



## Original Article

# Linking Elk Movement and Resource Selection to Hunting Pressure in a Heterogeneous Landscape

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**ABSTRACT** Elk (*Cervus elaphus*) are increasing in fragmented landscapes that result from exurban human development throughout western North America, which increases human–wildlife conflicts and poses a challenge to wildlife managers. Elk hunting must often be intensively managed to reduce population growth rate, crop depredation, and habituation to humans. However, little was known about the indirect effect hunting has on anti-predator behavior, movement, resource selection, and human–elk conflicts. We outfitted elk with global positioning system (GPS) collars in the wildland–urban interface (WUI) of Missoula, Montana, USA, 2007–2009, to test the indirect effects of hunting on elk. We used data from 9 GPS-collared adult female elk during 3 hunting seasons with increasing hunting pressure (2007–2009) to test relationships between movement rates measured by first passage time (FPT) and resource selection. Elk movement rates were lower approximately 750 m from houses and trails, resulting in resource selection for areas approximately 1,200 m from houses and trails; this suggested that habituation to humans contributed to human–wildlife conflict. Movement rates increased with increasing hunting pressure, and were lower in general versus focal hunting seasons and with archery versus rifle hunting. Thus, intensive hunting seasons in the WUI increased elk movement rates and exposure to hunter predation risk, as predicted. These results support the hypothesis that elk modify their behavior in relation to temporal and spatial variation in human predation risk. In the intensively managed WUI, our results demonstrate that even small increases in the area hunted and increases in intensity can indirectly change resource selection and movement rates of elk, potentially reversing recent trends of increasing habituation in WUI elk populations. © 2012 The Wildlife Society.

**KEY WORDS** anti-predator behavior, elk, first passage time, habituation, hunting, movement, resource selection, wildland–urban interface.

Human activities can affect animals through direct and indirect pathways (Sinclair and Byrom 2006, Creel and Christianson 2008). For example, humans can cause population declines either directly via over-harvest or indirectly through habitat fragmentation (Sawyer et al. 2007, Walker et al. 2007). Hunting by humans has direct effects on demography and indirect effects on animal behavior and life-history (Creel and Christianson 2008, Darimont et al. 2009). For example, under harvest pressure by humans, wild boar (*Sus scrofa*) invested more heavily in early reproduction at the cost of adult survival (Toigo et al. 2008). Even the risk of being killed by human hunters had a greater indirect effect on elk (*Cervus elaphus*) resource selection than did wolf (*Canis lupus*) predation risk (Gude et al. 2006). Under wolf and human predation risk, elk selected refuge areas

to avoid human predation risk in Montana, USA (Burcham et al. 1999, Gude et al. 2006, Proffitt et al. 2009). These examples demonstrate that the risk of mortality from a predator, including humans, can cause animals to change resource selection strategies to avoid risk. How animals adjust their movement behavior in response to spatio-temporal variation in predation risk, however, remains a neglected, but important, area of study in human–wildlife interactions (Lima and Bednekoff 1999).

Previous studies demonstrated that movement rates of elk are influenced by predation risk and forage availability (Fortin et al. 2005a, Frair et al. 2005). The risk-allocation hypothesis suggests that animals should show more frequent anti-predator behaviors under high risk, and forage during low risk (Lima and Bednekoff 1999, Ferrari et al. 2009). Many previous studies found that ungulates modify vigilance in proportion to predation risk, for example (Laundre et al. 2001, Liley and Creel 2008). Fewer studies have tested the resource selection and movement predictions of the

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risk-allocation hypothesis. Under the risk-allocation hypothesis, animals are predicted to slow down in areas and at times with high forage and speed up in areas and times of high predation risk (Ferrari et al. 2009). For example, Morales et al. (2005) identified “encamped” states in elk in which step lengths were small and turning angles were high; these were associated with foraging areas, whereas “exploratory” states were those with long step length and small turning angles.

Many resource selection studies have demonstrated spatial avoidance of predation risk (Hebblewhite and Merrill 2007), but from resource selection alone it is difficult to understand the mechanisms of risk avoidance. Gude et al. (2006) demonstrated that elk avoided human predation risk more than wolf predation risk, but they were unable to explain the behavioral mechanism explicitly. Did elk move more under human predation risk, or did they slow down and spend more time in safe patches as expected under the risk-allocation hypothesis? New movement analyses, such as first passage time (FPT; Fauchald and Tveraa 2003, Frair et al. 2005), provide novel approaches to test how predation risk influences the movement mechanisms of selection (Ferrari et al. 2009). For example, Frair et al. (2005) used FPT to demonstrate that human activity resulted in increased wolf predation risk, affected elk movement rates (Frair et al. 2005), and ultimately, reduced elk survival and fitness (Frair et al. 2007). Knowing whether changes in resource selection affect movements is important because movement could expose animals to increased risk of being encountered or detected by predators (Yoder et al. 2004). In many taxa, increased movement rates result in lower survival or fitness (Biro et al. 2003). Thus, understanding the effects of human predation risk on movement will be especially important in fragmented and heterogeneous human-dominated landscapes.

There are few landscapes more fragmented and rapidly changing in western North America than low-elevation valley bottoms (Radeloff et al. 2005, Haggerty and Travis 2006) that are also critically important winter ranges for ungulates (Toweill and Thomas 2002). The expansion of housing into ungulate winter range results in a complex matrix of land ownership that varies spatially in terms of human predation risk. In such landscapes, human predation risk varies from partial to complete exclusion, and is temporally regulated to mid-to-late autumn hunting seasons. As habitat fragmentation encroaches on ungulate winter range, ungulate exposure to humans is increasing, which increases the potential for habituation (Thompson and Henderson 1998). Humans also use differing hunting modes, similar to coursing (rifle hunting), and sit-and-wait predators (archery hunting), which may have different effects on risk allocation (Schmitz 2008). Thus, the winter range matrix of temporal and spatial variation in human predation risk will make elk management more complex because elk can change both movement and/or resource selection in response to human hunting (Thompson and Henderson 1998). Therefore, our objectives were to test the following predictions of the risk-allocation hypothesis: 1) FPT for elk will be lower (i.e., faster movement rates) in areas that allow hunting than in areas of refugia and hiding cover will reduce move-

