−0.09 (−0.10, −0.08)	−0.08 (−0.10, −0.07)
Distance to cover	−0.15 (−0.16, −0.13)	−0.39 (−0.41, −0.37)	−0.04 (−0.05, −0.03)	−0.17 (−0.18, −0.15)
Distance to road	0.18 (0.17, 0.19)	0.18 (0.17, 0.20)	0.34 (0.33, 0.35)	0.24 (0.23, 0.26)

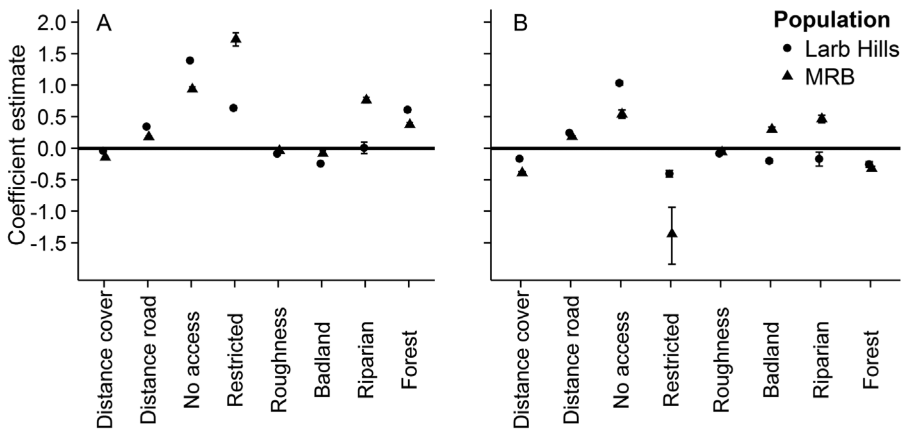

Figure 3. The estimated standardized population-level coefficients representing effects of covariates on third-order elk resource selection during the archery (A) and rifle (B) season in the Missouri River Breaks (MRB) and Larb Hills areas of northeastern Montana, USA, 2013–2014. Error bars represent the 95% confidence interval.

with no hunter access over areas with hunter access ($\hat{\beta} = 0.54$, 95% CI = 0.47–0.61; Table 4 and Fig. 3). During the rifle season, elk selection for locations with no hunter access was weaker than selection for these areas during the archery season (Table 4).

In Larb Hills, 50% of all archery season locations occurred in areas accessible to hunters, 40% occurred in areas with no hunter access, and 10% occurred in areas with restricted hunter access. The best archery season resource selection model varied among individuals. Elk most commonly selected for locations in areas with no hunter access ($n = 33$; Table 3). Of the 20 individual elk sampled in 2 years, 1 elk selected for locations with hunter access in both years, 17 selected locations that restricted or did not allowed hunter access in both years, and 3 elk selected for areas with hunter access in 1 year but not the second year. The best population-level archery season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk selected strongly for locations with no hunter access over areas with hunter access ($\hat{\beta} = 1.39$, 95% CI = 1.36–1.42; Table 4 and Fig. 3).

In Larb Hills, 66% of all rifle season locations occurred in areas accessible to hunters, 29% occurred in areas with no hunter access, and 5% occurred in areas with restricted hunter access. The best rifle season resource selection model varied among individuals. Elk most commonly selected for locations with no hunter access ($n = 27$) and away from roads ($n = 27$; Table 3). Of the 17 individual elk sampled in 2 years, 1 elk selected for locations with hunter access in both years, 13 selected for locations with restricted or no hunter access in both years, and 3 elk selected for locations with hunter access in 1 year but not the second year. The best population-level rifle season model included all covariates ($w_i = 1.0$). The standardized population-level coefficients indicated elk selected strongly for locations with no hunter access over areas with hunter access ($\hat{\beta} = 1.03$, 95% CI = 1.00–1.06; Table 4 and Fig. 3). The strength of selection for locations with no hunter access was stronger during the archery season as compared to the rifle season (Table 4).

