



Management and Conservation Article

Changes in Elk Resource Selection and Distributions Associated With a Late-Season Elk Hunt

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ABSTRACT Changes in resource selection associated with human predation risk may alter elk distributions and availability for harvest. We used Global Positioning System data collected from telemetered female elk (*Cervus elaphus*) to evaluate effects of refuges (areas where hunting was prohibited), spatial variation in hunting risk, and landscape attributes on resource selection within an established Greater Yellowstone Area, USA, winter range. We also evaluated elk distributions during and outside of a late-season hunting period. Refuge areas and landscape attributes such as habitat type and snow water equivalents (SWE) affected resource selection. Elk selection for flat grasslands increased as SWE increased, likely because these areas were windswept, leaving grasses exposed for foraging. Elk distributions differed during hunting and no-hunting periods. During the hunting period, elk shifted to privately owned refuge areas and the estimated odds of elk occupying refuge areas more than doubled. Risk-driven changes in resource selection resulted in reduced availability of elk for harvest. Elk selection for areas where hunting is prohibited presents a challenge for resource managers that use hunting as a tool for managing populations and influences grazing patterns on private ranchlands.

KEY WORDS *Cervus elaphus*, elk, Greater Yellowstone Area, human impacts, hunting effects, predator–prey, resource selection, winter range.

Understanding how human influences such as hunting interact with landscape attributes to affect ungulate spatial and temporal distributions and resource selection is important in understanding the ecology and appropriate management techniques for ungulates across the western United States. Effects of human hunting risk on elk resource selection are particularly important because risk-driven changes in selection during the hunting season may alter elk distributions, resulting in elk aggregations largely unavailable for harvest (Burcham et al. 1999). In the Greater Yellowstone Area, USA, several elk herds are over population objectives, and these refuge effects are particularly problematic to managers using harvest as a management tool (Montana Department of Fish, Wildlife, and Parks 2004). Refuge effects may also aggregate animals in high densities, enhancing potential risk of disease transmission. Further, if refuges are privately owned lands, changes in selection associated with hunting risk may alter elk impacts on plant communities, increase conflicts between elk and livestock producers, and lead to public perceptions of elk overabundance (Irby et al. 1996, Torstenson et al. 2002, Fortin et al. 2005, Gude et al. 2006).

Predation risk may influence resource selection because animals may accept reductions in forage quality or quantity to reduce risk, and these tradeoffs may result in altered animal distributions (Abramsky et al. 1996, 2002; Anderson et al. 2005; White et al. 2009b). Further, hunter avoidance may alter diet composition and impacts on resources (Morgantini and Hudson 1985, Schmitz et al. 1997, Dill et al. 2003). Elk typically respond to human predation risk by moving into areas of forest cover and low road density (Thomas et al. 1979, Unsworth et al. 1998, Skovlin et al. 2002); however, in heterogeneous mixed-ownership landscapes, responses may also include movement onto lands where hunting is prohibited (Burcham et al. 1999, Vieira et al. 2003).

Using data from Global Positioning System (GPS) location data, we investigated effects of refuge areas, spatial and temporal variation in hunting risk, and landscape attributes on resource selection by adult female elk in a Greater Yellowstone Area winter range. Within ungulate winter ranges, resource selection is influenced by snowpack; elk select for areas with less snow (Messer et al. 2009, White et al. 2009b). We predicted elk would select flat grasslands and selection for these areas would increase throughout the winter in response to higher exposed forage biomass in these windswept areas (Gude et al. 2006). Although effects of predation risk on resource selection may vary with season and study area, selection for preferred open grasslands may

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decline, and selection for more secure wooded areas may increase in response to predation risk (Thomas et al. 1979, Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005, White et al. 2009b). During the hunting period, we predicted that elk would increase selection for refuge areas (areas where hunting was prohibited), areas more distant to hunter access locations, and forested areas. Although we predicted elk would select against high-risk areas (areas that permitted hunting and areas near hunter access locations) during the day, we predicted that elk might select these high-risk areas during the night when hunting was prohibited.

STUDY AREA

We conducted this study 1 December–30 March during the winter of 2005–2006 and 1 December–27 February during the winter of 2006–2007 in the Madison Valley of southwest Montana, USA (44°58'N, 111°36'W; Fig. 1). The study area was 430 km². East of the highway bisecting the study 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 (Garrott et al. 2005). West of the highway was state-owned Wall Creek Wildlife Management area, an area closed to human activity during winter. The Madison River and United States Highway 287 act as a soft boundary to elk movements, though some interchange of elk does occur (Grigg 2007).