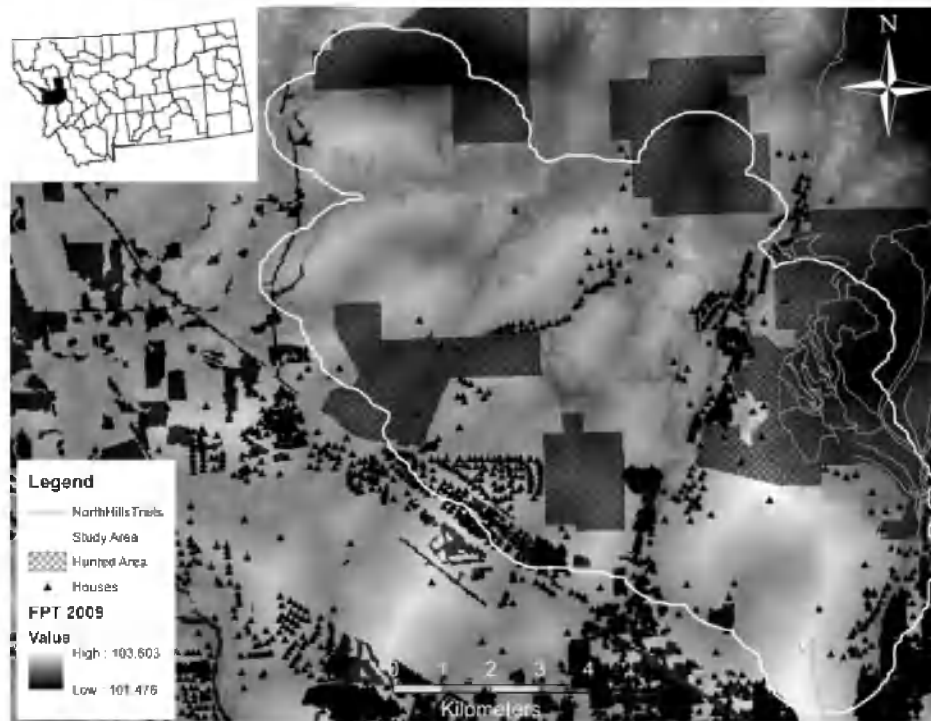
ment rates in hunted areas; 2) elk will move faster in areas of rifle predation risk than in areas of archery predation risk; 3) elk will increase movement rates with incremental increases in human predation risk as predation risk varies annually; and 4) elk will select for areas away from houses, roads, and trails. We tested these predictions over a 3-year period (2007–2009), during which hunting increased by nearly 30%, by measuring the effect of hunting access, hunting mode, distance to human influence (roads, trails, and houses), and the influence of cover on FPT and resource selection.

## STUDY AREA

Our study area focused on montane elk winter range in the North Hills of Missoula, Montana, USA (Fig. 1) from 2007 to 2009. This elk population size ranged from 300 in 2007 to 350 in 2009, but experienced an intrinsic growth rate of 11% from 1990 to 2007 (M. Thompson, Montana Department of Fish, Wildlife and Parks [MFWP], personal communication). The winter range was a matrix of housing subdivisions, private agricultural lands, National Forest, and the Rattlesnake Wilderness Area (U.S. Forest Service lands) along the northern boundary of the study area. Land use was a mix of cattle ranching and recreation (i.e., hiking, biking, and hunting). This matrix of land ownership exposed elk to varying intensity, duration, and modes (i.e., archery, rifle) of hunting pressure (Table 1, see Methods Section). Northern slopes were dominated by mixed-conifer forest, primarily Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*P. contorta*). Southern slopes were composed of ponderosa pine stands and mixed-bunchgrass communities dominated by native grasses: blue-bunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca altaica*), green needlegrass (*Nassella viridula*), needle-and-thread grass (*Hesperostipa comata*), timothy (*Phleum pratense*), and non-native Kentucky bluegrass (*Poa pratensis*) and cheat grass (*Bromus tectorum*). Elevation ranged from 1,100 m to 1,500 m from the southern to northern boundary, and topography was characterized by southwest rolling hills with slopes from 0% to 60%. The average annual precipitation was approximately 35 cm based on data from the National Oceanic and Atmospheric Administration (<http://www.wrh.noaa.gov/mso/climfacts.php>). The average summer temperature was 29° C and the average winter temperature was -9° C. White-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) were the other native ungulates in the study area. Despite the occasional presence of cougars (*Puma concolor*), humans were the main predators of elk in our study area (18% of mortality of radiocollared elk was hunting, compared with 9% non-hunting mortality,  $n = 3$  mortalities; Cleveland 2010).

## METHODS

We trapped and radiocollared adult female elk with GPS 4400M collars (Lotek, Newmarket, Ontario, Canada) during winters 2007–2009. We captured elk using clover traps (Thompson et al. 1989), a corral trap, and aerial helicopter



**Figure 1.** The location of the study and predicted first passage time (FPT) from the combined generalized linear mixed model for female elk, as a function of human predation risk (access) in Missoula County, in the wildland–urban interface of Missoula, Montana, USA. The study area was defined by the location data from 9 global-positioning-system-collared elk within the winter range of an urban elk herd in the North Hills of Missoula, Montana. The cross-hatched grids (Access) are the areas where human hunters had access to elk hunting during the course of the study (2007–2009). High FPT values represent increased time spent in that area.

darting in accordance with an approved animal use protocol (Animal Care and Use Committee 058-06MHECS-122706, University of Montana, Missoula, MT). Elk captured using aerial darting were immobilized with Thiafentanil and Xylazine, respectively, and reversed with Naltrexone at dosages recommended by Kreeger (2007). We used 6-hour location data from 9 GPS-collared elk on winter range for movement and resource selection function analyses to test predictions of the risk-allocation hypothesis during a 6-month focal period pre- to post-elk-hunting season from September to March. Global positioning system-collar fix-rates were high ( $\bar{x}$  fix rate >95%) and location error low ( $\bar{x}$  error = 34 m) enough to ignore habitat-induced bias or location error in movement or resource selection analyses

(Frair et al. 2010). We defined predation risk as the relative probability of death by human hunters for an elk, which was a function of the duration of hunting season as well as the number of hunters. During periods where hunting was illegal (out of season) or not allowed (e.g., private land, close to residential houses), predation risk was considered zero. Human predation risk on elk, as expressed by the combined number of huntable days by season type (days in which elk could be legally hunted), increased from 211 days in 2007–2008 to 271 days in 2008–2009. This represented an intentional increase of approximately 30% (M. Thompson, MFWP, unpublished data) in human predation risk with the goal of curbing wildland–urban interface (WUI) elk population growth (Table 1). This manipulation provided

**Table 1.** Elk hunting–season structure by season type, hunting mode, and total number of days in the wildland–urban interface of Missoula, Montana, USA, 2007–2008 and 2008–2009.

