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HUMAN PREDATION RISK AND ELK BEHAVIOR IN HETEROGENEOUS LANDSCAPES

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HUMAN PREDATION RISK AND ELK BEHAVIOR IN HETEROGENEOUS LANDSCAPES

By

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Thesis

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Human predation risk and elk behavior in heterogeneous landscapes

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Abstract:

Elk (*Cervus elaphus*) are increasing in fragmented landscapes that result from exurban human development throughout western North America. This problem is increasing human-wildlife conflicts and represents a significant new challenge to wildlife managers. Elk hunting must be intensively managed, if allowed at all, to reduce public relations problems. For example, the Montana Department of Fish, Wildlife & Parks has focused three hunts on a rapidly growing (~11% annually) elk herd in the wildland-urban interface (WUI) of Missoula, Montana, USA. Their goals were 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 first investigated the indirect effects of hunting on elk using an extensive comparison of elk anti-predator behavior across four human predation risk levels in western Montana. We collected 361behavioral observations across this predation risk gradient from October 2008 to March 2009. Vigilance was highest in highest predation risk areas and lowest in lowest risk areas. Vigilance and movement attenuated with the removal of human predation risk within 3-5 weeks under intermediate human predation risk in Missoula, Montana. I then used an intensive investigation of elk outfitted with global positioning system (GPS) collars in the WUI of Missoula to test the indirect effects of hunting on elk. We used data from nine GPS collared adult female elk during three hunting seasons with increasing hunting pressure (2007-2009) to test relationships between movement rates measured by first passage time (FPT) and resource selection. FPT decreased annually, by season type, and by hunting mode (archery vs rifle), and was negatively correlated with hunter predation risk. Elk slowed down ~750 meters from and selected for areas ~1200 meters from houses and trails, suggesting habituation to humans contributed to WUI human-wildlife conflict. These results support the risk allocation hypothesis that elk modify behavior in relation to temporal and spatial variation in human predation risk, and provide some of the first insights as to the indirect effects of hunting on elk in the WUI.

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Table of Contents

Human predation risk and elk behavior in heterogeneous landscapes

LIST OF TABLES

Chapter 2.

Chapter 3.

Appendix A.

Appendix B.

LIST OF FIGURES

Chapter 1.

Chapter 2.

Chapter 3.

Chapter 1. Introduction

There is a growing recognition of the importance of residential human development on wildlife habitat in the interface between wildland and urban areas (Radeloff et al. 2005). The wildland-urban interface (WUI) now occupies 9% of the US (Radeloff et al. 2005) and is growing fastest in the western states. The WUI influences timber sales (Dombeck et al. 2004), increases demand for fire fuels reduction (Ohlson et al. 2006), and facilitates the spread of invasive weeds (Radeloff et al. 2005). While the direct effects of WUI on forests are well known the indirect effects on wildlife have received less attention as few studies have investigated impacts of the WUI on wildlife (Bury 2004, Hagar et al. 2004, Converse et al. 2006).

Because humans frequently develop residential and industrial projects in ungulate winter range (Haggerty and Travis 2006), predicting the effects of the WUI on ungulates will be critical for elk (*Cervus elaphus*) conservation and management. Historically, elk were considered wilderness species (Toweill and Thomas 2002), but in the last few decades, biologists have documented growing resident elk populations in agricultural lands, managed forest lands, and in WUI areas (Thompson and Henderson 1998, Burcham et al. 1999). Elk populations are increasing in many WUI areas (e.g., Missoula and Gardiner, Montana, Ketchum, Idaho, Flagstaff, Arizona, Mammoth, Wyoming, Estes Park, Colorado, Banff and Jasper in the Canadian Rockies Hebblewhite et al. 2005, Snyder 2007), paradoxically suggesting that habitat fragmentation in the WUI may enhance elk populations. Despite this potential 'positive' effect on populations, state wildlife management agencies like Montana Fish, Wildlife and Parks (MFWP) have identified urban wildlife as a growing management issue. Many studies reported that elk select refugia where hunting is not permitted, reducing mortality rates (Burcham et al. 1999), an emergent management problem of the WUI (Figure 1). This reduces the 'administrative control' of growing elk populations by state wildlife management agencies, who really only have public hunting as an option to reduce growing elk populations, hampering their ability to manage complex objectives in the WUI (Haggerty and Travis 2006). Growing elk populations in WUI areas come with a host of associated ecological and management problems (Figure 1) including increased crop depredation, private property damage, loss of migration, increased risks of overgrazing, and the potential for elk habituation to humans (Thompson and Henderson 1998, Haggerty and Travis 2006, Hebblewhite et al. 2006, Snyder 2007).