Elevations ranged from 1,670 m to 3,064 m. A mixture of bunchgrass-dominated grasslands (e.g., *Festuca idahoensis* and *Pseudoroegneria spicata*) and sagebrush (*Artemisia* sp.) comprised approximately 55% of the study area, and sagebrush steppe, grassland hills, and coniferous forests (e.g., *Pinus contorta*, *P. flexilis*, *Abies lasiocarpa*, *Picea engelmannii*, and *Pseudotsuga menziesii*) were the other major habitat types (Despain 1990). The winter climate in the valley was characterized by long, cold winters and was strongly influenced by strong winds (Garrott et al. 2005, Grigg 2007). The valley was heavily windswept during winter, often leaving the open, low-elevation benches and higher elevation ridges largely snow free (Gude et al. 2006). Standing snow depths in areas with woody vegetation often exceeded 40 cm whereas depths in grasslands rarely exceeded 10 cm, other than in cornices and snowbanks (Gude 2004).

The study area served as a winter range for a migratory herd of approximately 5,000 elk and included portions of Montana elk hunting districts 360 (northern half of the study area) and 362 (southern half of the study area), where a winter rifle elk-hunting season was allowed after the general hunting season. This late elk hunt occurred in January, with limited permit hunting occurring 4 days (Friday–Monday) per week. Fifty hunters were permitted during each of the 4 weekly hunting periods. An additional 200 specially permitted antlerless elk hunters could hunt on the east side of the Madison Valley from September through mid-February; however, we did not consider these hunters in our analyses because the study area included <20% of hunting districts 360 and 362, and few of these hunters were within the study area during the analysis period. Because the

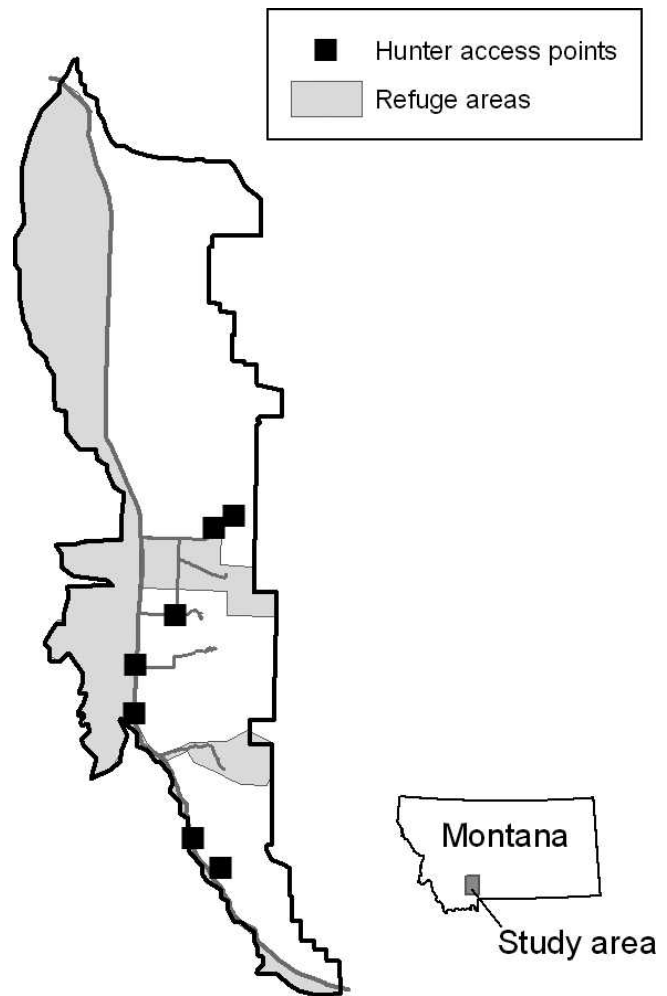


Figure 1. A public highway and network of roads through privately owned ranches passed through the Madison Valley elk winter range in southwest Montana, USA, and hunters accessed the study area through 7 primary points located along these roads during winters 2005–2006 and 2006–2007.

late-season elk hunt occurred on private ranches, access points for hunters were limited and tended to occur as parking areas associated with public roads. Hunters primarily accessed elk in the study area through 7 hunter access points, which were located near the main highway, as well as near a county road that bisected the study area (Fig. 1).

METHODS

Data Collection

We darted 20 and 25 adult female elk from a helicopter in February 2005 and 2006, respectively, and fit them with 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 (yr 1) and 52 (yr 2) weeks after deployment. We censored less than 4% of all locations with positional dilution of precision >10 because such locations often include location errors of ≥ 50 m (D'eon and Delparte 2005).

To investigate factors affecting elk resource selection, we compared used locations recorded from GPS collars to

randomly generated available locations. We treated day (0700–1730 hr) and night (2100–0600 hr) habitat selection separately because our predictions for the effects of covariates on selection differed between day and night. We randomly selected one day and one night location from each collared animal each day and treated these locations as our set of used locations. We considered these independent records because individual elk are capable of traveling throughout the entire study area in a 24-hour period (Proffitt et al. 2009). We classified instrumented animals as within the same group if multiple animals were within 100 m of each other at the same time, and we censored all but one observation from each group (<1% of all records were censored). To create a sample of available locations, we estimated a 95% kernel density distribution from all recorded GPS locations of instrumented animals and randomly selected available locations from within this distribution. We defined separate day and night distributions, and selected available locations from within the appropriate distribution. For each used point, we randomly selected 20 available locations and assigned corresponding time-varying characteristics, including date, snow water equivalent (SWE), and hunting season, for each used and available location.