Year	Season type	Dates of hunt	Hunting mode	Hunted days
2007–2008	Rattlesnake Wilderness	15 Sep–25 Nov	Rifle	71
	Archery	01 Sep–14 Oct	Archery	44
	General season	21 Oct–25 Nov	Rifle	35
	National Wildlife Federation	Non-hunted	None	0
	Game damage	15 Dec–15 Feb	Rifle	61
			Total	211
2008–2009	Rattlesnake Wilderness	15 Sep–30 Nov	Rifle	76
	Archery	06 Sep–19 Oct	Archery	43
	General season	26 Oct–30 Nov	Rifle	35
	National Wildlife Federation	06 Sep–19 Oct; 26 Oct–30 Nov	Archery	78
	Game damage	03 Jan–13 Feb	Rifle	41
			Total	273

a serendipitous management experiment to test for effects of increased risk on elk movement and resource selection.

### Testing the Risk-Allocation Hypothesis With Human Predation Risk on Elk

Under the risk-allocation hypothesis, elk were predicted to reduce movement rates in areas and at times with high forage quality and increase movement rates in areas and times of high predation risk (Lima and Bednekoff 1999, Ferrari et al. 2009, Bastille-Rousseau et al. 2010). The interplay between spatio-temporal responses, however, means that one cannot address only one dimension (time or space) of risk allocation. Consider the scenario where humans have a greater impact on elk resource selection and movements than do wolves (Gude et al. 2006), and equal number of elk locations in habitat A (moderate human predation risk) and B (moderate wolf predation risk), with equal availability of both patches. Under standard resource selection analysis, the risk-allocation hypothesis would not be supported because resource selection was equal for patches A and B. However, instead of only adjusting time spent in a patch, elk could change movement strategies in response to predation risk. For example, our primary hypothesis was that elk would increase movement to reduce predictability in a patch, but alternately, one might expect a reduction in the proportion of foraging bouts in riskier landscapes (Lima and Bednekoff 1999, Bastille-Rousseau et al. 2010). The optimal strategy depends on the relative spatio-temporal variance in predation risk and whether movement itself is risky (Lima and Bednekoff 1999, Ferrari et al. 2009). We tested the prediction from the risk-allocation hypothesis outlined in Table 2 for elk using analysis of FPT and resource selection across a heterogeneous winter range landscape with a wide range of spatio-temporal variation in human predation risk.

### First Passage Time and Analysis of Movement

Movement is the process by which animals make behavioral decisions to select resources in space and time (Turchin 1998). Animal movement can be thought of a series of

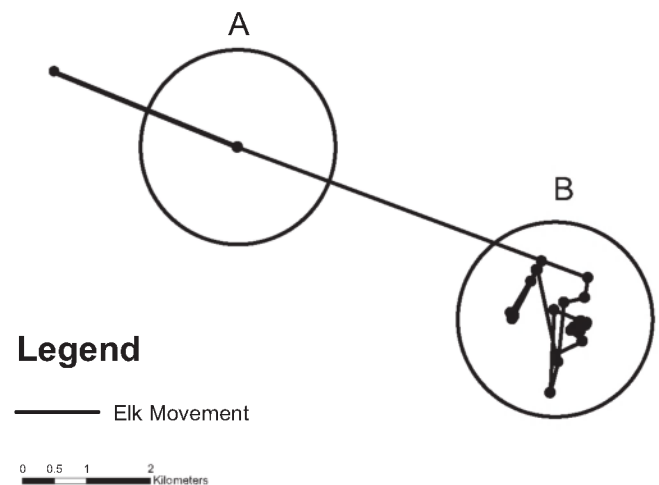
biological “moves” between safe foraging or resting “patches.” Movement analyses, such as FPT integrate step length, turning angles, and tortuosity to measure the amount of time it takes an animal to leave a specified patch (Fauchald and Tveraa 2003). First passage time thus measures the biologically relevant move from the animal’s perspective, and can help identify the relevant scale of biological moves (Fauchald and Tveraa 2003). We took the approach to use FPT to understand the patch size elk responded to, and then tested the effects of spatio-temporal variation in hunting pressure on FPT within these patches of GPS-collared adult female elk. By first examining the search radius that maximizes variance in FPT, ecologists can discriminate area-restricted search behavior, such as foraging, from long-distance movement between foraging patches (Fig. 2).

We first identified this patch size by measuring the FPT of GPS-collared elk forward and backward across circles of varying radii ( $t(r)$ ; excluding the first location) to derive the amount of time spent searching in the circle (Fauchald and Tveraa 2003). We calculated  $t(r)$  by taking the absolute value of forward movement plus the backward movement (Fauchald and Tveraa 2003) to test the maximized variance in FPT ( $S(r)$ ) that distinguishes area-restricted search within a patch from directed movement between patches (Fauchald and Tveraa 2003). Circles of radii between 25–100 m and 100–2,500 m were applied to each location, increasing in 25-m and 100-m increments, respectively, to determine the threshold where variation in area-restricted search was maximized. This radius where variation was maximized between patches defined the patch size in the landscape that elk responded to. First passage time was calculated using the Hawthtools 3.1 extension in ArcGIS 9.3.1.

We next tested whether human hunting seasons and modes changed the movement rates (FPT) of elk within patches of the identified radius above. Under the risk-allocation hypothesis, we predicted FPT to decrease during the hunting

**Table 2.** Predicted effects of selected covariates on first passage time (FPT) and resource selection under the risk-allocation hypothesis for 9 adult female elk in wildland–urban interface of Missoula, Montana, USA. The level of hunting access increases from 2007, 2008, and 2009, which has corresponding decreases in FPT and resource selection values. Negative signs and positive signs represent the expected increase or decrease in either FPT or selection for that variable.