In the Missoula valley for example, the elk herd wintering in the North Hills (Figure 2) grew from 40 in the 1980's (Weybright 1983) to ~300 elk in 2010 (MFWP, unpublished data). Historically, this elk herd used the National Wildlife Federation (NWF) lands (~324 hectares) in the WUI of Missoula as their core winter range. Since the 1980's, this herd has subsequently expanded use to low elevations throughout Grant and Butler creeks, resulting in increasing human conflicts with elk, particularly over crop depredation on ranches (Figure 2, Burcham et al. 1999). Ironically, habituating and increasing elk populations in these urban fringe ranches may cause sufficient economic damage as to favor further subdivision and urban growth, as ranchers sell of parts or all of their ranches (Figure 1, Haggerty and Travis 2006). These changes are also potentially associated with increasing elk habituation to humans, which can lead to reduction or loss of migratory behavior, and subsequent risk of overgrazing winter ranges by newly resident elk during summer (Figure 1). The main hypothesis for these changes in the North Hills elk herd is that protection of the Rattlesnake Wilderness and Recreation Areas north of Missoula, NWF lands, and growth of the WUI has rendered hunting marginally effective as a population control measure (MFWP unpublished data). With apparently low non-human predation (Appendix B), human predation is the only effective means to control population growth. Paradoxically, benefits for elk forage through fuels reduction and invasive weed control in the WUI (Radeloff et al. 2005) may potentially exacerbate problems of growing elk populations in the WUI.

In response to these challenges, I developed an elk research project in the wildland-urban interface of Missoula, Montana in January of 2007 in cooperation with MFWP, The University of Montana, The Rocky Mountain Elk Foundation, local ranchers, homeowners, and volunteers. My research goal was to test the indirect effects on hunting on elk behavior as predicted under the risk allocation hypothesis. The direct (lethal) effects of hunting are a well documented and widely used management tool for controlling ungulate populations (Burcham et al. 1999, Toweill and Thomas 2002, Wildlife-Division 2004). The lesser known but increasingly important indirect (non-lethal) effects of hunting may help managers better understand the process of habituation, and may improve the management of hunting in fragmented landscapes settings.

First, in Chapter 2, I focused on comparing elk behavioral responses across a wide range of risk levels in 4 sites in western Montana to better understand how elk within the WUI behaved with respect to completely habituated and 'wild' elk subject to high predation risk from human and native carnivore predation. I examined the effects of human predation risk on anti-predator behavior (e.g., vigilance and movement levels) to test the predictions of the risk allocation hypothesis that animals should modify behavior when subject to varying levels of predation risk (Lima and Bednekoff 1999). Behavioral measurements began in October, 2008 and ended in March 2009, totaling 361 observations across four risk levels (High Risk – human and wolf, Moderate – human (North Hills), Moderate – wolf (Northern Range), and Low Risk). The effect of hunting on behavioral categories (grazing, vigilant, movement) significantly differed across all risk levels and time since hunting (p-value ≤0.005). Movement and vigilance anti-predator behaviors attenuated to low risk predation risk levels within five weeks of cession of hunting season in the moderate risk (human) area, but stayed constant in areas with either high or low predation risk. Grazing levels did not correspond to changes in predation risk, contrary to predictions. These results confirmed that WUI elk were behaviorally intermediate between 'wild' and the habituated elk of Mammoth/Gardiner, and showed behavioral flexibility in allocating their antipredator behavior to avoid human predation risk.

Armed with this understanding of how elk within the WUI responded to spatio-temporal variation in predation risk, I focused intensively on understanding how WUI elk moved and selected resources in response to human activity within the WUI. I outfitted adult female elk (n=21) with radio collars, 10 with global positioning system (GPS) and 11 with very high frequency (VHF) collars, to document annual and winter home range size (Figure 1), movement patterns, and resource selection. I used data from nine GPS collared adult female elk (39,000 telemetry locations from 2007-2009) to develop movement (first passage time) and resource selection models to better understand how temporal and spatial variation in human predation risk influences elk movement rates and resource selection in the heterogeneous wildland-urban interface landscape (Chapter 3). In Chapter 3, I show that elk movement rates slow down ~750m from human related covariates such as distance to houses and trails which were surrogates for human predation risk. In contrast to movement, WUI elk showed resource selection for areas farther than when moving from humans, selecting for areas 1200m from human activity for areas to forage and bedding behavior. Furthermore, movement rates increased with annual increases in human predation risk during the hunting season from 2007 to 2008 (p-value = 0.093), and 2008 to 2009 (p-value 0.031). In contrast, there were no differences in movement rates (p-value = 0.50?) by elk during periods when they were not hunted. Rifle hunting had the greatest impact on moving compared to archery and non-hunting times (p-values < 0.011). During the periods of highest predation risk, elk selected for high vegetation cover, and as predation risk from humans decreased, elk selection for spatial covariates related to forage increased, confirming that elk were able to respond to human predation risk through risk-forage trade-offs because of the temporal variation in human predation risk.