We evaluated 3 predation risk factors potentially affecting daytime elk resource selection: refuge area, hunting period, and distance to hunter access points. We defined a refuge as an area where hunting was prohibited during the late-season rifle hunt. In the study area, all areas west of the highway and 2 areas of private land east of the highway were closed to hunting (Fig. 1). We treated refuge as a static landscape predictor (not a time-varying covariate) to determine if refuge areas affected selection patterns throughout the winter. We considered hunting period a time-varying indicator variable that contrasted periods of hunting and no hunting, and the interaction term refuge \times hunting period represented the effects of a refuge area during the hunting period. Although hunting occurred only 4 days per week during January, we treated the entire month as the hunting period and treated all other times as the no-hunting period. We censored records from the week preceding and week following the hunting period because we considered these transition periods. We predicted that selection for refuges would be equal to their availability during the no-hunting period, and selection for refuges would increase during the hunting period.

Finally, we calculated distances between each used and available location and the nearest hunter access point, and we treated this distance as a static landscape predictor to determine if proximity to hunter access locations affected selection throughout winter. The distance to hunter access \times hunting period interaction represented effects of proximity to hunter access points during the hunting season, and we considered this interaction term a metric of spatial variation in predation risk. We predicted elk might select for areas near hunter access locations because these access locations were located at the core of the study area, but that selection for areas distant to hunter access locations would

increase during the hunting period. Further, we predicted similar day and night resource selection during the no hunting period; during the hunting period, we predicted increased selection for risky areas (i.e., non-refuge areas and areas near hunter access) at night.

We also evaluated 2 landscape attributes potentially affecting elk resource selection: habitat type and SWE. We classified habitat type into 4 categories: grassland flats, sagebrush steppe, grassland hills, and forested areas. Snow water equivalent integrates the depth and density of snowpack into a measure of the amount of water contained within the snowpack, and we measured it at the nearest snowpack telemetry (SNOTEL) site (Beaver Creek, MT) located 30 km southeast and approximately 300 m higher in elevation than the study area (Natural Resources Conservation Service SNOTEL data). Although we expected SWE measurements at the SNOTEL site to be greater than actual SWE within the study area, the general patterns of snow accumulation throughout the winter, which we predicted would affect elk selection, were similar (validated using 2004–2005 unpublished data, this study).

From the sample of used points (one observation per animal per day), we constructed a 95% fixed kernel density estimator to estimate elk distributions during the hunting period and no-hunting period (Beyer 2004). Because a different sample of animals were collared each winter, we mapped distributions from 2005–2006 and 2006–2007 independently to determine if spatial variations in distributions of the 2005–2006 animals were similar to the distributions of the 2006–2007 animals.

Statistical Methods and Model Evaluation

We used log odds ratios to determine the likelihood of elk occupying specific habitat types throughout the winter, and we compared log odds ratios to identify shifts in habitat use associated with the hunting period. We first sorted used and available locations by date into 3 periods, which corresponded to changes in snowpack and hunting period: early winter (low snowpack, pre-hunting, 1–25 Dec), mid-winter (moderate snowpack, hunting period, 1–28 Jan), and late winter (heavy snowpack, post-hunting, 6 Feb–30 Mar). We obtained the odds ratio for each period by dividing the odds of a used location occurring in a given habitat during the hunting period by the odds of an available location occurring in a given habitat during the hunting period. The odds ratio compared the odds of actual use to the odds of use expected under random selection. We calculated the asymptotic standard error and constructed 95% confidence intervals on the log odds ratio (Agresti 2002).

We developed a set of 18 competing a priori models representing potential effects of human predation risk and landscape attributes on resource selection within the winter range. We used a matched case-control logistic regression approach (Collett 2003; Proc Logistic, SAS Version 9.2, www.sas.com, accessed 12 Dec 2008). We matched each used location (a case) to 20 available locations (controls) temporally. Because we matched used and available locations in time, all time-varying covariates including SWE and

hunting period were matched. Therefore, we could not estimate the main effect of SWE or hunting period on resource selection, but we could estimate interactions of SWE or hunting period and non-time-varying covariates (habitat type, refuge, distance to hunter access) on resource selection.