Variables	First passage time	Resource selection function
Access	--	--
Distance to houses	-	-
Access × highcover	+	Neutral
Year	--	n/a
Rifle season	--	n/a
Archery season	Neutral	Neutral
Distance to trails	++	+
Housing density	--	-
Normalized difference vegetation index	++	++
Highcover	Neutral	-
Distance to roads	+	+



**Figure 2.** An example of first passage time (FPT) from a global-positioning-system-collared adult female elk (Elk 2; tracked during 2007–2009) from the wildland–urban interface of Missoula, Montana, USA. Both circles have a radius of 1,600 m (drawn to scale). (A) represents a low FPT, and (B) represent a high FPT.

season and to increase outside of the hunting season. We also predicted that rifle hunters (coursing predators) would decrease FPT when compared with archery hunters (sit-and-wait; Table 2). Finally, because predation risk increased 30% from 2007 to 2009, we also predicted an annual decrease in FPT. We tested these predictions on FPT with 2 complimentary analyses. First, we conducted simple descriptive 1-way analyses of variance (ANOVA) across the 4 hunting seasons (i.e., non-hunted, archery, rifle, game damage; Table 1), hunting mode (i.e., archery, rifle), and time (i.e., yr, month; Zar 1999). We used simple post hoc tests to test for differences in one-way ANOVAs.

Second, we tested how spatio-temporal covariates influenced FPT at the area-restricted search threshold we identified in the first step by using a general linear modeling approach to accommodate data complexity more adequately than ANOVA. We used a generalized linear mixed-model (GLMM) with the identity (Gaussian errors) link function (Bolker et al. 2009) of FPT fit to a function of hunting and landscape covariates following

$$\text{FPT}_i = \beta_0 + \gamma_{0i} + \beta_{1i}X_{1...} + \beta_{ni}X_n + \epsilon \quad (1)$$

where  $\beta_0$  is the intercept,  $\gamma_{0i}$  is the random intercept for individual elk  $i$ ,  $\beta_x$  is the individual selection for resource  $X$ , and  $\epsilon$  is the residual variation unexplained by the model. We added a random effect ( $\gamma_{0i}$ ) for each elk to account for individual variation in elk movement behavior (Freitas et al. 2008). We predicted that elk movement rates will increase (i.e., exploratory movements and a low FPT) with increasing human predation risk (as expressed by increased hunter access) in space and time (Table 2; Morales et al. 2005). Furthermore, if movement rates decreased following the cessation of hunting, then the prediction that elk selected for refuge from human hunting would be upheld. We expected other factors, such as topography, vegetation cover, and proximity to humans to also potentially influence FPT of elk in predictable ways based on previous studies (Frair et al. 2005, Anderson et al. 2008). We summarize these effects below in the covariates section.

### Resource Selection Functions

We predicted that factors that increase elk movements should decrease the strength of selection as measured by time in a patch because of the inverse relationship between time spent in a patch and movement rate (Table 2; Bastille-Rousseau et al. 2010). We developed resource selection functions for elk as a function of human predation risk using a used-available design (Manly et al. 2002) by comparing used locations to random available locations along GPS-collared elk movement paths. We used a matched-case control logistic regression to evaluate the effect of landscape covariates on elk resource selection (Hosmer and Lemeshow 2000, Compton et al. 2002). We generated 2 locations from the empirical step length and turning angle distribution of the movement pathways (Forester et al. 2009). We conducted 2-staged modeling where we estimated a matched-case logistic regression for each elk and then averaged among individuals (Fieberg et al. 2010). Two-stage regression

modeling approximates mixed-effects models by treating the individual as the sampling unit, but is statistically more straightforward than adding a random effect for each individual elk to matched-case control models that do not have an intercept (Hosmer and Lemeshow 2000). We estimated individual elk resource selection along movement paths using fixed-effects conditional logistic regression for each individual elk ( $i$ ) by using

$$w(x)_i = \frac{\beta_{1i}X_{1...} + \beta_{ni}X_n + \epsilon}{1 + \beta_{1i}X_{1...} + \beta_{ni}X_n + \epsilon} \quad (2)$$

where ( $i$ ) is the individual elk,  $\beta$  is the individual selection for resource covariate  $X_n$ , and  $\epsilon$  is the residual variation unexplained by the model. The probability  $w(x)_i$  is a relative probability because of the problem of defining availability in use-availability resource selection designs (Johnson et al. 2006).

### Covariates Influencing FPT and Resource Selection

We used spatial measures of hunter accessibility, distance from trails, roads, and houses (m), housing density (no. of houses/km<sup>2</sup>), distance to streams, normalized difference vegetation index (NDVI), elevation, slope, hillshade, and landcover variables to develop *a priori* models of elk resource selection (Burnham and Anderson 2004). Spatial data for hunter access, trails, roads, houses, streams, and a digital-elevation model were all obtained from Montana Cadastral Mapping (<http://www.gis.mt.gov>). We spatially defined hunted (access) and refugia landcover classes from parcel data that identified landowners that were involved in cooperative hunting agreements with MFWP and by following legal hunting-district boundaries (MFWP Hunting Regulations 2007–2009). As a surrogate for spatial human predation, we estimated human activity as function of distance from known human use areas (trails, roads, and houses; Merrill et al. 1999) in the Spatial Analyst Extension of ArcGIS 9.1. We measured housing density by measuring the centroid of individual landowner parcels. We then screened the data to insure a house was in the parcel, and then calculated the number of houses/km<sup>2</sup>. We obtained 30-m-pixel resolution digital-elevation model, slope, and aspect covariates, and calculated hillshade using the default in ArcGIS 9.1 (NE 315°) to obtain a continuous variable where high variables represent warm southwest hillsides. We measured changes in primary productivity using NDVI data from the Moderate Resolution Imaging Spectroradiometer satellite at a 250-m<sup>2</sup> resolution (Pettorelli et al. 2005). We included 2 measures of NDVI measured in winter (NDVI\_W) and summer (NDVI\_S) to represent the seasonal transition from high forage biomass in the autumn to spring green-up. We defined autumn forage biomass using NDVI at the 193rd day of the year (NDV\_S), and spring green-up as the 81st day of the year. High NDVI values for both winter and summer were representative of tree cover. We used the 30-m-resolution landcover map (U.S. Forest Service's Northern Region Vegetation Mapping Project) to represent vegetation landcover (Brewer et al. 2006). We reclassified landcover covariates into open habitats composed

of grasses, shrubs, and sparsely vegetated areas (OPEN), and closed habitats composed of tree-dominated landscapes (CLOSED).

