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Management and Conservation

Effects of Hunter Access and Habitat Security on Elk Habitat Selection in Landscapes With a Public and Private Land Matrix

KELLY M. PROFFITT,[1] *Montana Department of Fish, Wildlife, and Parks, 1400 South 19th Avenue, Bozeman, MT 59718, USA*
JUSTIN A. GUDE, *Montana Department of Fish, Wildlife, and Parks, 1420 East 6th Avenue, Helena, MT 59620, USA*
KENNETH L. HAMLIN, *Montana Department of Fish, Wildlife, and Parks, 1400 South 19th Avenue, Bozeman, MT 59718, USA*
MATTHEW ADAM MESSER, *Montana Department of Fish, Wildlife, and Parks, 1420 East 6th Avenue, Helena, MT 59620, USA*

ABSTRACT Traditional elk habitat management on public land has focused on providing security habitat for bull elk during the hunting season to provide for both adequate hunter opportunity and bull survival. This paradigm has given less consideration to adult female elk habitat use, patterns of adjacent land ownership, and hunter access. This paradigm also was developed when elk population sizes were much smaller in many areas. In many Rocky Mountain states, the focus of elk population management has recently shifted to reducing or maintaining elk population sizes, necessitating a better understanding of the implications of security habitat management, as well as patterns of adjacent land ownership and hunter access, on adult female elk. We addressed this need by testing the hypotheses that during the hunting season: 1) adult female elk selection for areas prohibiting or limiting hunter access is stronger than elk selection for publicly owned and managed elk security habitat, 2) these effects occur during the archery hunting period and intensify during the rifle hunting period, and 3) the effects of hunter access on selection are consistent among herds that occupy landscapes characterized by a matrix of public and private lands. We used global position system locations collected from 82 females in 2 different Greater Yellowstone Ecosystem (GYE) elk herds to evaluate effects of hunter access, security habitat as defined by the Hillis paradigm, and other landscape attributes on adult female elk resource selection during the pre-hunting, archery, rifle, and post-hunting periods. We found that female elk selection for areas restricting public hunting access was stronger than selection for security habitat in both study areas, and that the density of roads open to motorized use was the strongest predictor of elk distribution. Increases in selection for areas that restricted hunting access occurred during the rifle hunting period, and we did not find consistent evidence these movements were triggered by the archery hunting period. Our results provide evidence that in landscapes characterized by a matrix of public and privately owned lands, traditional concepts of elk security habitat need to be expanded to also include areas that restrict hunter access to plan for elk population management that is regulated through adult female harvest. Future efforts should investigate whether elk use of areas that restrict hunter access are flexible behavioral responses to hunting risk, or if these behaviors are passed from generation to generation such that a learned pattern of private land use becomes the normal movement pattern rather than a short-term behavioral response. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Cervus elaphus*, elk, Greater Yellowstone Ecosystem, Hillis paradigm, hunter access, hunting effects, resource selection, security habitat.

Elk distributions and habitat selection patterns during the hunting period have received considerable study and have been used as the foundation for elk habitat management (Thomas et al. 1979, Unsworth et al. 1998). Traditionally, elk habitat management has been structured around a model that focuses on cover, forage, and road management as the determining parameters of habitat quality (Lyon and Canfield 1991). Management objectives typically have aimed to reduce disturbances associated with roads and preserve timbered habitat to create habitat security for bull elk during the fall hunting seasons (Hillis et al. 1991). Providing adequate security areas makes elk harder for hunters to find, increases elk survival during the hunting season, and therefore allows liberal hunting opportunities that are less costly in terms of elk vulnerability (Hurley and Sargeant 1991, Leptich and Zager 1991, Unsworth and Kuck 1991).

However, the challenges facing elk management have changed in some parts of the western United States (Haggerty and Travis 2006). In many parts of Montana, for example, elk population sizes have doubled since the

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[1]*E-mail: kproffitt@mt.gov*

1980s when the analyses underpinning traditional elk security concepts were completed (Montana Fish, Wildlife and Parks 2005). The focus of elk management in many areas has therefore changed from a strategy designed to ensure elk security and population growth to strategies designed to maintain or reduce elk population sizes through regulated harvest of adult females (e.g., Montana: Montana Fish, Wildlife and Parks 2005; Idaho: Rachel 2010; Wyoming: Wyoming Department of Game and Fish 2010). Traditional elk security concepts, which are based on road density and forested cover (Hillis et al. 1991), and habitat management objectives may need to be re-evaluated and refined in areas where achieving adequate adult female harvest to reach population management goals has been difficult.

Further, newer, non-traditional landowners tend to be amenity-based, rather than commodity-based and may be less inclined to allow general public hunter access to private lands (Gosnell et al. 2006, Haggerty and Travis 2006). Changes in land ownership and its effects on hunter access and elk distributions during the hunting period are often not considered in traditional elk habitat management strategies for adjacent public lands. However, in the rapidly changing landscape of the west, elk may employ flexible strategies for identifying and selecting secure habitat during the hunting season. Instead of using elk security habitat on public lands, elk may find more complete security during hunting seasons by moving to private lands that restrict hunter access or prohibit hunting (Burcham et al. 1999, Proffitt et al. 2010). This response to hunting risk may result in elk herds that spend increasing amounts of time on privately owned lands and limit the ability to manage herd sizes through harvest (Haggerty and Travis 2006). Rather than focusing management actions on creating habitat security on public lands to increase elk populations, many elk managers are now faced with the task of reducing elk populations and providing hunting opportunities on a landscape where elk occupy a matrix of public and private lands with differing amounts of public access. Hunter access to elk is requisite for hunting to be an effective tool to stabilize or reduce elk populations, and management strategies to manage elk associated with these private land refuges need to be defined. Thus, traditional concepts of elk security habitat which consisted of large tracts of heavily timbered and low road density public lands may need to be refined to include private lands that prohibit or restrict hunter access.