These data provide wildlife managers perhaps the first understanding of the influence of hunting on elk behavior, movement, and resource selection in the WUI, and has important implications for management of elk in the WUI and other fragmented landscapes. Our results from the extensive comparison of elk behavior and detailed focus on the WUI in Missoula also confirm that human hunting seems to have more dramatic effects on elk distribution than predation by carnivores such as wolves and other native predators (Gude et al. 2006). The knowledge that elk behavior attenuates to levels of knowingly habituated elk (e.g., Mammoth/Gardiner) within five weeks after hunting season suggests that hunting seasons could be structured to maintain higher anti-predator behavior (i.e., a hunting season every 3-5 weeks) if habituation is a concern to managers (Thompson and Henderson 1998). By this logic, punctuated elk hunting seasons would restore a more natural 'predator resembling' pattern of overwinter mortality that should discourage habituation. When used in combination with block management programs designed to encourage hunter access to private land refuges, such 'punctuated' elk hunting seasons may help address the growing problem of elk use of private land refuges and associated agricultural damage from elk aggregation (Thompson and Henderson 1996, Burcham et al. 1999, Haggerty and Travis 2006). Ironically, the proliferation of game damage hunts on private lands indirectly supports our conclusions that extended hunting seasons may be needed where private lands create predation refugia. Other alternatives to 'punctuated' hunting seasons exist, but include costly aversive conditioning methods with near daily conditioning by humans on foot or horseback, dogs, or a combination of aversive conditioning tools

(Kloppers et al. 2006; Spaedtke 2009). For most state wildlife management agencies, hunting will continue to be the main realistic tool to use to help maintain ‘wild’ elk movements and behavior in WUI and other fragmented landscapes.

The analysis of elk movement and resource selection also has important implications for exurban development in low elevation elk winter range. Our movement analyses showed that elk movements were lowest 750m from residential houses and that they selected areas 1200m from houses for foraging and bedding. Combined, these results suggests that residential development should be a minimum of 1,500m apart (i.e., 2 times 750m) to ensure movement corridors remain viable, and that as housing development increases in the WUI, elk may lose the ability to move between important winter range habitats. Alternately, without human predation risk, over time, this ‘avoidance’ of human activity may diminish, increasing habituation. Combined, our results describe the behavior, movement and resource selection of a partially habituated elk herd resulting from close contact to human development in a WUI on low elevation elk winter range. Failure to reverse the trend of habituation, whether through ‘punctuated’ elk hunting, changes to residential zoning, or more active measures such as aversive conditioning, will likely lead to loss of migration, increased residency time on winter ranges year round, and the ensuing negative ecological effects of resident habituated elk herds (e.g., Figure 1).

Chapters 2 and 3 are intended for scientific publication with coauthors and are written in second voice ‘we’ as a result. Authorship for Chapter 2 will be S. M. Cleveland

and M. Hebblewhite, and for Chapter 3, S. M. Cleveland, M. Hebblewhite, K. R. Foresman, P. R. Krausman, M. J. Thompson and R. E. Henderson.