We predicted that landscape covariates (distance to houses, trails, and roads) that decreased FPT would consequently be avoided in resource selection analysis (Table 2). For example, as forage biomass increased, elk were predicted to spend more time foraging in a patch, decreasing FPT and increasing the signal for resource selection. Hiding cover, as represented by percent canopy cover, was expected to increase FPT, as would steeper slopes that reduce movement rates (Fortin et al. 2005*b*). Slope and hiding cover were predicted to be selected more strongly during hunting seasons to avoid predation. We did not include a year covariate as we had done in FPT analysis because available and used locations were paired temporally, such that a used location in 2007 could not have an available hunting level in 2008. We tested for interactions between access and hiding cover (by including a multiplicative term between the categorical covariates of cover and access) given previous evidence that elk select for closed forests when subject to predation risk (Creel et al. 2005). In addition, we screened for quadratic relationships of selection for distance to streams, trails, roads, and houses to determine whether elk were selecting for intermediate distances to these variable (Hosmer and Lemeshow 2000).

### FPT and Resource Selection Model Selection and Analyses

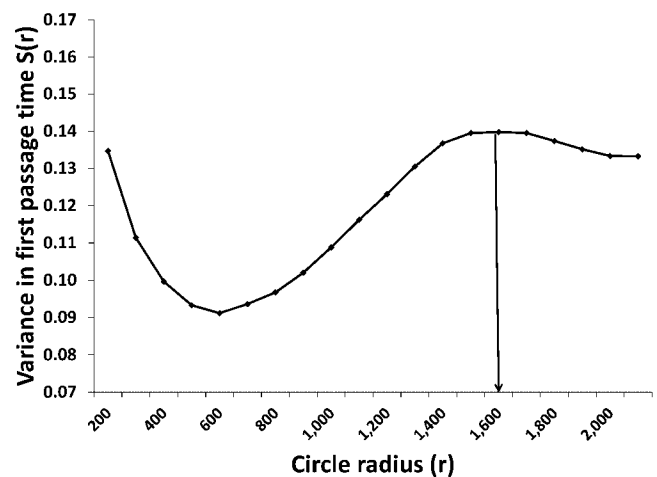
We tested the predictions of the resource allocation hypothesis (Table 2) for both FPT and resource selection in a stepwise model-selection procedure following recommendations from Hosmer and Lemeshow (2000). We first screened explanatory variables for multicollinearity (using a correlation coeff.,  $r$  approx. = 0.50) by using univariate analysis while accounting for confounded variables (Hosmer and Lemeshow 2000). We then manually built 3 different suites of models using stepwise model selection following Hosmer and Lemeshow (2000), which considered only human-only covariates, environmental-only covariates, and a combined model. We selected the top FPT or resource selection model from either human, environmental, or combined models using Akaike's Information Criterion (AIC; Burnham and Anderson 2004). We chose this "hybrid" model-selection form to avoid allowing collinear or confounded variables in the same models (Hosmer and Lemeshow 2000).

The fit of FPT GLMMs was evaluated with the coefficient of determination. We evaluated model fit for resource selection models using a modified version of  $k$ -folds cross-validation adapted for matched-case control designs.  $K$ -folds iteratively builds resource selection models on  $k$  random "partitions" of data and then tests the predictive capacity of the model against out-of-sample data not used in model development (Boyce et al. 2002). We adopted this approach to the matched-case design using a jackknife  $k$ -folds cross-validation, where we excluded one elk, estimated resource selection with the remaining elk, and then tested predictive accuracy for each elk's locations and averaged across elk to evaluate predictive capacity for the population (*sensu* Boyce

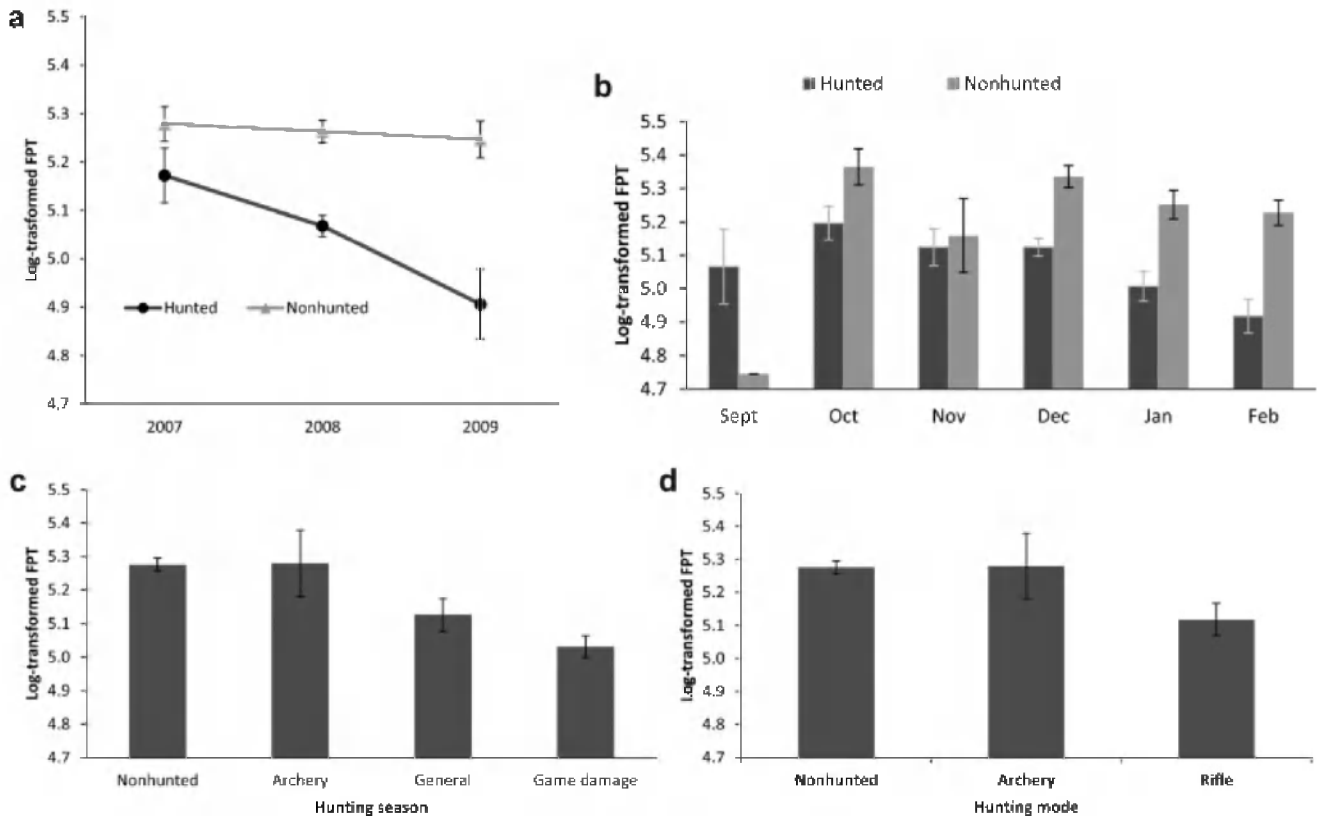
et al. 2002). If a resource selection model has high predictive capacity, then the rank observation of all out-of-sample locations should be well-predicted within ranks of increasing habitat "bins" from 1 (poor habitat) to 10 (excellent habitat). We tested for high predictive capacity of excluded elk locations using spearman rank correlation (Boyce et al. 2002). All statistical analyses were conducted using STATA 10 (College Station, TX).