The purpose of this project was to quantify the relative effects of hunter access, security habitat, and other landscape attributes on adult female elk resource selection in 2 different Greater Yellowstone Ecosystem (GYE) elk herds during the fall hunting period. General patterns of adult female elk resource selection during the hunting seasons are well documented (e.g., Unsworth et al. 1998, McCorquodale 2003). However, the relative effects of the archery and the rifle periods on adult female elk habitat selection patterns are not well studied, and the relative strength of selection by female elk for areas with limited hunter access on private land and public land security habitat have not been compared. Our goals were to test the hypotheses that during the hunting season: 1) female elk selection for areas prohibiting or severely limiting hunter access is stronger than selection for publicly owned and managed elk security habitat, 2) these effects become manifest during the archery hunting period and intensify during the rifle hunting period, and 3) the effects of hunter access on selection are consistent between our 2 study herds that occupied similar landscapes characterized by a matrix of public and private lands.

STUDY AREA

We collected data from adult female elk in 2 GYE herds: the East Madison Valley herd (2005–2006) and the West Paradise Valley herd (2009; Fig. 1). The East Madison Valley served as

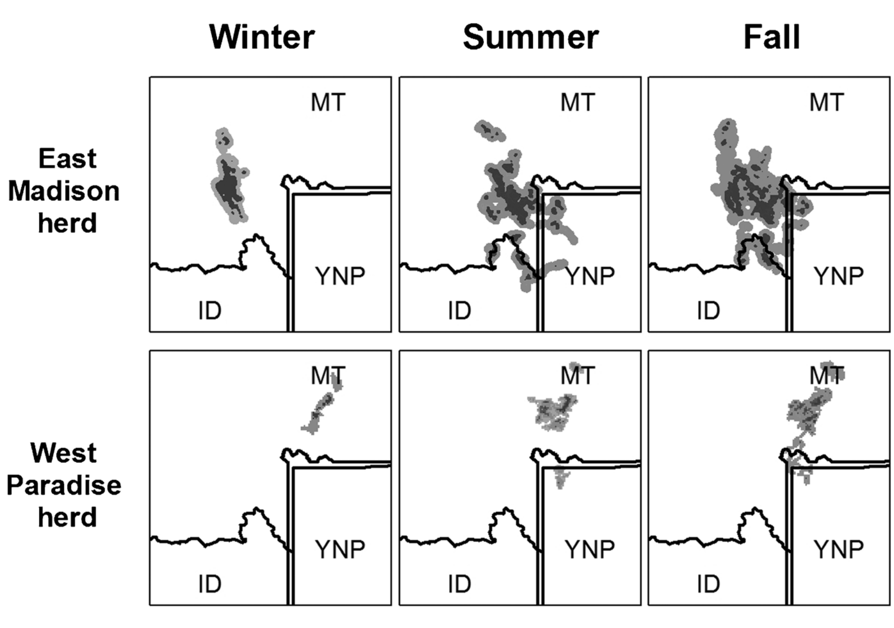

Figure 1. The 60% (darker gray) and 90% (lighter gray) kernel density distribution of telemetry-collared adult female elk in the East Madison Valley and West Paradise Valley elk herds, during winter (1 Jan–28 Feb), summer (1 Jul–31 Aug) and fall (1 Sep–30 Nov) 2005–2006 (East Madison Herd) and 2009 (West Paradise Herd). Figures show elk distributions in Montana (MT), Idaho (ID), and Yellowstone National Park (YNP).

a winter range for a migratory herd of approximately 5,000 elk (see Gude et al. 2006 for additional information). Wintering area lands were primarily large tracts of private ranchlands grazed by livestock and surrounded by National Forest, Bureau of Land Management, and state-owned lands. Summer ranges for this elk herd included mountainous National Forest lands to the south and east of the wintering area, as well as the western edge of Yellowstone National Park (YNP). One pack of 3–6 wolves used this area during the study period. During the fall hunting season, these elk primarily occupy Montana Hunting Districts 362, 361, and 310, or YNP. In Hunting Districts 361 and 362 in the Madison Valley, unlimited brow-tined bull and antlerless hunting were permitted throughout the general archery and rifle period during 2005–2006. Hunter effort averaged an estimated 1,250 hunters, 9,600 hunter-days, and approximately 400 elk were harvested annually in these Hunting Districts. Approximately 30–40% of the hunters in these districts held archery stamps annually. In district 310, the Gallatin Canyon, unlimited brow-tined bull and antlerless hunting were permitted during the general archery period during 2005–2006, and unlimited brow-tined bull hunting was permitted during the general rifle period during 2005–2006. Hunter effort was an estimated at 750 hunters, 4,800 hunter-days, and approximately 60 elk were harvested annually in Hunting District 310. Approximately 40–50% of the hunters in Hunting District 310 hold archery stamps annually. No hunting is permitted within YNP.

The western Paradise Valley area between Eightmile Creek and Tom Miner Basin served as a wintering range for a herd of approximately 3,000 elk. Wintering areas for the western Paradise Valley herd also were large tracts of private ranchlands grazed by livestock and surrounded by National Forest. Summer ranges included higher elevation National Forest lands, lower elevation privately owned areas adjacent to the wintering range, and the northwestern portion of YNP. No known wolf pack was established in the area during the study period, although transient wolves likely used the area. During the fall hunting period, animals in this herd primarily occupied Montana Hunting District 314. Unlimited brow-tined and antlerless elk hunting is permitted during archery and rifle periods. One thousand additional antlerless licenses were available during the 2009 hunting season. Hunter effort was estimated at 2,000 hunters, 14,000 hunter-days, and approximately 800 elk were harvested annually in Hunting District 314. Approximately 25–30% of the hunters in Hunting District 314 hold archery stamps annually.