We used Akaike's Information Criterion (AIC) and Akaike model weights (w_i) to quantify support from the data for each of our hypothesized models and to address model-selection uncertainty (Burnham and Anderson 2002). We conducted a post hoc, exploratory analysis evaluating distance to hunter access in the asymptotic form to evaluate the hypothesis that risk initially diminished with increasing distance to hunter access points and after a certain distance, effects of hunter access locations diminished. We also treated data from 2005–2006 and 2006–2007 as separate datasets, fit the top ranked model to each dataset, and compared estimated coefficients between years to identify potential inter-annual differences in resource selection. Finally, we altered our definition of the hunting period to evaluate if elk responded to temporal variation in predation risk. We treated only the 4 days per week when hunting was permitted as the hunting period, and we treated 3-day intervals of no hunting within the hunting period and all times outside of the hunting period as the no-hunting period. We predicted selection during the 3-day, no-hunting intervals would be more similar to selection during the hunting period than to selection during the no-hunting period.

RESULTS

We collected location data from 43 elk over 2 winters, and 3,222 used and 64,440 available daytime locations were included in analyses. Global Positioning System fix success was 98.8%. Of all used day locations, 816 occurred during the month-long hunting period and 723 occurred in refuges. Snow water equivalents ranged from 7.4 cm to 50.5 cm ($\bar{x} = 26.4$), and winter 2005–2006 had higher average SWE ($\bar{x} = 27.9$) than winter 2006–2007 ($\bar{x} = 16.8$). Distance to hunter access points ranged from 161 m to 13,687 m ($\bar{x} = 3,817$). During day, elk were most commonly located in grassland flats ($n = 2,070$) and less commonly in grassland hills ($n = 547$), forested areas ($n = 363$), and sagebrush steppe ($n = 242$). The 95% volume contour used to define available daytime locations included 53% grassland flats, 14% grassland hills, 26% forested area, and 7% sagebrush steppe habitats. Overall, 42% was a refuge area. The refuges were comprised of 64% grassland flats, 11% grassland hills, 21% forested area, and 4% sagebrush steppe.

Our analysis included 1,375 used and 27,500 available night locations. Of the used night locations, 344 occurred during the hunting period and 393 occurred in a refuge. Distance to hunter access points ranged from 132 m to 12,866 m ($\bar{x} = 3,352$). During night, elk were most commonly located in grassland flats ($n = 1,013$), and less commonly in grassland hills ($n = 172$), forested areas ($n = 111$), and sagebrush steppe ($n = 79$). The 95% volume contour used to define available nighttime locations included 64% grassland flats, 15% grassland hills, 16%

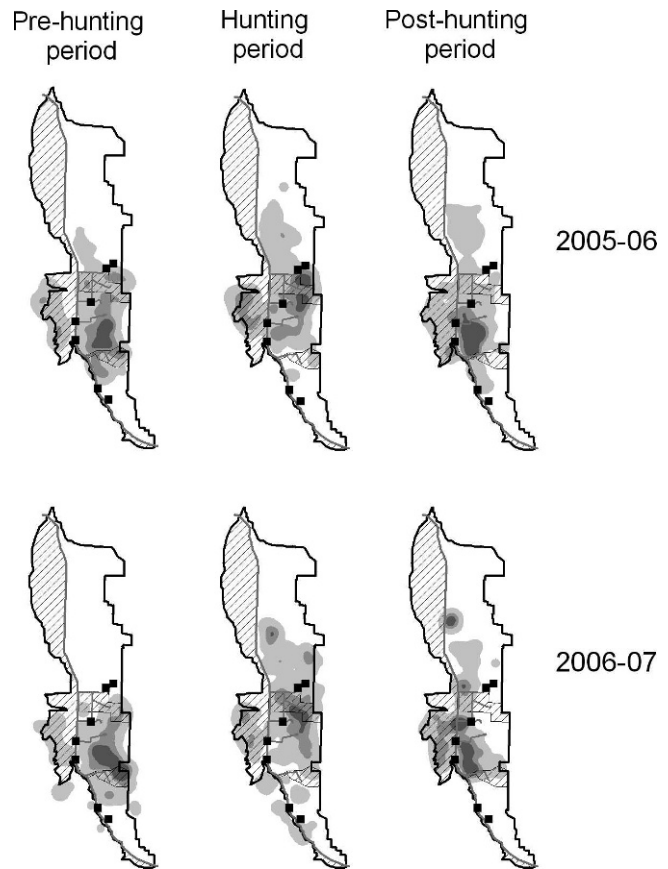


Figure 2. The 50% (darker gray), 75% (medium gray), and 95% (lighter gray) volume contours of daytime female elk probability density distributions during the pre-hunting, hunting, and post-hunting periods in the Madison Valley, Montana, USA, during winters 2005–2006 and 2006–2007.

forested area, and 5% sagebrush steppe habitats. Overall, 44% was a refuge area, and refuge habitat composition was the same as previously described.