## RESULTS

We obtained approximately 39,000 GPS telemetry locations from 9 GPS-collared elk during the focal sampling period (Sep–Mar) over the 3 years of the study (2007–2009). The variance in area-restricted search was maximized at 1,600-m radii (Fig. 3). Using this threshold of 1,600 m to discriminate movements between patches, FPT varied as a function of year, month, hunting season, and hunting mode (Fig. 4). Focusing first on the effect of changing hunting seasons between years, FPT decreased (i.e., movement rates increased) as hunting pressure increased (Table 1) during the hunting season from 2007 to 2008 ( $F_{x,y} = 15$ ,  $P = 0.093$ ), and from 2008 to 2009 ( $F_{x,y} = 14$ ,  $P = 0.031$ ), but was not significantly different during the non-hunting periods in the same years ( $F_{x,y} = 13$ ,  $P = 0.707$ ) and ( $F_{x,y} = 14$ ,  $P = 0.719$ ), respectively. However, when just considering FPT when elk were spatially available to be hunted ( $F_{x,y} = 13$ ,  $P = 0.148$ ), FPT of within-year hunted and non-hunted elk was not significantly different in 2007, but FPT was significantly lower in 2008 ( $F_{x,y} = 15$ ,  $P < 0.001$ ) and 2009 ( $F_{x,y} = 13$ ,  $P < 0.001$ ), which supported the hypothesis that increasing hunting pressure decreased FPT and increased movement (Fig. 4a). First passage time was significantly lower between the archery and rifle hunt than non-hunted periods ( $F_{x,y} = 24$ ,  $P < 0.011$ ; Fig. 4c), yet multiple comparisons revealed that only rifle hunting decreased FPT relative to both archery and non-hunting periods (Fig. 4d). Monthly



**Figure 3.** The variance in log first passage time (FPT)  $S(r)$  as a function of area to define area-restricted search (ARS), given an increasing circle radius ( $r$ ), for female elk in the wildland–urban interface of Missoula, Montana, USA (2007–2009). ARS is maximized at a radius of 1,600 m.



**Figure 4.** Log-transformed first passage time (FPT) values with standard errors from 9 global-positioning-system-collared adult female elk in the wildland-urban interface of Missoula, Montana, USA as a function of (a) year, (b) month across all years (2007–2009), (c) hunting season across all (2007–2009) years, (d) hunting mode across all years (2007–2009). Year 2007 represents the lowest human predation risk, with risk increasing in 2008 and 2009.

FPT was lowest during September, peaked in October and December, and dropped again in February (Fig. 4b). First passage time during hunting season was significantly lower than non-hunted times for all months except September and November (Fig. 4b).

The top FPT model combined human and environmental factors, with a  $\Delta AIC > 1,100$  compared with the next-ranked model with only human or environmental factors. Therefore, we only report the top human and environment model here. Individual variation in FPT was substantial (random effect for individual elk variance = 0.235) in the top model. Human-related covariates (access, yr, mode) caused the biggest reductions in FPT, and hence greatest increases in movement rates (Table 3). Elk FPT showed a quadratic relationship with distance to houses (Table 3), with FPT increasing until elk were approximately 750 m from homes and then declining thereafter (Fig. 5a). Important environmental covariates that increased FPT were distance (in meters) to streams ( $\beta = 0.0002$ ) and hillshade ( $\beta = 0.0002$ ), whereas FPT declined in areas of highcover ( $\beta = -0.09$ ; Table 3). Distance to streams was highly correlated with distance to roads (correlation coef. = +0.50); therefore, we interpret distance to streams interchangeably with distance to roads in our analysis.

The top model describing adult female elk resource selection was also the combined human and environmental model ( $r^2 = 0.83$ ,  $\Delta AIC > 683$ ). Distance to houses and distance

to trails were the only human variables that had a significant influence on resource selection. Elk selected for intermediate distances from both houses and human trails. Elk selected intermediate distances of 1,200 m from human activity, and approximately 2,000 m from trails (Table 3). Hunter access was statistically insignificant in the model ( $P = 0.34$ ) but was retained regardless to test Prediction 1 (Table 3). Elk selected for high NDVI values during winter months ( $\beta = 16.19$ ), which we interpreted as selection for tree cover because NDVI was highest in closed forests in our study area. Conversely, during autumn, elk avoided high NDVI values ( $\beta = -16.26$ ; Table 3), suggesting elk selected for hiding cover during high-risk times and selecting for high forage biomass during less risky times. The  $k$ -folds cross-validation of the top resource selection functions model predicted the rank order of observed habitat selection of the withheld elk very well across all individual elk (Spearman's rank correlation,  $r_s = 0.946$ ,  $SE = 0.017$ , range = 0.861–1.0).