METHODS

Data Collection

We captured and collared 49 adult female elk on the Madison Valley winter range and 45 adult female elk on the western Paradise Valley winter range. We darted all animals from a helicopter in February and fitted them with global positioning system (GPS) collars (Model GPS3300L; Lotek, Newmarket, ON, Canada) programmed to record locations every 30 minutes. Collars were equipped with a release mechanism to drop the collar 48, 52, or 72 weeks after deployment. We censored all locations with positional dilution of precision >10 because such locations often include location errors of ≥ 50 m (D'eon and Delparte 2005).

We used only data collected 1 month before, during, and 1 month after the fall hunting period in analyses (1 Aug–31 Dec). We monitored individual animals for a maximum of 1 fall sampling period. Archery hunting occurred during the last 4 weeks in September and the first 2 weeks in October. No hunting occurred during the third week in October. Rifle hunting occurred during the last week in October and throughout November. The exact dates of the general archery and rifle periods varied by year, as rifle hunting ends the Sunday following Thanksgiving. We treated the archery and rifle hunting periods as 2 distinct time periods, and we censored the week of no hunting between the archery and rifle period.

To investigate factors affecting elk resource selection during the fall hunting periods, we compared all used locations recorded from GPS collars to randomly generated available locations. To create a sample of available locations, we estimated a population level seasonal range (late-summer pre-hunting period, archery hunting period, rifle hunting period, winter post-hunting period) and randomly generated 20 available locations corresponding to each used location from within the appropriate seasonal range.

We evaluated 9 covariates potentially affecting female elk resource selection during the fall and early winter: 6 landscape attributes, 1 metric of hunter access, and 2 metrics of habitat security. The 6 landscape attributes we evaluated included vegetation type, elevation, slope, snow water equivalence (SWE), probability of wolf occupancy, and snow cover extent. We used the 2001 national land cover dataset (http://www.mrlc.gov/) to broadly classify vegetation type as: forest, shrublands, grasslands (including crop and pasturelands), and other (rock, talus, water, lithic ridges). Because few "other" vegetation types occurred in the area and these habitat types were typically located adjacent to forested areas, we lumped other and forested areas into a single category. We estimated elevation from a 30-m Digital Elevation Map (DEM), and derived slope in degrees from the DEM. We measured SWE at the Beaver Creek, Montana station snowpack telemetry site; it integrated the depth and density of snowpack into a measure of the amount of water contained within the snowpack. The snowpack telemetry site was located 30 km southeast of the Madison study area and 120 km southwest of the Paradise Valley study area. We evaluated the interactive effects of SWE with vegetation type to represent the hypotheses that the strength of selection for different vegetation types varied as SWE varied. We used an existing map depicting the estimated probability of wolf occupancy at a 3-km resolution, developed using forest cover, human population density, elk density, and sheep density as predictors (Oakleaf et al. 2006). We estimated the extent of snow cover in 2-week periods using a 500-m resolution moderate-resolution imaging spectroradiometry (MODIS; Hall et al. 2000).

We evaluated the potential effects of hunting access on resource selection by developing a categorical covariate (access) contrasting areas that permitted public hunting access and areas that prohibited or restricted public hunting access. We treated all public lands that permitted hunting and privately owned lands that were enrolled in the State of Montana's Block Management Program (which allows public hunting access) as areas of public hunting access. We treated YNP and all private lands not enrolled in the block management program as areas that may have restricted or prohibited public hunting access. We therefore assumed that although many private lands did permit some hunting opportunity and access (i.e., for family, friends, or paying clients), the restricted hunting access and level of hunting risk was more similar to no access areas than areas that permitted public hunting access.

We evaluated habitat security as a covariate potentially affecting resource selection. We defined security habitat as public lands that 1) permitted public hunting access, 2) included a minimum of 1 km^2 of continuous forest, and 3) were located more than 0.8 km from the nearest road or trail opened to motorized travel during the hunting season (Hillis et al. 1991). This is the definition of security habitat incorporated into National Forest management plans in our study areas. We calculated continuous forest using a moving window and allowed a maximum of 10% of the 1 km^2 forest to be comprised of non-forested habitat to allow for small breaks in the forest (Hillis et al. 1991). We treated security habitat as a dichotomous variable. Additionally, because some National Forest management plans in our study areas consider only road density as a metric of elk habitat security, we evaluated road density, measured as the length of road per square mile as a second metric of elk habitat security, as per these management plans.

Statistical Analysis

We used log odds ratios to determine the likelihood of elk occupying publicly accessible hunting areas throughout the study periods, and we compared log odds ratios to identify shifts in selection associated with the hunting periods. We first sorted all used and available locations by date into 4 periods: pre-hunting period (1 Aug—start of archery period), archery hunting period, rifle hunting period, and post-hunting period (end of rifle period—31 Dec). We obtained the odds ratio for each period by dividing the odds of a used location occurring in an area permitting public access by the odds of an available location occurring in an area permitting public access, and the odds ratio compared the odds of actual use to the odds of use expected under random selection. This method assumes that available habitat did not vary during the archery period or during the rifle period. We calculated the asymptotic standard error and constructed 95% confidence intervals on the log odds ratio (Agresti 2002). We also calculated the log odds ratio of elk occupying security habitat and areas with >1 mile of motorized access road per square mile throughout the study periods, and we compared log odds ratios to identify shifts in selection for security habitat associated with the hunting periods.

We constructed models of elk resource selection during the fall study period by comparing used and available locations to estimate resource selection function (RSF) models. To estimate selection coefficients, we used a conditional logistic regression model from the survival package in Program R (R Version 2.12.2, http://cran.r-project.org, accessed 24 Jul 2012). Prior to developing our a priori model list, we screened covariates for correlations and excluded pairs with Pearson's correlation coefficients correlations $|r| \geq 0.7$ and variance inflation factors >5 from entering the same model.