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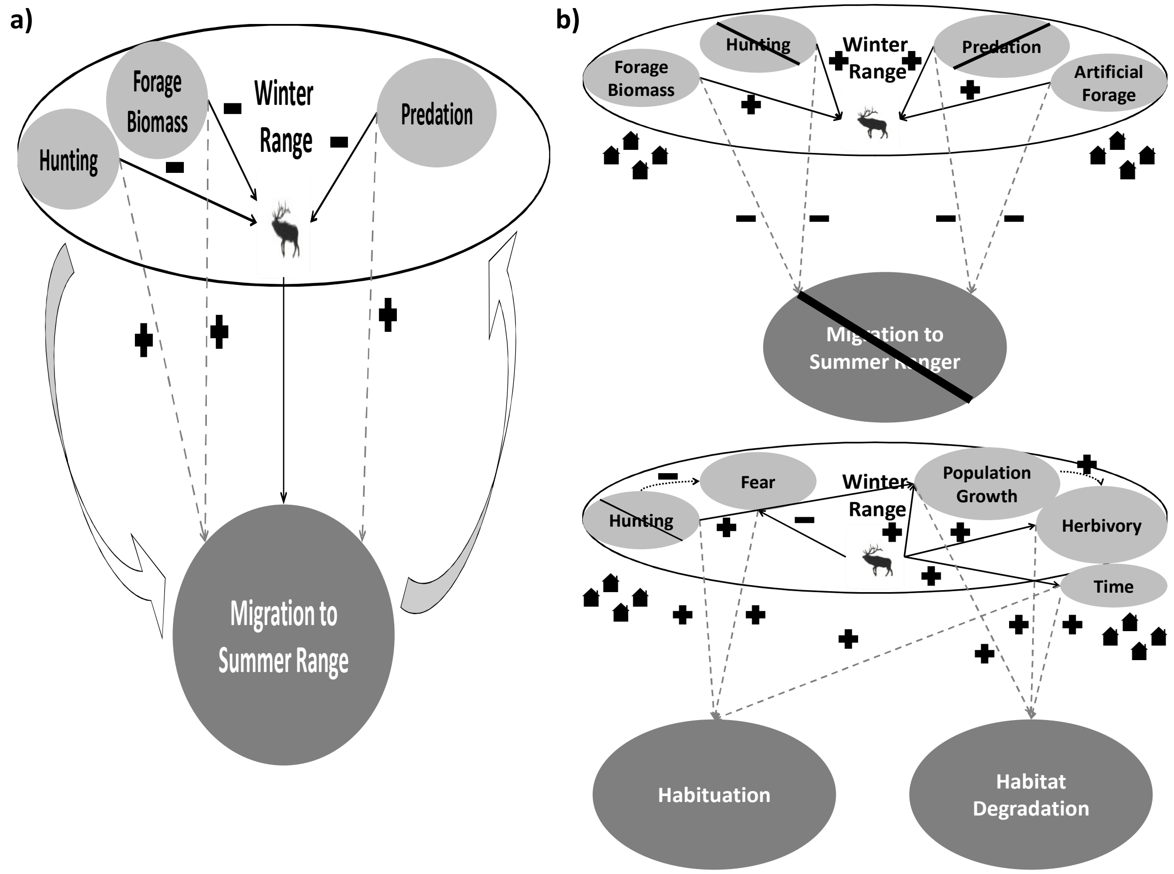

Figure 1. A conceptual figure of a wild elk herd (a) becoming a resident wildland-urban interface elk herd (b) that leads to habituation and the ecological and social consequences associated with habituation and residency with this shift in behavior. In a) elk on the winter range are negatively (-) influenced by hunting and predation which encourages (+) migration to the summer range. The winter range has increased forage biomass which is positive for elk, but over the course of the winter the forage is depleted through grazing and the nutritional quality of forage on the summer range increases encouraging migration to the summer range. The more positive drivers associated with migration (gray dashed lines) the more likely migration is to occur between winter and summer ranges. In b) two of the primary drivers of migration (hunting and predation) are lost; humans artificially increase available and high nutritional value forage (i.e., lawns, golf courses, alfalfa fields) further reducing the nutritional advantages of migration. This leads to loss of migration, increases in population growth with no hunting or predation pressure, which in turn decreases fear of humans. As population growth increases and residency time on the winter range increases, there are corresponding increases in herbivory which leads to habitat degradation. The more time spent with humans without a negative stimulus (i.e., hunting) the more habituation increases which increase human wildlife conflicts.