Effects of Hunter Access on Elk Selection Coefficients

Across 45 individuals in MRB and Larb Hills and 80 elk-years, the strength of selection for distance to roads, distance to cover, and terrain roughness varied during the archery season with the accessibility of individuals' archery season range. Elk with home ranges having a higher proportion of area accessible to hunters showed stronger selection for locations away from roads ($P = 0.04$, $R^2 = 0.05$; Fig. 4A), stronger selection for locations near dense cover ($P = 0.04$, $R^2 = 0.05$; Fig. 4B), and stronger selection for rougher terrain ($P = 0.001$, $R^2 = 0.13$; Fig. 4C). During the rifle season, elk with more accessible home ranges showed stronger selection for areas near dense cover ($P = 0.05$, $R^2 = 0.05$; Fig. 4E), but the strength of selection for distance to roads and terrain roughness did not vary as compared to elk with less accessible home ranges.

DISCUSSION

In our prairie-breaks study area, elk selected for areas with restricted or no hunter access during the archery and rifle hunting seasons. This behavioral decision to use areas that restrict hunter access as security from harvest-risk during the hunting seasons has been documented in other parts of Montana and the western United States and is an increasing problem that challenges wildlife managers to maintain growing elk populations within socially acceptable levels (Burcham et al. 1999, Skovlin et al. 2002, Proffitt et al. 2013). Although the overall level of hunter access is high in both the Larb Hills and MRB areas, our results suggest that location and size of areas that restrict hunter access may be an important factor in determining elk distributions. In the Larb Hills area, lands restricting hunter access were arranged in a large (~150 km^2) contiguous block near the center of the hunting season ranges. In spite of a relatively small proportion of the overall elk seasonal range having restricted hunter access, elk in Larb Hills disproportionately selected home ranges and locations within home ranges in the area that restricted hunter access. Thus, even relatively small geographic areas within an elk population range being