We conducted a multivariate analysis of the effects of vegetation, landscape features, and hunting period on elk resource selection using a hierarchal information-theoretic approach. We developed separate models for each of the study areas and treated individual animals as the sample unit. We first evaluated 6 models representing effects of landscape attributes on resource selection and incorporated influential landscape attributes into all subsequent models evaluating effects of hunting period on resource selection. We developed 10 a priori models representing potential effects of hunter access, security habitat, and length of road per square mile on elk resource selection during the fall hunting periods (Table 1). For each animal, we evaluated the 6 landscape models and used Akaike's Information Criterion (AIC) to determine the best approximating model from the candidate landscape model set (Burnham and Anderson 2002). Next, we incorporated the influential landscape attributes in the hunting period models and used AIC to determine the best overall approximating model for each animal (Rittenhouse et al. 2008).

We treated individual animal selection coefficients as a random sample from a normal distribution with the mean representing the population-level effect of a covariate on the relative probability of selection (Marzluff et al. 2004, Sawyer et al. 2006). We estimated the population level resource selection coefficients by taking the average of the standardized coefficients from the most supported model for each individual. We conservatively estimated the variance of each population-level selection coefficient by calculating the variance of each coefficient across all individuals (Rittenhouse et al. 2008).

We compared standardized population-level selection coefficients between study areas to determine similarities and differences in resource selection at the 2 sites. To validate models, we used the unstandardized population-level selection coefficients to generate predictions. First, we validated predictions externally in the other study area and second, we validated predictions internally from the model development area. We randomly selected 1 location per animal per day and treated these data as the validation set. We generated and validated predictions during the archery period and the rifle period. We averaged the SWE value over the study period and used the averaged SWE value for predictions. We classified pixels of the predictive map into 20 equal-interval RSF intervals that corresponded to the relative probability of use (i.e., 0–5%, 5–10%, 10–15%, etc.; Durner et al. 2009). We plotted data corresponding to the appropriate time

Table 1. A priori models and biological hypotheses representing the potential effects of hunter access, security habitat, and road density on elk resource selection during the hunting season in 2 Greater Yellowstone Ecosystem elk herds, 2005–2006, 2009. Covariates evaluated include vegetation cover type (Hab), snow water equivalence (SWE), slope, elevation (Elev), snow cover extent (Extent), wolf risk (Wolf), hunter access (Access), security habitat (Security), road density (Roads), archery hunting period (Archery), and rifle hunting period (Rifle).

Model	Covariates	Hypothesis
Effects of landscape attributes on elk resource selection		
1	Hab × SWE + Extent	Vegetation cover type and snowpack affect resource selection
2	Hab × SWE + Slope + Elev + SWE × Elev	Vegetation cover type, snowpack, and topography affect resource selection
3	Hab × SWE + Wolf	Vegetation cover type, snowpack, and wolf risk affect resource selection
4	Hab × SWE + Slope + Elev + SWE × Elev + Extent	Vegetation cover type, snowpack, topography, and wolf risk affect resource selection
5	Hab × SWE + Extent + Wolf	Vegetation cover type, snowpack, and wolf risk affect resource selection
6	Hab × SWE + Slope + Elev + SWE × Elev + Extent + Wolf	Vegetation cover type, snowpack, topography, and wolf risk affect resource selection
Effects of hunting risk on elk resource selection		
1	Hab × Archery + Hab × Rifle	Elk alter selection for vegetation type during hunting periods
2	Access ×Archery + Access × Rifle	Elk increase selection for areas of restricted hunter access during hunting periods
3	Security × Archery + Security × Rifle	Elk increase selection for public land security habitat during hunting periods
4	Roads × Archery + Roads × Rifle	Elk avoid roads during the hunting periods
5	Hab × Archery + Hab × Rifle + Roads × Archery + Roads × Rifle	Elk alter selection for vegetation type and avoid roads during hunting periods
6	Hab × Archery + Hab × Rifle + Access × Archery + Access × Rifle	Elk alter selection for vegetation type and increase selection for areas of restricted access during hunting periods
7	Hab × Archery + Hab × Rifle + Security × Archery + Security × Rifle	Elk alter selection for vegetation type and increase selection for security habitat during hunting periods
8	Access × Archery + Access × Rifle + Security × Archery + Security × Rifle	Elk increase selection for areas of restricted access and security habitat during hunting periods
9	Roads × Archery + Roads × Rifle + Access × Archery + Access × Rifle	Elk avoid of roads and select for areas of restricted hunter access during hunting periods
10	Roads × Archery + Roads × Rifle + Security × Archery + Security × Rifle	Elk avoid of roads and select security habitat during hunting periods

period (archery or rifle period) on the predictive map and calculated the frequency distributions of observed elk locations within RSF intervals.

RESULTS

East Madison Herd

We included 268,972 used locations collected from 43 individual animals and 5,379,440 available locations in our analyses. Of the used locations, 26% were located in shrublands, 25% in grassland, and 49% in forests and other areas (>48% in forests and <1% in other cover types). Fifty-eight percent were located on public lands that permitted hunting and 42% were located on privately owned lands where hunting was restricted. Thirty-five percent of the available area had restricted hunter access. Sixteen percent of used locations were located in security habitat. Length of motorized road per square mile surrounding used locations ranged from 0 km to 11.6 km, with a median of 0. Snow water equivalence averaged 5.6 cm in 2005 and 3.3 cm in 2006. The 8-year average (2002–2009) SWE for this time period (1 Aug–31 Dec) was 4.2 cm and annual average SWE values ranged from 2.7 cm to 5.6 cm.