## DISCUSSION

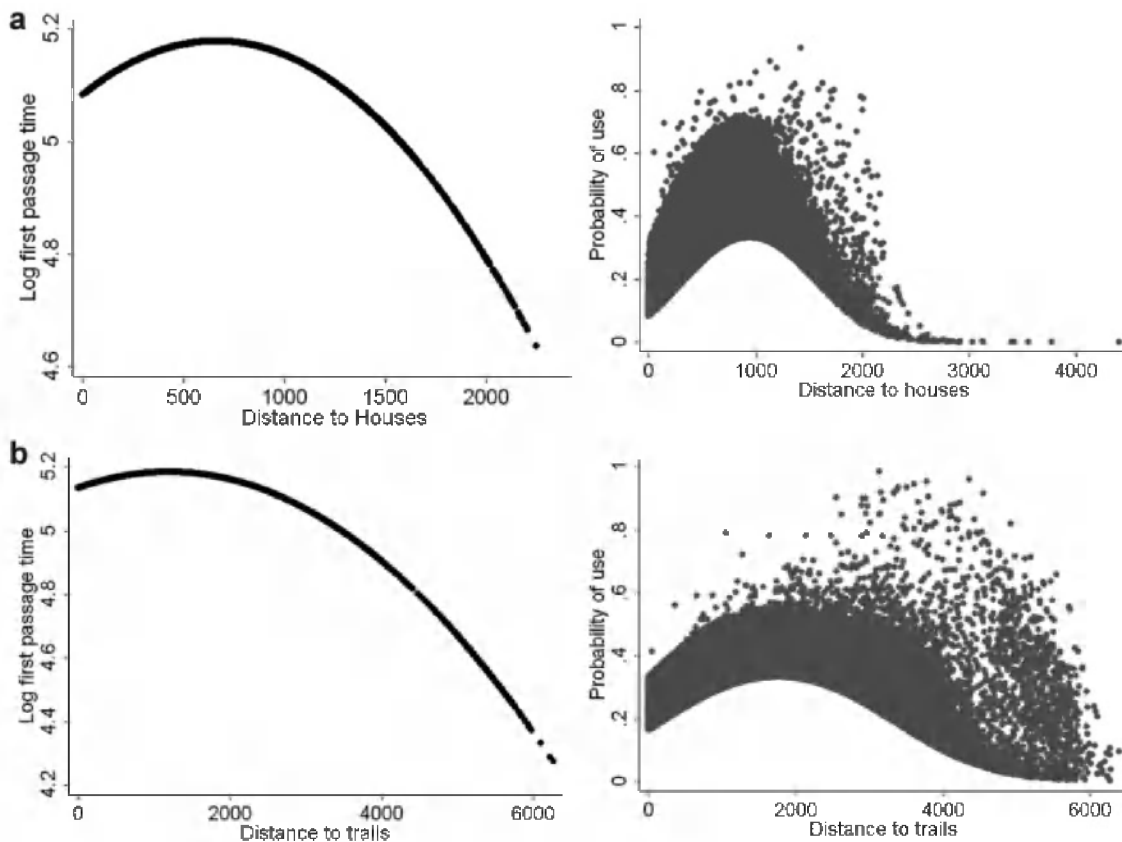
We found that spatio-temporal variation in human predation risk drove patterns of elk movement, but not necessarily resource selection, in a heterogeneous WUI landscape. As expected under the risk-allocation hypothesis, elk FPT declined with increasing movement rates, where, and when they were exposed to more human predation risk. The only

**Table 3.** Highest ranked first passage time (FPT) and resource selection function models based on Akaike Information Criterion (AIC) values of competing models from 9 global-positioning-system-collared adult female elk in the wildland-urban interface of Missoula, Montana, USA. Bolded variables are those whose effect on elk differed between FPT or resource selection but were significant in FPT analysis or were of interest in hypothesis testing. Distances are expressed in meters and housing density is the number of houses per km<sup>2</sup>.

Variables	First passage time			Resource selection functions		
	$\beta$	SE	<i>P</i> -value	$\beta$	SE	<i>P</i> -value
Access	-0.29	0.007	<0.0005	-0.11	-0.037	<b>0.3350</b>
Distance to streams	0.0002	0.00004	<0.0005	0.0007	0.00022	0.0334
Distance to houses	0.0002	0.00002	<0.0005	0.003	0.0011	0.0047
Distance to houses2	-0.0000007	0.00000001	<0.0005	-0.000002	-0.0000005	0.0181
Access × Highcover	0.076	0.0119	<0.0005			
Year	-0.05	0.002	<0.0005			
Rifle	-0.11	0.004	<0.0005			
Distance to trails				0.001	0.0003	0.0183
Distance to trails2				-0.0000003	-0.00000009	0.0065
Housing density				-0.006	-0.0020	<b>0.1507</b>
Hillshade	0.0002	0.0000613	0.0070	-0.003	-0.0010	<b>0.1022</b>
Highcover	-0.09	0.005	<0.0005			
Lowcover				-9.25	-3.085	0.0298
Normalized difference vegetation index-winter				16.19	5.41	<0.0001
Normalized difference vegetation index-summer				-16.26	-5.42	<0.0001
Slope				0.014	0.0046	<b>0.8104</b>
Constant	103.17	3.788	<0.0005			

exception was when elk were able to hide under cover as a strategy to reduce exposure to human predation risk, similar to recent studies of elk movement (Conner et al. 2001, Frair et al. 2005, Anderson et al. 2008). In contrast, hunting access was not the strongest influence on elk resource selection;

instead, resource selection was influenced more strongly by forage-related covariates, also echoing recent studies that emphasized the importance of elk selection for forage biomass (Sheehy and Vavra 1996, Sawyer et al. 2007). This discrepancy in our analysis between movement and resource



**Figure 5.** The distance (m) to houses (a), and trails (b), where first passage time and the relative probability of resource selection was maximized from generalized linear models developed from 9 global-positioning-system-collared adult female elk. The data were collected from 2007 to 2009 in the wildland-urban interface of Missoula, Montana, USA.



selection highlights the importance of considering the mechanics of movement in how animals select resources (Turchin 1998). Unfortunately few studies consider both movement and resource selection analysis, yet had we conducted only one analysis, our understanding of elk–human interactions in the WUI would have been much poorer.