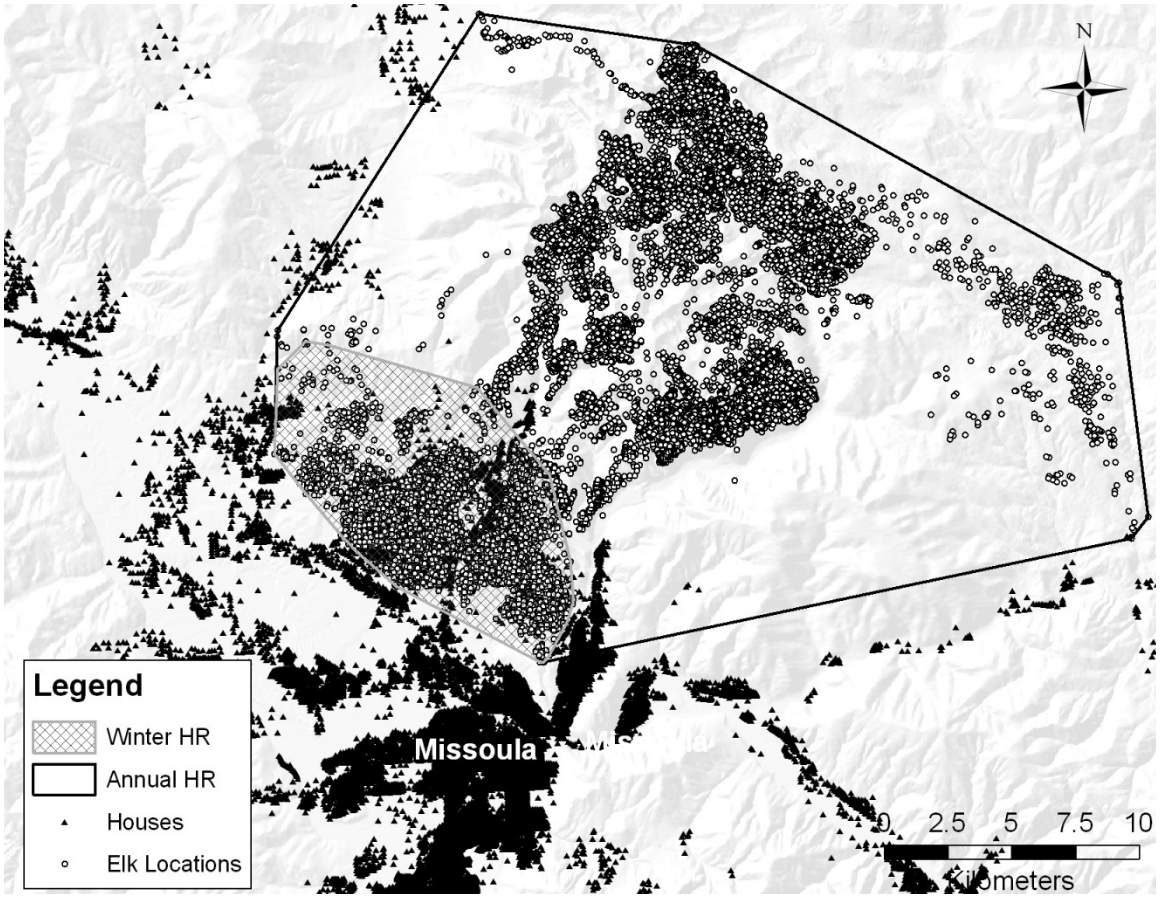

Figure 2. The annual (60,675 ha) and winter (8,865 ha) minimum convex polygon (MCP) home range from GPS collared adult female elk (n=9) of an urban elk herd in the wildland-urban interface of Missoula, Montana, USA. Data was collected from 2007-2009.

Chapter 2. Temporal and spatial variation in anti-predator behavior of elk.

Introduction

Herbivores balance forage intake, energetic cost, and predation risk when selecting resources to maximize fitness across spatial and temporal scales (Altendorf et al. 2001, Creel et al. 2005, Lind and Cresswell 2005, Gude et al. 2006). At the largest scales, ungulates such as wildebeest (*Connochaetes taurinus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) migrate to procure forage resources and avoid predation risk (Senft et al. 1987, Fryxell et al. 1988). Within their home ranges, ungulates select areas with low predation risk to improve reproductive success and survival (Hebblewhite et al. 2005, Berger 2007, Moe et al. 2007, Tremblay et al. 2007, Proffitt et al. 2009, Valeix et al. 2009). For example, female moose (*Alces alces*) calve in areas that grizzly bears (*Ursus arctos*) avoid or in areas with reduced risk (Bowyer et al. 1999, White and Berger 2001). Elk select open grasslands with higher forage quality in the absence of wolves (*Canis lupus*) and forested areas with lower quality forage in the presence of wolves (Creel et al. 2005, Gude et al. 2006). Elk select areas close to human refugia if hunting by humans is excluded to avoid predation by non-human predators (Burcham et al. 1999, Hebblewhite et al. 2005, Kloppers et al. 2005, Snyder 2007). At the finest scales, ungulates adopt behavioral strategies minute-by-minute to avoid predation risk through vigilance behavior, grouping, and resource selection (Lima and Dill 1990).