Elk Distributions

Daytime elk distributions differed between hunting and no hunting periods. During the hunting period, the core distribution of elk was centered on a privately owned ranch that prohibited hunting. During the no-hunting period, the core distribution of animals was centered on a nonrefuge grassland flats area. Distributions of elk were similar between years, and a shift in distribution of elk to the refuge occurred during the January hunting season in 2005–2006 and 2006–2007 (Fig. 2). Distributions of elk differed somewhat during the pre-hunting period (Dec). In 2005–2006, a year with higher December SWE levels, the core elk distribution was located at a lower elevation flat grassland area near the highway, whereas in 2006–2007, a year with low December SWE, the core distribution was located in a higher elevation area of mixed grassland hills and forested areas. Distributions during the hunting and post-hunting periods were similar in 2005–2006 and 2006–2007.

Log-Odds Ratios

Our prediction that daytime selection for forested habitats increased during the hunting period was not supported

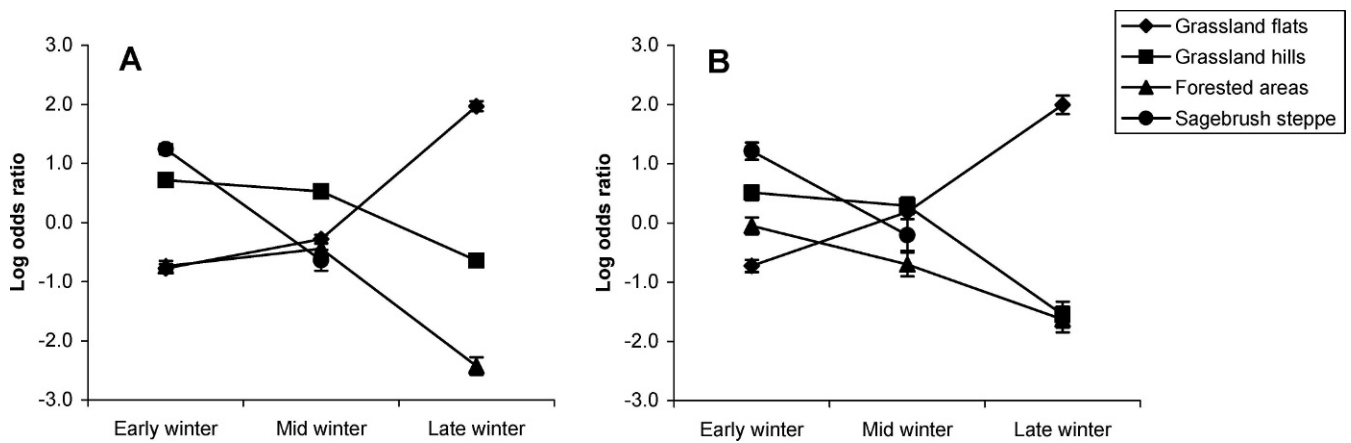


Figure 3. Log-odds of elk selection within 4 habitat types in the Madison Valley, Montana, USA, early winter (low snowpack, pre-hunting period), midwinter (moderate snowpack, hunting period), and late winter (heavy snowpack, post-hunting period) during winters 2005–2006 and 2006–2007. (A) Daytime locations; (B) nighttime locations. A log odds ratio of zero corresponds to independence. Error bars represent 95% confidence intervals.

(Fig. 3). We estimated the log-odds of occupancy in forested areas was -0.74 (95% CI = -0.92 to -0.56) during early winter, -0.44 (95% CI = -0.61 to -0.27) during the mid winter hunting period, and -2.43 (95% CI = -2.71 to -2.14) during late winter. During early winter, elk were more likely to occur in grassland hills and sagebrush steppe habitats and less likely to occur in grassland flats. As winter progressed, elk increased selection for grassland flats and selected against occupying grassland hills and forested areas. In late winter, elk did not occupy the sagebrush steppe habitat.

Habitat specific selection for refuges also varied during winter, and elk selected for grassland hills refuges during the hunting season (Fig. 4). Elk selected for grassland flats refuges approximately equal to their availability throughout the winter. Elk selection for grassland hills refuges was proportional to their availability during the pre- and post-hunting periods, and selection increased during the hunting period. Elk selected for forested refuges during the

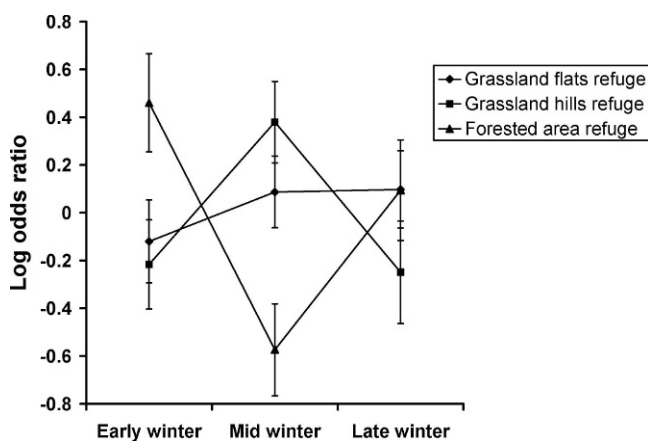


Figure 4. Log odds of daytime elk selection for refuge areas of different habitat types in the Madison Valley, Montana, USA, early winter (low snowpack, pre-hunting period), midwinter (moderate snowpack, hunting period), and late winter (heavy snowpack, post-hunting period) during winters 2005–2006 and 2006–2007. Error bars represent 95% confidence intervals.

pre-hunting period and selected against forested refuges during the hunting period. During the post-hunting period, elk selection for refuges was proportional to their availability.