Elk were less likely to occupy areas that permitted public hunting access during the rifle period and post-hunting period (Fig. 2A). We estimated the log odds of elk occupancy in areas that permitted public hunting access was 1.32 (95% CI = 1.30, 1.34) during the pre-hunting period, 0.86

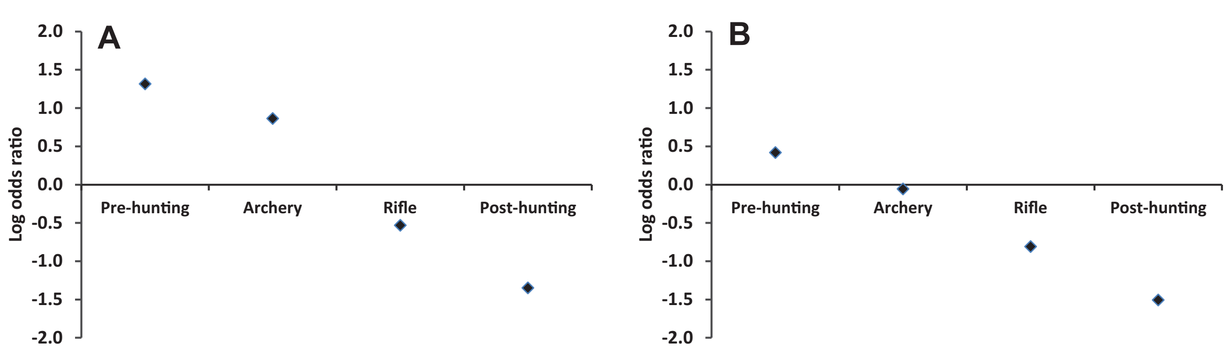

Figure 2. Log odds of adult female elk selection for areas with public hunting access during the pre-hunting, archery, rifle, and post-hunting periods. Panel A represents the East Madison herd (2005–2006) and Panel B represents the West Paradise herd (2009). A log odds ratio of 0 corresponds to independence. Error bars represent 95% confidence intervals, and may appear too small to be viewed.

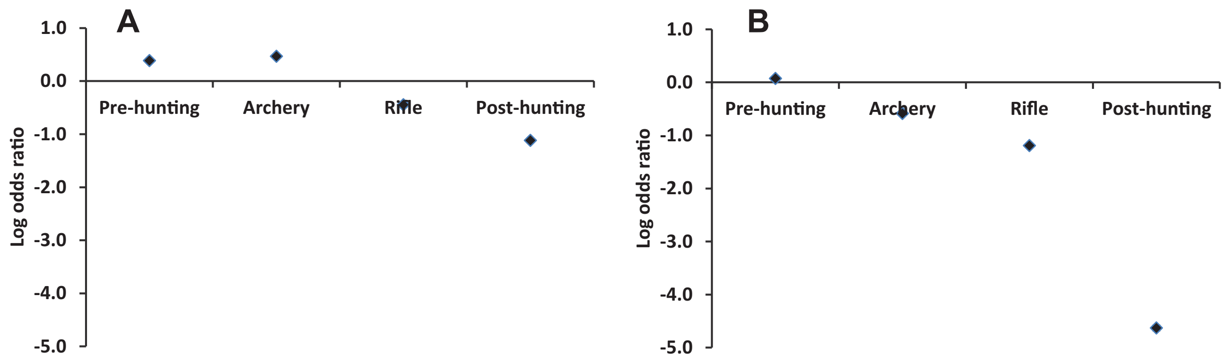

Figure 3. Log odds of adult female elk selection for security habitat during the pre-hunting, archery, rifle, and post-hunting periods. Panel A represents the East Madison herd (2005–2006) and Panel B represents the West Paradise herd (2009). A log odds ratio of 0 corresponds to independence. Error bars represent 95% confidence intervals, and may appear too small to be viewed.

(95% CI = 0.86, 0.88) during the archery period, −0.53 (95% CI = −0.55, −0.51) during the rifle period, and −1.35 (95% CI = −1.37, −1.33) during the post-hunting period. Elk were more likely to occupy security habitat during the pre-hunting and archery periods than during the rifle or winter periods (Fig. 3A). We estimated the log odds of elk occupancy in security habitat was 0.39 (95% CI = 0.37, 0.41) during the pre-hunting period, 0.47 (95% CI = 0.45, 0.49) during the archery period, −0.45 (95% CI = −0.47, −0.42) during the rifle period, and −1.12 (95% CI = −1.16, −1.08) during the post-hunting period. Elk were less likely to occupy areas with greater motorized access road density, and the odds of elk occupying greater road density areas was least likely during the post-hunting period (Fig. 4A). We estimated the log odds of elk occupying an area with >1 mile of open road per square mile was −1.94 (95% CI = −1.98, −1.90) during the pre-hunting season, −1.61 (95% CI = −1.64, −1.58) during the archery season, −0.39 (95% CI = −0.40, −0.37) during the rifle season, and −3.06 (95% CI = −3.08, −3.05) during the post-hunting season.

The most supported landscape model explaining variations in elk resource selection during the fall study period contained the covariates vegetation × SWE, slope, elevation, elevation × SWE, snow extent, and wolf risk. The most supported landscape model ranked as the top model for 40 of the 43 elk (Table 2). The most supported hunting risk model contained the covariates hunter access × hunting period, and roads × hunting period. The most supported risk model ranked as the top model for 39 of the 43 elk (Table 2). Population level standardized coefficient estimates indicated that elk strongly selected for areas with less open roads during the entire study period, and selection away from roads was strongest during the archery period (Table 3). Elk selected for areas that permitted public access during the archery season, but selected for areas that restricted public access during the rifle period. We found little evidence that elk selected for security habitat during the study period. Elk selection for grasslands and shrublands over forested areas increased as SWE increased. Relative to the effects of roads, hunter access, and SWE–habitat interactions, other covariates had a minimal effect on elk resource selection.