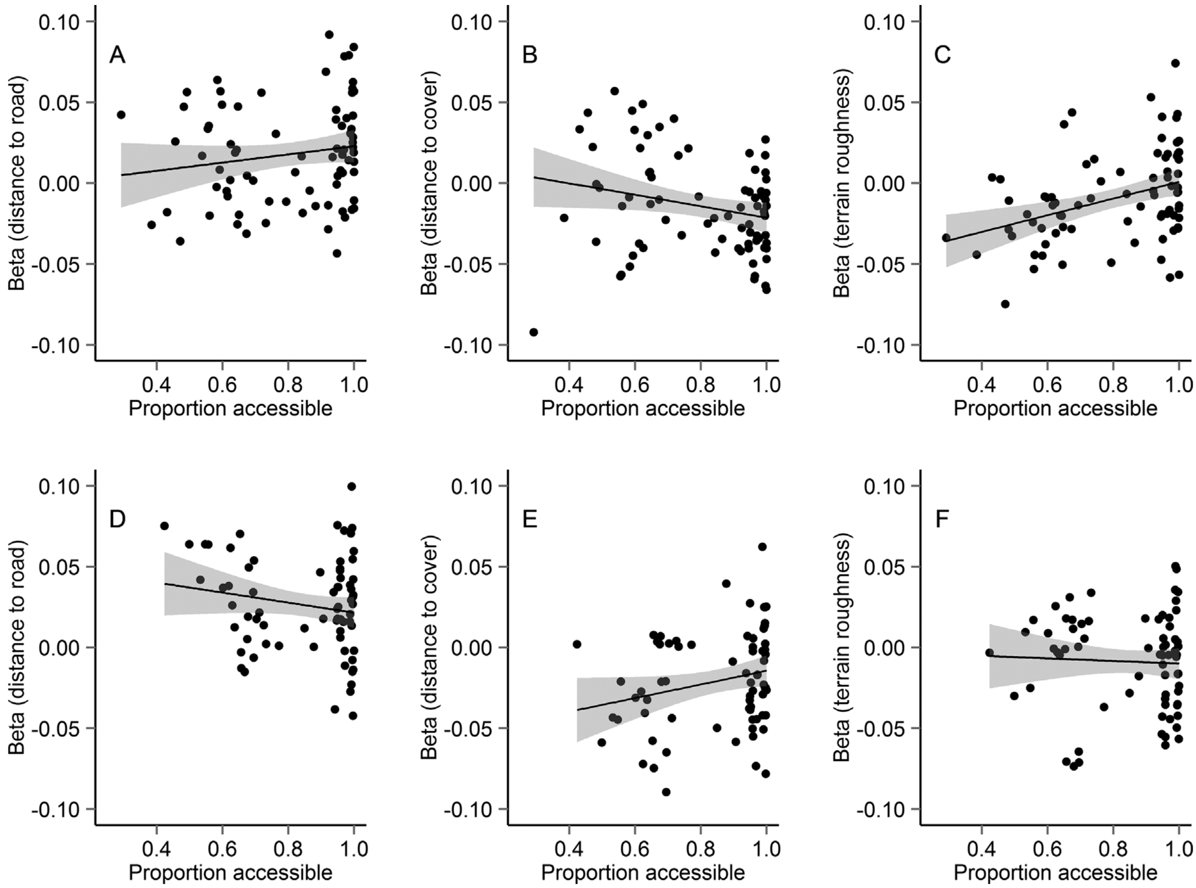

Figure 4. Resource selection coefficients representing the effects of varying proportions of hunter access within elk home ranges on individual elk selection for distance to roads, distance to cover, and terrain roughness in the Missouri River Breaks area of northeastern Montana, USA, 2013–2014. Panels A–C represent selection patterns in the archery season and D–F represent selection patterns in the rifle season.

managed for restricted hunting access may have a disproportionate effect on elk distributions and prevent effective harvest of female elk to maintain elk populations within socially acceptable levels.

Although hunter access may limit the effectiveness of harvest regulations at meeting population objectives in the Larb Hills population, our results suggest that it is unlikely that hunter access is limiting sufficient adult female elk harvest to maintain or reduce the MRB population. In both the MRB and Larb Hills, we found that the majority of adult female elk mortality occurred as hunter harvest during the rifle hunting period, which is consistent with 77% and 79% of the annual hunter harvest in the MRB and Larb Hills, respectively, during the last decade occurring during the rifle season (MFWP, unpublished data). During the rifle season, elk in MRB did select for home ranges and locations in areas with no hunter access. However, areas with no hunter access comprised only a small (<5%) portion of the rifle season elk range and elk primarily used areas accessible to hunters (i.e., 91% of all rifle season elk locations occurred in areas accessible to hunters). Further, individual animal resource selection function analyses indicated only a small proportion of the population selected for home ranges or locations within home ranges with no access during the rifle season. Our resource selection modeling results highlight 2 important issues: population-level coefficients may not accurately represent individual animals' patterns of selection and highly significant and strong population-level selection coefficients may not have highly significant or strong biological meaning. In contrast, Larb Hills elk selected for rifle season home ranges and locations in areas with restricted or no hunter access. In the Larb Hills analyses, treating either the individual elk or the population as the sampling unit, selection for areas that restricted or did not allow hunter access was a behavioral strategy frequently employed by individuals and the population. At the population level for both the Larb Hills and MRB, third-order selection coefficients may have underestimated the strength of selection for areas with hunter access because individuals in these areas were disproportionately harvested, resulting in underrepresentation in the dataset used to estimate population-level selection.

Elk selection for areas with restricted or no hunter access may partially explain recent declines in hunter success, and may limit the effectiveness of further increasing hunter opportunity in an attempt to achieve a sufficient harvest to reduce elk populations to objective levels, unless hunter access issues are simultaneously addressed. Further increasing hunter opportunity has the potential to result in increasing elk selection for areas that restrict hunter access as hunter activity on publicly accessible lands increases, and could exacerbate the problem. Such an approach could also potentially result in lower hunter satisfaction because of hunter crowding issues or perceived hunter crowding issues on lands that are open to public hunting, which has been an issue in the past in this area (Lewis and Herbert 2001). In the Missouri River Breaks, stakeholders may need to determine whether they are willing to tolerate larger elk populations, tolerate higher number of hunters or longer season length, or provide some level of hunting access on currently restricted private land to more hunters to harvest antlerless elk so the population can be reduced to objective levels.