How animals move is influenced by landscape heterogeneity, foraging behavior, and predation risk, which may result in differences between resource selection and movement (Morales et al. 2005, Bastille-Rousseau et al. 2010). Bastille-Rousseau et al. (2010) showed that a discrepancy between movement and resource selection could result because of changes in inter-patch movement decisions, which our results corroborate because elk changed movement, but not resource selection, as human predation risk increased. The threshold between within-patch and between-patch movements (1,600 m) was also similar to elk in Frair et al.'s (2005) study in a wolf predation system, which suggests that elk were making decisions at a similar spatial scale under predation risk of wolves (Frair et al. 2005) and humans. We also observed a peak in variance in FPT at very small radii that may be because of small-scale foraging decisions or GPS-induced error in apparent movement (Frair et al. 2010). Our results demonstrated that elk movement strategies supported the risk-allocation hypothesis for movement, but not for resource selection, because human predation risk increased by year (Fig. 4a), by differing hunting modes (Fig. 4d), and by season type (Fig. 4c). MFWP increased hunting pressure from 2007 to 2009, and we documented a corresponding decrease in FPT, as expected under Prediction 3. Elk responded the strongest by increasing movement rates in response to rifle hunting (couraging predator), supporting predictions of the risk-allocation hypothesis, but in contrast to the effect seen by Schmitz (2008) that found ambush predators had the largest effect on prey resource selection. This difference could, in part, be due to the large impact humans have on elk (Gude et al. 2006), or to the fact that there were insufficient numbers of archery hunters to illicit a response, or the fact that archery hunting was not really equated with a sit-and-wait hunting strategy. Interestingly, FPT of elk did not differ during the non-hunting and archery seasons. However, the FPT of 2 rifle-hunting seasons differed from other season types significantly (i.e., general rifle season vs. game-damage rifle season). The significant decline in FPT with game-damage rifle hunting illustrates that focused hunting seasons have a greater impact on elk movement than do more general hunting seasons designed to directly reduce elk populations. Movements also increased in response to hunting season structure from a more general to a focused hunting season over time within a season from October to February (Fig. 4b). Thus, wildlife managers seeking to manage ungulates in the WUI and other fragmented landscapes might need to make a trade-off between the direct (reduce elk no.) and indirect effects (increase movements and dispersion of elk) of human harvest on elk.

Understanding effects of hunting on movements was all the more important because of its minimal effect on resource

selection in the WUI. Hunter access (which decreased FPT) and distance to streams (which increased FPT) were the primary drivers of FPT in our top model (Table 3). In contrast, human related variables (access; distance to streams, houses, and trails; and housing density) had less of an impact on resource selection, which was driven more by environmental variables (forage, open habitats, and slope). For example, hunter access had scant impact on resource selection in the top resource selection model, contrary to other studies (Gude et al. 2006, Proffitt et al. 2009). This difference was likely a result of the increased landscape heterogeneity in the WUI. Humans were still influencing the system with nonlinear relationship of distance to trails and distance to houses (Fig. 5). In addition, elk selected for areas farther from streams and roads (because of the correlation in our area of 0.5 between them), which is well-supported in the literature (Lyon 1979, Rowland et al. 2000). Elk selected for forested areas during winter, as indicated by high NDVI values, which represented forested landscapes, and they selected for open grasslands in the autumn. These results were similar to Creel et al. (2005) and Gude et al. (2006), who showed that elk selected for areas of forage availability irrespective of human predation risk.

The results of this study are somewhat limited by sample size ( $n = 9$ ), except this elk herd of >300 rarely split into >3 groups, and groups were never observed without a GPS-collared elk. Another potential limitation of our study is that we used the surrogates of hunting access and distance to human-related variables (trails, houses, and streams) to approximate the human predation risk. Although we feel this is an acceptable method to determine the additive effects of humans (Merrill et al. 1999), our insights of actual hunting pressure would have been more accurate if we had temporal and spatial data of elk hunters on the landscape. Also, human predation risk is obviously not the only form of mortality for elk because 50% of our collared elk died (admittedly from a small sample) from non-human harvest causes. Thus, non-human predation risk could potentially confound our results. However, our results emphasize that, in 2007, there was no difference in FPT of hunted and non-hunted elk, but over time as hunting pressure (and thus human-caused mortality) increased, FPT declined. This supports our interpretation that human predation risk, not risk from non-human predators, was driving changes in elk movement. Regardless, few wildlife management agencies are able to track the numbers of hunters on the landscape. Our results demonstrated a significant effect of increased hunting season length alone, without known hunter numbers, on elk movement, and resource selection. This reinforces the importance of managing hunting-season length, and not specifically numbers of hunters, in developing management strategies to address elk harvest in fragmented landscapes.

## MANAGEMENT IMPLICATIONS

Our results support the efficacy of highly focused and orchestrated hunts to increase elk movement, because the focused game-damage rifle season had the greatest effect on

increasing movements and thus, dispersion of elk. We also observed an attenuation of vigilance and movement rates for WUI elk within 3–5 weeks of the end of hunting season (Cleveland 2010). This suggests that altering hunting timing, duration, and location can decrease the refuge effect by reducing the spatio-temporal predictability of predation refugia. Punctuated hunting seasons may offer a valuable management tool to break the habituation cycle. The mode of hunting was also important because archery had little effect on movement and resource selection. If increasing elk dispersion is important, either to decrease crop damage or increase vulnerability to harvest, rifle-hunting seasons had the greatest effect on movement rates. If increased movements increase vulnerability to human harvest, as suggested for wolf predation (Hebblewhite and Merrill 2007), increased movement rates may result in direct reductions in elk populations.

These highly orchestrated WUI hunts also seem effective at reducing the risk of habituation, an important credibility challenge to wildlife managers (Thompson and Henderson 1998). In our study area, elk selected areas 1,600 m from houses and started to slow down at 750 m from houses (Fig. 5). This suggests that humans are still viewed as a potential predation risk, but their willingness to be close to a potential predator (humans) suggests they are showing signs of habituation (Thompson and Henderson 1998). This information will allow managers to structure hunting access in a fashion to reduce conflict between WUI residents and hunters in the area by potentially allowing hunting access a minimum of 750 m from homes. Knowing that elk will move quickly through areas 750 m from houses suggests a minimum of 1,500 m of buffer between subdivisions is required to insure movement corridors remain functional. Maintaining migratory behavior of elk populations is imperative to the maintenance of ecosystem function (White et al. 1998, Hebblewhite and Merrill 2009), because resident elk populations degrade range condition (Baker et al. 1997, Snyder 2007). The 1,500-m buffer zones may provide a useful guideline by which to prioritize conservation easements in the WUI to insure continued migration of WUI elk populations.

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