Effects of Landscape Attributes and Predation Risk on Elk Resource Selection

We found strong support for our predictions that hunting risk and landscape attributes influenced elk resource selection during daytime. The most supported model included the covariates habitat, habitat \times SWE interaction, refuge, refuge \times hunting period interaction, distance to hunter access, and distance to hunter access \times hunting period interaction ($w_i = 1.0$, Table 1). Coefficient estimates supported predicted effects of covariates on resource selection (Table 2). The refuge area coefficient estimate was negative, indicating selection for areas that allowed hunting; however, the refuge \times hunting season interaction coefficient estimate was positive, indicating support for our prediction that during the hunting period, elk increased selection for areas that prohibited hunting. Based on coefficient estimates from the top ranked model, estimated log-odds of daytime elk occupancy in a refuge area increased from -1.4 (95% CI = -1.5 , -1.3) during the no-hunting period to -0.47 (95% CI = -0.65 , -0.29) during the hunting period.

The coefficient estimate for distance to hunter access points was negative, indicating selection for areas near hunter access locations, and the coefficient estimate for the distance \times hunting period interaction was positive, indicating that during the hunting period elk increased selection for areas distant to hunter access locations. However, coefficient estimates were near zero and estimated log-odds of elk occupying a non-refuge area 100 m from a hunter access location was -0.0120 (95% CI = -0.0121 to -0.0119) during the no hunting period and -0.009 (95% CI = -0.012 to -0.006) during the hunting period. In early winter, elk selected grassland hills, sagebrush steppe, and forested areas over grassland flats. However, habitat \times SWE interactions were negative, indicating selection for

Table 1. Model selection results for a priori models investigating effects of landscape and predation risk covariates on daytime elk resource selection in the Madison Valley, Montana, USA, during the winters of 2005–2006 and 2006–2007.

Model covariates ^a	K^b	ΔAIC^c	w_i^d
Habitat ^c + (Habitat × SWE) + Refuge + (Refuge × Hunt) + Dist + (Dist × Hunt)	10	0	1.0
Habitat + (Habitat × SWE) + Refuge + (Refuge × Hunt)	8	288	0.0
Habitat + (Habitat × SWE) + Refuge	7	380	0.0
Habitat + Dist + Refuge	5	982	0.0
Habitat + Refuge + (Refuge × Hunt) + (Habitat × Hunt)	8	994	0.0
Habitat + (Habitat × SWE)	6	1,037	0.0
Habitat + Refuge + (Refuge × Hunt)	6	1,168	0.0
Habitat + Refuge	4	1,254	0.0
Dist + Refuge + (Refuge × Hunt)	3	1,419	0.0
Dist + Refuge	2	1,508	0.0
Dist + Refuge + (Dist × Hunt)	3	1,509	0.0
Habitat + Dist	4	1,707	0.0
Habitat + Dist + (Dist × Hunt)	5	1,709	0.0
Habitat + (Habitat × Hunt)	6	1,734	0.0
Refuge + (Refuge × Hunt)	2	1,741	0.0
Refuge	1	1,828	0.0
Habitat	3	1,883	0.0
Dist	1	2,109	0.0

^a Covariates evaluated included habitat type (Habitat), snow water equivalent (SWE), refuge area (Refuge), hunting period (Hunt), and distance to hunter access points (Dist).

^b No. of parameters.

^c The Akaike's Information Criterion (AIC) value of the top ranked model was 22,757.

^d Akaike wt.

^e Habitat was a categorical covariate representing grassland flats, grassland hills, sagebrush steppe, and forested areas.

grassland flats increased as SWE increased. Coefficient estimates in the second ranked model were similar to the best ranked model, and given the relatively small effect of distance to hunter access locations, the second ranked model may be considered the most parsimonious model.

Contrary to our predictions that elk may select for high-risk areas during the night, we found elk avoided high-risk areas even though no hunting occurred during night. The most supported model of night resource selection included covariates habitat, habitat × SWE interaction, refuge, refuge × hunting period interaction, distance to hunter access, and distance to hunter access × hunting period interaction ($w_i = 1.0$). Coefficient estimates predicted effects of covariates on night selection were similar to effects

of covariates on day selection (Table 2). Based on coefficient estimates from the top ranked model, estimated log-odds of nighttime elk occupancy in a refuge area increased from -1.13 (95% CI = -1.28 to -0.98) during the no hunting period to -0.30 (95% CI = -0.57 to -0.03) during the hunting period.