In Lima and Dill's (1990) citation classic, they proposed that anti-predator behavior, such as vigilance and flight response should change with temporal and spatial variation in predation risk (Lima and Dill 1990). Animals should behave differently across the landscape assuming they can determine which areas are more risky than others. Animals then adjust behavioral patterns resulting in spatial and temporal avoidance of the riskier areas (Lima and Zollner 1996). These ideas lead to the development of the risk allocation hypothesis that suggests prey species should alter their foraging inversely in space and time with predation risk (Lima and Bednekoff 1999). As predation risk increases, anti-predator behavior (i.e., vigilance) should increase and there should be a corresponding decrease in other costly behaviors (i.e., grazing). Conversely, under reduced risk, animals should have decreased vigilance and increased foraging. The risk allocation hypothesis predicts that because anti-predator behaviors are energetically costly, animals must adjust to these temporally varying risks. This prediction has found wide support across predator-prey systems. For example, reindeer (*Rangifer tarandus*) increased flight distance after hunting by humans was initiated on a previously non-hunted population (Reimers et al. 2009). Impala (*Aepycerus melampus*) densities, flight response, and vigilance levels were higher in protected areas than adjacent areas where only partially protected from illegal harvest (Setsaas et al. 2007). Impala and wildebeest (*Connochaetes taurinus*) also increased vigilance levels in areas of high predation risk from reintroduced lions (*Pathera leo*) and cheetahs (*Acinonyx jubatus*) when compared to areas with no predators (Hunter and Skinner 1998). In Yellowstone National Park (YNP) where human hunting is prohibited, elk increased flight distance from recreating humans in areas of non-human predation risk compared to habituated elk in Mammoth, Wyoming without predation risk (Cassirer et al. 1992). Gude et al. (2006) reported that elk group size was influenced more by humans than wolves and the probability of elk presence in preferred open grasslands was negatively correlated with time since wolf presence, supporting the risk allocation hypothesis. These results show that ungulates adjust temporally to varying risk levels, but how quickly behavioral responses occur and attenuate after predation risk stimuli is still largely unknown (Ferrari et al. 2009).

Selection of spatial refugia from predation can lead to significant ecological and socio-political problems. Elk that select refugia may become sedentary rather than migrate between summer and winter ranges which alters predator-prey relationships (Kloppers et al. 2005, Hebblewhite et al. 2006, Snyder 2007). By foregoing migration, sedentary elk must forage year round in what was previously used only as winter range, increasing the demand on forage resources, which can lead to trophic consequences from increased herbivory (Ripple et al. 2001, Creel et al. 2005, Fortin et al. 2005, Hebblewhite et al. 2005). Many ungulate winter ranges are in close proximity to humans, which reduces both human (because hunting near homes is illegal) and non-human predation, leading to rapidly growing elk populations (Snyder 2007). These urbanized elk populations pose a new challenge to wildlife managers because managers have limited ability to regulate harvest levels to control population growth (Thompson and Henderson 1998, Haggerty and Travis 2006, Berger 2007). As humans pose little to no threat in the urban setting, urbanized elk lose their fear of humans and become habituated (Whittaker and Knight 1998). A growing problem facing wildlife managers is managing habituated wildlife populations such as deer (Warren 1997), elk (Thompson and Henderson 1998), and bears (Beckmann and Berger 2003) in wildland-urban interface settings. Habituated elk can begin in inhabit urban areas, leading to direct human wildlife conflict, including property damage and human injury (Snyder 2007). Especially for elk, managers lack information that can correct habituation, and do not know how long it takes to alter this change in behavior (Whittaker and Knight 1998, Kloppers et al. 2005).

Previous studies have shown that elk and other ungulates spatially avoid predation risk (Creel et al. 2005, Hebblewhite et al. 2005, Berger 2007). For example, in Chapter 3 we show that elk avoided human related covariates such as distance to houses and trails which are surrogates for human predation risk. In addition, we found elk movement rates increased both temporally and spatially in relation to human predation risk as predicted under the risk allocation hypothesis. This confirms that elk may increase movement away from predation as an anti-predator strategy (Fortin et al. 2005, Anderson et al. 2008). The few studies that have examined this relationship have examined grouping behavior before and during exposure to predation risk, and how naive prey lose their naiveté to predators over time (Hunter and Skinner 1998). Few studies have examined how long anti-predator behavior lasts (i.e., attenuation time) following reduction in predation risk, or how quickly habituation responses occur (Ferrari et al. 2009).

Human hunting provides rich opportunities to test the risk allocation hypothesis presented by Lima and Bednekoff (1999). Elk hunting by humans is temporally and spatially constrained by hunting regulations and access laws (Gude et al. 2006). Under the risk allocation hypothesis we would therefore predict temporal and spatial variation in anti-predator responses of elk. In this study, our goals were to test the following predictions of the risk allocation hypothesis for elk living under different combinations of human and non-human predation risk. We predicted that 1) elk anti-predator behavior, measured by vigilance, should vary spatially with predation risk; 2) elk vigilance should attenuate when human predation risk is removed; 3) increased vigilance should impart a cost of reduced grazing opportunities (Fortin et al. 2004), and 4) elk should increase movement behavior as an anti-predator strategy as spatio-temporal predation risk increases. These predictions have important implications for management of habituated ungulate populations (McShea et al. 1997, Thompson and Henderson 1998, Wolff and Van Horn 2003, Kloppers et al. 2005, Snyder 2007) to which we return in the discussion.