The across study-area validation revealed that the population-level Madison model had good predictive ability in the Paradise Valley study area during both the archery and the rifle hunting periods. Eighty percent of the Paradise elk archery locations occurred in the >75% RSF interval and 88% occurred in the >50% RSF interval. Forty-one percent of the Paradise elk rifle locations occurred in the >75% RSF interval and 71% occurred in the >50% interval. Internal

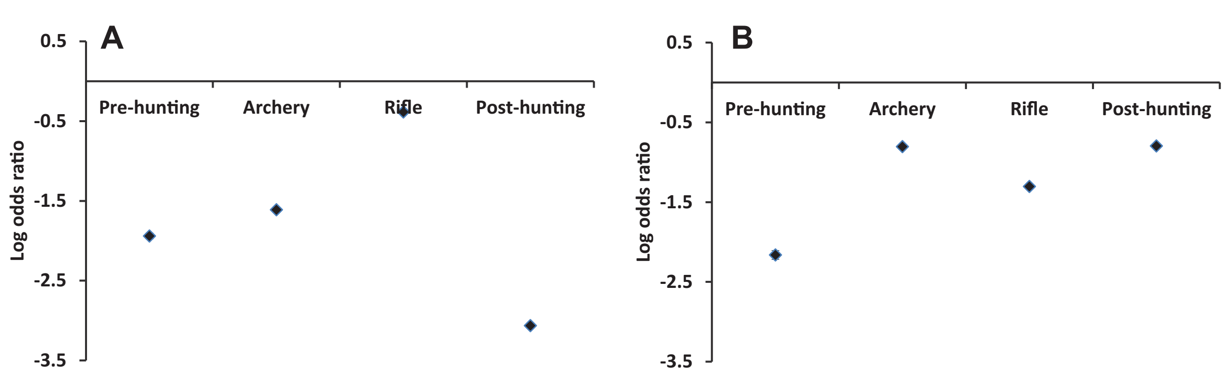

Figure 4. Log odds of adult female elk selection for areas with >1 mile of open road per square mile during the pre-hunting, archery, rifle, and post-hunting periods. Panel A represents the East Madison herd (2005–2006) and Panel B represents the West Paradise herd (2009). A log odds ratio of 0 corresponds to independence. Error bars represent 95% confidence intervals, and may appear too small to be viewed.

Table 2. Number of times each landscape and hunting risk model of elk resource selection during the fall hunting season received the most support in the East Madison Valley and Western Paradise Valley, Montana, USA (2005–2006, 2009). Covariates evaluated include vegetation cover type (Hab), snow water equivalence (SWE), slope, elevation (Elev), snow cover extent (Extent), wolf risk (Wolf), hunter access (Access), security habitat (Security), road density (Roads), archery hunting period (Archery), and rifle hunting period (Rifle).

Model	Covariates	No. times	
		Madison Valley	Paradise Valley
Landscape models			
6	Hab × SWE + Slope + Elev + SWE × Elev + Extent + Wolf	40	34
4	Hab × SWE + Slope + Elev + SWE × Elev + Extent	3	4
2	Hab × SWE + Slope + Elev + SWE × Elev	0	1
Hunting risk models			
9	Roads × Archery + Roads × Rifle + Access × Archery + Access × Rifle	39	21
10	Roads × Archery + Roads × Rifle + Security × Archery + Security × Rifle	2	8
5	Hab × Archery + Hab × Rifle + Roads × Archery + Roads × Rifle	1	5
6	Hab × Archery + Hab × Rifle + Access × Archery + Access × Rifle	1	0
8	Access × Archery + Access × Rifle + Security × Archery + Security × Rifle	0	5

study-area validation with withheld data revealed the Madison model also accurately predicted the relative probability distribution for Madison elk in the archery and rifle periods. Ninety-four percent of the archery locations occurred in the >75% RSF interval and 97% occurred in the >50% RSF interval. Forty-two percent of the withheld rifle locations occurred in the >75% RSF interval and 60% occurred in the >50% interval.

Western Paradise Valley Herd

We included 249,815 used locations collected from 39 individual animals and 54,996,300 available locations in our analyses. Of the used locations, 32% were located in shrublands, 23% in grassland, and 45% were located in forests and other areas (>44% in forests and <1% in other cover types). Thirty percent of locations were located on lands that permitted hunting access and 70% were located on privately owned lands and the enclosed public lands where hunting was restricted. Sixty-two percent of the available area had restricted hunter access. Thirteen percent of the used locations were located in security habitat. Length of road per square mile surrounding used locations ranged from 0 km to 7.1 km, with a median of 0. Snow water equivalence averaged 3.8 cm in 2009, and the 2002–2009 average was 4.2 cm.

Similar to the East Madison herd, during all study periods, Western Paradise Valley elk were less likely to occupy areas that permitted public hunting access, and this effect

Table 3. Population-level estimates for the effects of landscape and hunting risk covariates on female elk resource selection during the fall hunting season in the East Madison Valley and Western Paradise Valley, Montana, USA, during 2005–2006 (East Madison Valley) and 2009 (Western Paradise Valley). Forest was treated as the base vegetation category and areas that restrict public hunting access were treated as the base access category. Estimates are based on 30-minute interval location data collected from a sample of 43 radio-collared individuals in the East Madison Valley and 39 individuals in the Western Paradise Valley. We averaged the estimates of standardized coefficients from the most supported model for each individual to obtain the population level estimates. Covariates included vegetation cover type (e.g., shrub, grass), snow water equivalence (SWE), snow cover extent, slope, elevation, wolf risk (Wolf), archery hunting period (Archery), rifle hunting period (Rifle), hunter access (Access), security habitat (Security), and road density (Roads).