Comparison of estimated day and night coefficients revealed that although predicted effects of covariates on resource selection were consistent, estimated coefficients for forested areas and grassland hills habitats, refuge area, and distance to hunter access differed between day and night (95% confidence intervals did not overlap). During day and night, selection was strongest for grassland flats habitats. Relative to grassland flats, selection for forested areas was

Table 2. Comparison of day and night coefficient values and 95% confidence intervals from the best ranked model representing the effects of habitat, snow water equivalency (SWE), refuge area (Refuge), hunting period (Hunt), and distance to hunter access locations (Dist) on elk resource selection in the Madison Valley, Montana, USA, during the winters of 2005–2006 and 2006–2007.

Covariate	$\hat{\beta}_{\text{Day}}$			$\hat{\beta}_{\text{Night}}$		
	Estimate ^{a,b}	Lower CI	Upper CI	Estimate ^{a,b}	Lower CI	Upper CI
Forested areas ^c	-1.34	-1.48	-1.21	-1.02	-1.26	-0.79
Grassland hills	-0.28	-0.38	-0.17	-0.78	-0.97	-0.59
Sagebrush steppe	-2.92	-3.43	-2.40	-4.00	-5.14	-2.85
Forested areas × SWE	-1.07	-1.22	-0.92	-0.79	-1.01	-0.56
Grassland hills × SWE	-0.75	-0.87	-0.64	-0.79	-0.97	-0.61
Sagebrush steppe × SWE	-3.87	-4.34	-3.40	-4.51	-5.40	-0.98
Refuge	-1.41	-1.52	-1.30	-1.13	-1.28	-0.98
Refuge × Hunt	0.94	0.76	1.22	0.83	0.57	1.10
Dist	-0.34	-0.38	-0.29	-0.48	-0.56	-0.41
Dist × Hunt	0.09	0.01	0.18	0.14	-0.01	0.29

^a Covariate estimates are from the top-ranked model that included the covariates: Habitat + (Habitat × SWE) + Refuge + (Refuge × Hunt) + Dist + (Dist × Hunt).

^b For comparing relative effects of covariates on variations in selection, we based coefficient estimates on centered and scaled covariates.

^c The grassland flats habitat was considered the base category. Coeff. estimates describe how selection for other habitat types compared to selection for grassland flats.

stronger during night and selection for grassland hills was stronger during day. During day, selection for non-refuge areas was stronger, although during the hunting period the effects of refuge on selection were similar during day and night (95% CI on refuge use overlapped).

Exploratory modeling revealed that the log-transformed distance to hunter access covariate did not improve model fit (day Δ AIC = 227, night Δ AIC = 74). Treating the 3-day no-hunting intervals within the hunting period as part of the no-hunting period did not improve model fit (Δ AIC = 48.9), indicating selection during the 3-day no-hunting intervals was more similar to selection during the hunting period than selection during the no-hunting period. We found some evidence of differences in daytime resource selection patterns between years. Coefficient estimates from winter 2005–2006 and 2006–2007 datasets predicted effects in the same direction as the combined years model with the exception of the 2005–2006 grassland hills covariate and the 2006–2007 distance to hunter access–hunting period interaction. The estimated log-odds of elk occupancy in a refuge area during the hunting season estimated during 2005–2006 and 2006–2007 were each within the confidence interval of estimated log-odds from the combined model.

DISCUSSION

We found evidence that human predation risk, as well as landscape attributes such as habitat type and snowpack, influenced adult female elk resource selection within a Greater Yellowstone Area winter range. Increased selection for refuge areas during the hunting season resulted in distributions that reduced elk availability for harvest, which represents a challenge to wildlife managers using harvest as a management tool (Haggerty and Travis 2006). Although it has long been accepted that human predation risk and landscape attributes influence elk distributions, quantifying the spatial and temporal scales to which elk respond may guide wildlife managers in designing harvest schedules to reduce elk use of refuges. Additionally, quantifying effects of hunting risk and landscape attributes on elk resource selection provides wildlife managers with baseline information against which to judge the effectiveness of alternate harvest schedules aimed at mitigating refuge effects.

Throughout the Rocky Mountains, elk behavioral responses to human predation risk include changes in grouping behaviors and movement rates, as well as distributional shifts from areas that allow hunting to areas where hunting is prohibited (Burcham et al. 1999, Vieira et al. 2003, Gude et al. 2006, Proffitt et al. 2009). After we accounted for the effects of landscape attributes, our best resource selection model estimated odds of elk occupying a refuge area more than doubled during the hunting period. Outside the hunting period, elk selected for non-refuge areas, which suggests non-refuge areas had greater abundance or availability of forage and provides indirect evidence that risk-driven changes in selection associated with hunting may result in trade-offs between forage quality or abundance and security. Although other landscape attributes such as land use or proximity to residences had the potential to

influence resource selection, we chose not to evaluate these attributes because there was only a low level of human activity associated with ranching and low density of residences across the study area. Further, this use was consistent throughout the winter and likely had little influence on elk use of refuges or the other attributes we were interested in quantifying.