We found that in addition to using areas that restricted hunter access, elk in the study area responded to hunting risk by selecting locations near dense cover and away from roads and the strength of these responses increased for elk that had home ranges with higher levels of hunter access. The effect of roads on elk distributions during the archery and rifle seasons was scale dependent in both populations. The overall weak second-order selection for or against roads at the home range scale may result from roads being distributed throughout the study area, making selection for home ranges in roadless areas impossible. However, within home ranges, third-order selection for locations away from roads was important in both populations during the archery and rifle seasons, as expected. Although elk selection for areas with hiding cover and away from roads is documented in other areas (Hillis et al. 1991, Unsworth et al. 1993, McCorquodale et al. 2003), traditionally secure areas in the Rocky Mountains region are characterized as large blocks (i.e., $\geq$101 ha) of forested cover >0.8 km from a road. These types of areas did not exist in our prairie-breaks study area. Instead, roads are evenly distributed and hiding cover is sparsely distributed in small patches throughout the elk population ranges. Rather than select for secure blocks of habitat with cover and no roads, elk in these areas selected for areas away from roads, smaller patches of dense cover, and rougher terrain to mitigate hunting risk. Additionally, our results indicated that individual elk employed a variety of strategies to mitigate hunting risk. Elk selection varied among individuals and was likely dependent on the relative benefit or risk associated with a combined set of features in a given area.

Elk use of areas that restricted or do not allow hunter access may represent either long-term behavioral adaptations developed and passed down through generations (Boyce 1991), or short-term behavioral responses to fluctuating hunting pressure (Millspaugh et al. 2000, Proffitt et al. 2010). We found that the strength of selection for areas that restricted hunter access varied with the level of hunter pressure between the archery and rifle seasons. The archery and rifle season selection differences that we observed suggests that selection for areas that restrict hunter access may be a short-term response that is at least partially conditional on factors such as hunter pressure that vary on a seasonal or annual basis. If so, managers may have the opportunity to influence elk distributions by manipulating levels of hunting pressure on public and private lands. Additionally, in the prairie-breaks region in Montana, habitat is relatively homogeneous and elk do not have distinct summer, fall, and winter ranges. This homogeneity in habitat allows elk to use any portion of their annual range during the fall hunting seasons, and results in weaker second-order selection for home ranges, in contrast to other areas where variability in terrain and habitat require animals to use distinct seasonal ranges (DeCesare et al. 2012). This habitat homogeneity and behavioral plasticity may increase the likelihood that applying some level of hunter pressure to areas that currently restrict hunter access will result in a redistribution of elk. However, although we found short-term behavioral responses to fluctuating hunting pressure between archery and rifle hunting seasons, individual elk selection patterns were generally consistent between years, which could represent a long-term behavioral adaptation that is more difficult to affect through redistribution of hunting pressure.

The effects of the archery and rifle seasons on elk distributions vary across studies and likely correlate with hunting pressure. Multiple studies have documented that elk more strongly respond to the rifle hunting season with the archery season having relatively little effect on elk distributions (Millspaugh et al. 2000, Johnson et al. 2004, Proffitt et al. 2013); however, in these areas, hunting pressure was higher during the rifle season than the archery season. In our study area, hunting pressure was greater in the archery season than the rifle season. Accordingly, we found that elk selection for most covariates associated with mitigating hunting risk was greater during the archery than the rifle season, similar to other areas with high archery hunting pressure (Vieira et al. 2003). If elk move to areas restricting hunter access during archery season, these effects may carry over into rifle season, leaving fewer elk accessible for harvest during rifle season when the majority of the harvest occurs. We found that elk in MRB moved to more publicly accessible lands during rifle season, but a higher number of elk in Larb Hills remained in areas restricting hunter access after the archery season, limiting the number of elk available for harvest during the rifle season.

MANAGEMENT IMPLICATIONS

In areas where elk populations have exceeded socially acceptable population levels, increasing female elk harvest is necessary to curtail further population increases and reduce the population to acceptable levels. In many areas, hunting licenses are limited because the habitat is relatively open and hunters are concerned with perceived overcrowding during archery and rifle seasons. Given elk populations have exceeded socially acceptable levels, stakeholders may need to decide to accept the current elk populations or give up the exclusivity of the hunting experience. However, increasing the number of hunters may not necessarily result in increasing female elk harvest rates. Increasing hunting pressure on publicly accessible lands could increase the differential in harvest risk across publicly accessible and restricted hunter access lands, resulting in increasing number of elk selecting for areas of restricted hunter access. Additionally, increasing hunter numbers could increase the harvest of elk using publicly accessible lands, reducing this segment of the elk population while allowing the segment of the population that preferentially uses private lands that restrict access to further increase. Ultimately, this situation would not reduce elk populations to objective levels but would increase the proportion of the population using areas hunters cannot access. Cooperation among stakeholders to provide some level of hunter access to elk is necessary for curtailing further elk population increases and maintaining a distribution of elk across public and private lands.

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