Resource attribute	East Madison Valley Herd		West Paradise Valley Herd	
	$\bar{x}$	SE	$\bar{x}$	SE
Shrub	0.443	0.126	0.499	0.065
Grass	0.538	0.098	−0.027	0.141
Shrub × SWE	1.485	0.157	0.830	0.049
Grass × SWE	1.202	0.149	0.639	0.077
Snow extent	−0.460	0.106	−0.633	0.141
Slope	0.049	0.048	0.124	0.041
Elevation	0.004	0.099	−0.176	0.130
SWE × Elevation	−0.607	0.083	−0.801	0.203
Wolf	0.218	0.141	0.103	0.099
Shrub × Archery	0.037	0.041	0.031	0.021
Grass × Archery	−0.019	0.025	0.009	0.076
Shrub × Rifle	0.011	0.034	−0.114	0.049
Grass × Rifle	−0.022	0.016	0.010	0.025
Access	1.060	0.556	−0.666	0.568
Access × Archery	3.239	1.150	−1.085	0.559
Access × Rifle	−1.545	0.562	−1.775	0.976
Security	−0.015	0.042	−0.679	0.495
Security × Archery	−0.035	0.034	−0.217	0.621
Security × Rifle	−0.003	0.029	−0.807	0.760
Roads	−6.603	3.919	−20.692	11.808
Roads × Archery	−99.827	22.581	−37.415	27.246
Roads × Rifle	0.969	5.968	−89.750	34.310

intensified during the rifle period (Fig. 2B). We estimated the log odds of elk occupancy in areas that permitted public hunting access was 0.42 (95% CI = 0.40, 0.44) during the pre-hunting period, −0.06 (95% CI = −0.07, −0.04) during the archery period, −0.81 (95% CI = −0.83, −0.79) during the rifle period, and −1.51 (95% CI = −1.54, −1.48) during the post-hunting period. Similar to elk from the East Madison herd, Western Paradise Valley elk were less likely to occupy security habitat during the rifle and post-hunting periods than during the pre-hunting and archery periods (Fig. 3B), and overall Western Paradise Valley elk showed less preference for security habitat than elk in the East Madison. We estimated the log odds of elk occupancy in security habitat was 0.07 (95% CI = 0.06, 0.09) during the pre-hunting period, −0.59 (95% CI = −0.61, −0.56) during the archery period, −1.19 (95% CI = −1.22, −1.16) during the rifle period, and −4.63 (95% CI = −4.69, −4.57) during the post-hunting period. Western Paradise Valley elk were less likely to occupy areas with >1 mile of motorized access road per square mile during all time periods. The odds of Western Paradise Valley elk occupying these areas was least likely during the pre-hunting period (Fig. 4B). We estimated the log odds of elk occupying an area with >1 mile of open road per square mile was −2.16 (95% CI = −2.21, −2.11) during the pre-hunting season, −0.80 (95% CI = −0.83 −0.78) during the archery season, −1.30 (95% CI = −1.33, −1.27) during the rifle season, and −0.80 (95% CI = −0.82, −0.77) during the post-hunting season.

Model selection results for elk resource selection in the western Paradise Valley herd were similar to results from the East Madison Valley herd. The most supported landscape model explaining variations in elk resource selection during the fall study period contained the covariates vegetation × SWE, slope, elevation, elevation × SWE, snow extent, and wolf risk. The most supported landscape model ranked as the top model for 34 of the 39 elk (Table 2). The most supported hunting risk model contained the covariates hunter access × hunting period, and roads × hunting period. The most supported risk model ranked as the top model for 21 of the 39 elk, and the covariates for roads, hunter access, and hunting periods were consistently contained in the most supported models for the remaining 18 animals (Table 2). Population level standardized coefficient estimates indicated that elk strongly selected for areas with less open roads during the entire study period, and selection away from roads was strongest during the rifle period (Table 3). Elk selected against areas that permitted public access during the entire study period, and the strength of selection against areas that permitted public access increased during both the archery and rifle hunting periods. We found no evidence that elk selected for security habitat during the study period. Elk selection for grasslands and shrublands over forested areas increased as SWE increased. Relative to the effects of roads and hunter access, other covariates had a minimal effect on elk resource selection.

The across study-area validation revealed that the population-level Paradise model had good predictive ability in the Madison population during the archery hunting period, but poorly predicted Madison elk distributions during the rifle hunting period. Ninety-one percent of the Madison elk archery locations occurred in the >75% RSF interval and 96% occurred in the >50% RSF interval. Ten percent of the Madison elk rifle locations occurred in the >75% RSF interval and 21% occurred in the >50% interval. The Madison elk used public lands accessible to hunters more than predicted by the Paradise model, resulting in the poor predictive performance of the Paradise model in the Madison Valley. Internal study-area validation revealed the Paradise model had good predictive ability during the archery period, but predicted poorly during the rifle period. Sixty-five percent of the withheld archery locations occurred in the >75% RSF interval and 88% occurred in the >50% RSF interval. Six percent of the withheld rifle locations occurred in the >75% RSF interval and 43% occurred in the >50% interval. Paradise elk used areas with restricted public hunting access less than predicted by the model, likely because a portion of these areas were privately owned ranchlands with little hiding cover that may have had some degree of harvest risk from outfitted clients. Overall, the predictive ability of the Paradise Valley model was lesser than the Madison model.

DISCUSSION

Our results provide evidence that in landscapes characterized by a matrix of public and privately owned lands, adult female elk selected for areas that restricted public hunting access and areas with lesser motorized access road density, but did not increase selection for security habitat during hunting seasons. Model coefficient and log odds ratio results were generally consistent between herds, providing support for the generalizability of these results; however, we did find elk may avoid areas with hunter access during the rifle hunting period more strongly in some areas than in others. Our results therefore support the premise that when elk herd size management via adult female harvest is the goal, the traditional concept of elk security habitat needs to be expanded to account for areas that restrict hunter access, particularly during rifle seasons.

Adult female elk selection for areas of restricted hunter access was only present during the archery period in 1 of our 2 study areas. However, elk selection for areas that restricted hunting access occurred during the rifle hunting period and persisted throughout the post-hunting period in both areas. These results contrast with findings from 2 similar studies in Colorado that document elk shift the timing of their movements to private lands in response to the beginning of the archery hunting season (Conner et al. 2001, Vieira et al. 2003). Differences in these results may be due to differences in the level of archery hunting pressure, or related to topographical and migration differences between areas (Conner et al. 2001).