Although previous studies found elk increased selection for forested areas in response to predation risk, we did not find strong evidence elk increased selection for forested areas during the hunting period (Unsworth et al. 1998, Creel et al. 2005). Elk used forested areas more frequently during the hunting period than before or after the hunting period, but confidence intervals on the log-odds ratio of elk occupying forested areas overlapped during the pre-hunting and hunting periods. Grassy patches may be smaller in forested areas, and forest browse may have lower digestibility and higher protein content than grasses (White et al. 2009a); therefore, risk-driven shifts into forested areas likely result in dietary changes (Morgantini and Hudson 1985). In landscapes that provide both natural escape habitat (i.e., forested cover) and refuge areas consisting of mixed forest and grassland habitats, elk may maximize security and foraging by selecting for grassland areas within refuges, and refuges may minimize security-foraging trade-offs.

Previous studies found that winter diet of elk consists primarily of grasses and that animal distributions may track available forage biomass (Frank et al. 1998, Christianson and Creel 2007). Consistent with these predictions, we found elk selected for sagebrush steppe and grassland hills in early winter, but as snow mass increased, selection for grassland flats increased. Flat grasslands were heavily windswept during winter, which left grasses exposed, and selection for these areas likely increased with SWE due to availability of exposed forage. Surprisingly, we found that selection for flat grasslands was less during a year of high SWE, perhaps because all habitats, including flat grasslands, retain snow cover during winters with high SWE.

Increases in selection for non-hunttable refuge areas during the 1-month hunting period provided evidence elk identify and respond to spatial and temporal variation in predation risk. Similarly, Unsworth et al. (1998) observed that elk avoided roads and hunter access locations during the hunting period but not outside of hunting periods. Although we found little evidence that elk avoided areas near hunter access locations during the hunting period, detecting these effects at our study site may have been difficult because refuge areas were located near hunter access locations, potentially confounding effects of hunter access locations on selection. Gude et al. (2006) found elk used habitats outside of the hunting period that were dangerous during the hunting period, despite the presence of human activity year round, suggesting that elk were able to discern temporal variation in predation risk.

We observed similarity of hunting period shifts in resource selection during day and night, which suggests that although elk may respond to variations in predation risk over weekly or monthly time scales, elk did not respond over

diurnal time scales. During night, when hunting was not permitted, elk selection for refuge areas increased during the hunting period, suggesting that although no immediate risk existed, elk continued to perceive risk associated with daytime hunting throughout the night. This result may partially reflect correlations between elk locations during day and night; however, we predicted that responses would diminish during night hours because elk are capable of moving throughout the study area over short time periods (Proffitt et al. 2009). Creel et al. (2005) documented elk responses to wolf predation risk at time scales of ≤ 1 day, suggesting that either elk responses to predation risk differed between sites or elk responded to wolf risk over shorter time intervals than human risk.

Wolf predation risk may have influenced elk selection for windswept grassland areas, although we were not able to evaluate these effects because wolf GPS collars failed partway through the study. One pack of 9 wolves used the study area during winter 2005–2006 and one pack of 6 wolves used the study area during winter 2006–2007. Previous studies reported contrasting effects of wolves on selection for open grasslands (Creel et al. 2005, Mao et al. 2005). Snowpack may influence an elk's ability to flee coursing predators and increase vulnerability to attack, and selection for grassland flats may also reflect risk-driven decisions to occupy areas increasing ease of movement and maneuverability (Mech and Peterson 2003, Smith et al. 2004). Alternatively, wolf predation risk may increase selection for forested areas where predation risk or detection is lower (Creel et al. 2005). Elk behavioral responses to wolf predation risk may have influenced habitat selection decisions; however, previous studies at this site showed elk responses to wolf predation risk were less than responses to human predation risk, and wolf predation risk likely had little influence on elk selection of refuge areas (Proffitt et al. 2009).

MANAGEMENT IMPLICATIONS

Elk selection for open grassland refuge areas, rather than forested areas, suggests that traditional concepts of elk security should be expanded in heterogeneous landscapes to include mixed-habitat refuge areas. Further, wildlife managers should consider boundary and refuge effects when designing hunts because opening small areas within winter ranges to hunting may result in elk selection for closed areas, reduced harvests, and potentially increased game damage claims. Incorporating short-duration temporal variability in predation risk may not be an effective strategy in reducing selection for refuges. However, incorporating spatial variation in hunting risk across the landscape and into refuge areas may be effective in reducing elk selection for refuges. If addition of at least some hunter access results in elk perceiving former refuge areas as insecure, selection for refuges is likely to diminish and more effective population management may be achieved. Where managers want to increase harvest, harvest schedules aimed at reducing elk use of refuge areas should be implemented. We recommend future studies quantify elk use of refuges and compare the

effectiveness of various harvest regimes in reducing elk selection for refuges.

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