Materials and methods

Study area

We conducted behavioral observations at different predation risk levels (hereafter, risk levels) at four different sites across western Montana and northern Wyoming that had similar climate, topography, and wildlife communities, but that differed in human and non-human predation risk: 1) Dome Mountain, Montana, 2) the

North Hills, Missoula, Montana, 3) Mammoth, Wyoming and Gardiner, Montana, and 4) the Northern Range, Yellowstone National Park, Montana and Wyoming (Figure 1, Table 1). We define predation risk as the cumulative probability of death by all potential predators on the landscapes (Lima and Dill 1990). Under our definition, a site with wolves and human hunters would have higher predation risk than a site with just humans or wolves, and predation risk also increases with increasing predator density (Lima and Dill 1990). Our four sites therefore experienced varying levels of predation risk from human and non-human predators. The North Hills and Dome Mountain had similar human hunting seasons with a general rifle season (October 26-November 30, 2008), an archery hunting season (September 6-October 19, 2008) and a late season rifle hunt (North Hills; January 3-February 15, 2008; Dome Mountain; January 2-26, 2008, MFWP 2008). However, predation risk was higher in Dome mountain because hunting regulations allowed for a maximum of 100 hunters/week compared to 6/week in the North Hills (Table 1). Furthermore, Dome mountain also experienced predation risk by wolves during winter (Hamlin and Cunningham 2009) compared to the North Hills where wolves were absent. In comparison, Gardiner and the Northern range experienced no human hunting, but varying levels of predation by non-human predators. Elk on the Northern Range experience primarily wolf predation risk during winter (Evans et al. 2006), and Mammoth and Gardiner have no human hunting and little documented wolf presence within the townsites. Our four sites also experienced recreational activities other than hunting (i.e., hiking, biking).

Data collection

We recorded elk behavior (i.e. grazing, vigilant, bedded, moving, and standing) across the four risk levels as a function of the main treatments; predation risk (both human and non-human) and time since hunting season, following methods of other recent authors (Lung and Childress 2007, Winnie and Creel 2007, Liley and Creel 2008). We recorded behavior during and after the hunting season to determine the proportion of time elk spent in each behavioral category in the two human hunted sites (North Hills, Dome Mountain) and the two sites without hunting by humans (Gardiner/Mammoth and Northern Range) from October 2008 through March 2009. A grazing elk was defined as one with its head down and biting vegetation. Previous authors have used varying definitions of vigilance, which has lead to criticisms that vigilance may not necessarily impose energetic costs and hence impart no foraging trade-off (Fortin et al. 2004). We defined vigilant animals as those animals with head up, not chewing, and ears pointed in the same direction as their gaze (Winnie and Creel 2007). This definition ensures an energetic cost as rumination requires chewing, thus vigilant animals that do not chew suffer an energetic cost. Vigilant animals could be vigilant in a bedded and standing body position, but were simply recorded as vigilant. Bedded animals were those in a recumbent position, which does not exclude rumination. Finally, moving animals were those animals walking or running, and standing animals are those animals upright in a non-bedded position and not moving. Elk groups were defined as animals within 5 body lengths of the nearest neighbor (Winnie and Creel 2007). We opportunistically located elk groups, and then sampled their behavior using instantaneous scan sampling (Altman 1974) at a distance of 0.05-2.0 km to ensure our presence had no effect on behavior. In addition, all groups were sampled in open non-forested areas to minimize loss of visibility due to visual obstruction (see discussion).

We tested the predictions of the risk allocation hypothesis that elk behavior varies with predation risk level, and that anti-predator behavior will attenuate following the hunting season. Data were grouped into risk levels and categorical time periods (i.e., hunting season and weeks following hunting season) for statistical analysis. We controlled for other potentially confounding variables known to affect elk behavior in previous studies, including group size, temperature, group position, age, and sex (Winnie and Creel 2007, Liley and Creel 2008). We scanned elk groups 3 to 6 times with the unaided eye (e.g., for habituated Gardiner/Mammoth elk), binoculars, or spotting scopes at 5 minute intervals and categorized behaviors by sex and age (female, calf, brow-tine male, spike, unknown), position in group (periphery or interior) and by behavioral status as defined above (Winnie and Creel 2007). We then pooled repeated scans within one observation period to produce a single data point, thus a single proportion of time spent in each age-sex-position class for each group was calculated (Altman 1974). If the group left the area or became vigilant at the onset of our presence the test was abandoned and a new group was found. If elk behavior was influenced during sampling by other factors (i.e., domestic dog and/or human recreational harassment), data collection was terminated at that scan interval, although behavior measured prior to the disturbance were retained.