The traditional concept of elk security habitat is aimed at providing adequate adult male elk survival while not limiting elk hunter opportunity (e.g., Leptich and Zager 1991). Given different behavioral patterns of male and female elk, male elk may use security habitat to a greater degree than reported here for adult female elk. Previous studies indicate that during the autumn, male elk use mature, semi-closed, forested areas more than females and selected for areas of lesser road densities than females (McCorquodale 2003). Therefore, we may expect male elk to show a stronger preference for security habitat than we observed in female elk and the security habitat concept may still apply to the issue for which it was developed.

Our results infer that in the matrix of public and private land ownership in which we worked, publicly managed security habitat is not adequate to maintain adult female elk accessible to the public during hunting seasons. During hunting seasons, adult female elk increased selection for areas that may have restricted public hunting access. This situation can result in elk herd distributions during hunting seasons primarily centered on privately owned lands that limit public access during hunting seasons (e.g., Burcham et al. 1999, Hamlin and Cunningham 2009: 49–53). Although previous work has documented strong, immediate, small-scale, and short-term behavioral changes in elk selection for areas that restrict hunter access in response to hunting risk (Proffitt et al. 2010), our results here show that a potential landscape-level effect may also occur. Further, in the study area, female elk tend to remain on these lower-elevation privately owned ranchlands throughout the winter and sometimes into the calving period (Montana Department of Fish, Wildlife, and Parks, unpublished data).

Road density was the strongest predictor of elk distributions and, similar to other studies, elk in both study areas selected for areas of lesser open road density throughout the fall study period (Rowland et al. 2000, McCorquodale 2003). These findings suggest that motorized road access management may be successful at maintaining elk distribution on publicly owned lands. In this region, some Forest Management Plans have recently revised elk habitat management standards to include only open road densities, rather than road density and forested cover (i.e., the Hillis paradigm of security habitat; Hillis et al. 1991). Results of this study indicate that road density was a stronger predictor of elk distributions during the hunting period than was security habitat. This suggests that standards based solely on road densities may be adequate for managing female elk distributions on public lands during the hunting periods in some areas.

The relatively low female elk utilization of security habitat observed here is likely related to elk movements to refuge areas that restricted hunter access and is likely not representative of female elk use of security habitat in other areas that lack accessible refuge areas. Therefore, in areas where both summer and winter ranges are primarily publicly owned and allow hunter access, forest standards based solely on road densities may or may not be appropriate for providing female elk security during the hunting season. We did not consider the appropriateness of standards based solely on road density for providing male elk security during hunting seasons in this study.

Recent strategies to limit the size of elk herds in our study areas have consisted of large, limited-entry hunts for adult female elk and liberalization of general hunts to include harvest of adult females. Because of this history, the patterns of selection we observed may in fact be related more to selective hunting pressure on a landscape scale than localized, individual elk behavioral choices. Elk herds are typically composed of individual elk that exhibit different movement strategies, including non-migratory or very short-distance migrants, as well as long distance migrants (Irwin 2002). Elk herds in southwest Montana are also known to be composed of elk that employ different movement strategies (e.g., Hamlin and Ross 2002: 148–157). Migration and movement strategies may or may not be passed between generations in Rocky Mountain Elk as they are in other ungulates (e.g., Clutton-Brock et al. 1982: 185–186, Sweanor and Sandgren 1988). If migratory or movement behaviors are passed generation to generation, harvest may act as a landscape-scale selective force, increasing herd segments using private lands that limit public hunter access and reducing adult female survival in herd segments using public lands. A pattern similar to this was hypothesized to have preferentially selected for migratory segments of elk herds in Wyoming through the 1970s and 1980s (Rudd et al. 1983, Boyce 1991). Once movement patterns are lost from elk herds, they have also proven difficult and costly to restore (Allred 1950).

Conversely, the pattern of selection we observed may result from individual behavioral choices made by adult female elk in response to the presence of hunters and human activity, which individual elk tend to avoid during hunting seasons (Skovlin et al. 2002). These choices may be flexible, such that if hunting pressure is relaxed in certain areas, elk may quickly begin using those areas again. This pattern of flexible, small-scale, and short-term elk behavioral responses to hunting pressure has been documented in response to late-season (winter) elk hunts in the East Madison herd (Gude et al. 2006, Proffitt et al. 2010).

This distinction has important applications for elk management because different hunting season structures may be necessary to manage herds with distinct segments that occupy public and private lands. If hunting opportunity exists solely or disproportionately on public lands, hunting may selectively reduce numbers in the public land herd segment. If animals learn migratory and movement patterns as calves, over time this could result in the loss of the public land herd segment and limited private land hunts will not be effective in rebuilding the public lands segment of the herd over the short term. To rebuild the public segment of the herd over time, public lands hunting pressure may need to be reduced or eliminated while hunting pressure on private lands is increased, to affect differential mortality rates in different herd segments. Conversely, if elk selection for lands inaccessible to hunters represents a flexible behavioral strategy, elk re-distribution onto public lands may be achievable in the short term via elk avoidance of hunters, with only limited hunter access onto lands that currently are not open to hunting.

MANAGEMENT IMPLICATIONS

Elk selection for areas with limited public hunting access and lesser motorized road densities, combined with either differential adult female harvest pressure on herd segments that use areas with public hunting access or elk avoidance of areas used by hunters, has the potential to reduce the number of elk using public lands. These results reinforce the need for wildlife managers to work closely with public land management agencies and private landowners to manage the size of elk herds. Focusing harvest pressure on private lands currently restricting hunter access while limiting harvests on public lands may be an effective strategy for redistributing elk onto public lands in areas where elk distribution is focused on private lands with limited public hunting access. The speed with which this happens depends largely on whether landscape-scale elk movements are passed between generations or are individual, flexible behavioral strategies. The basis of elk movement strategies is largely unknown, and this requires further research. Additionally, management of motorized road access by land management agencies may influence female elk distributions onto public lands during the hunting periods. If these strategies are successful, and provided that adequate elk forage is available on public lands, publicly managed security areas may become a more central part of adult female elk habitat use during hunting seasons than we documented here.

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