Statistical methods

We used ANOVA to test our main hypothesis that anti-predator responses will attenuate following removal of human predation risk. We analyzed the main treatment effects (i.e., hunting season and weeks since hunting season [time], risk level) for each behavioral category (proportion of time spent grazing, vigilant, bedded, moving, and standing). We repeated analyses for each different behavior. The duration of time since hunting (time) varied between sites because of differences in the date of the end of hunting season in each site.   We arcsine square-root transformed the proportion of a specific behavior to achieve normality, and analyzed each individual behavior using a fixed-effect analysis of variance (ANOVA) (Zar 1999) as a function of our main treatment effects using STATA 10 (College Station, Texas, USA). We tested our main hypothesis while controlling for the effects of sex, age class, time of day (time), temperature, and position within group (interior or peripheral). Post-hoc least squares difference tests were conducted to determine when and where significant differences between and among risk levels occurred for each behavior using SPSS 16.0 (Chicago, Illinois, USA, Zar 1999). Group size and temperature were the only continuous covariates; all other independent covariates were categorical. We did not include distance to forest in analysis because it had no significant effect on elk behavior in similar study areas in Montana (Winnie and Creel 2007).

Results

We collected 361 behavioral observations across all four risk levels (High Risk – human and wolf, Moderate – human (North Hills), Moderate – wolf (Northern Range), and Low Risk) from October, 2008 to March, 2009 (Table 1, Table 2). Dome Mountain (High Risk n=70), was significantly more vigilant than Missoula (Moderate Risk (NH) n=102), Gardiner/Mammoth (Low Risk n=104), and the Northern Range (Moderate Risk (NR) n=87). Individuals on the periphery of all groups were significantly more vigilant than interior individuals (Table 3). We were unable to collect data for the first three weeks following the end of hunting season in the high, moderate (NR), and low predation risk study areas due to logistical problems. The effect of hunting on all behavioral categories (except standing) significantly differed across all risk levels and time since hunting, as indicated by the significant interaction of risk level *time (p-value ≤0.005). Group size only affected grazing and movement behaviors (Table 3).

Behavioral responses – grazing

The proportion of time elk spent grazing was significantly influenced by all variables except position within the group and temperature (Table 3). In general, elk grazed more in the evening than morning (p-value = 0.043) or mid-day (p-value <0.001). The exception to this generalization was in the Mammoth/Gardiner study area where grazing was highest during mid-day when compared to morning (p-value 0.001) and evening (p-value <.001). Elk in the Northern Range study area grazed significantly less than all other study areas (p-values: High Risk 0.018, Moderate Risk (NH) <0.001, Low Risk 0.004) and had the least within study area variation in time spent grazing (p-value 0.615).

Behavioral responses – vigilant

Vigilance was significantly explained by time of day, position with the group, and risk level*time (Table 3). Group size did not influence vigilance. Within risk-level variation in vigilance was only significant for Dome Mountain and Missoula. Dome Mountain vigilance was significantly less than hunting season levels by week 4, but rebounded to hunting season levels by week 5. Vigilance in the North Hills attenuated by week 5 following hunting season (Figure 3).

Behavioral responses – movement

Elk moved significantly less in the morning than mid-day (p-value <0.001) or evening (p-value 0.002). The exception was Mammoth/Gardiner when movements did not statistically vary during the day. The only weekly variation in movement occurred in Missoula where hunting season movements were significantly less during the hunting season than weeks after hunting season (Figure 4). There were no consistent predation risk effects on bedding or standing behavior, nor were these behaviors' necessarily related to our predictions from the risk allocation hypothesis. Therefore, we report changes to bedding and standing behavior as a function of the same factors as grazing, vigilance and movement in Appendix A.

Discussion

Animals must decide how to allocate resources as a function of predation risk (Lima and Bednekoff 1999). We predicted elk vigilance would vary 1) spatially by risk level; 2) attenuate temporally following the removal of human predation risk; 3) increasing vigilance should result in a trade-off of decreasing grazing; and 4) movement behavior should increase with increasing predation risk. Our predictions were upheld in most sites supporting the utility of the risk allocation hypothesis to understand indirect effects of human hunting on elk in the wildland urban interface. Elk vigilance was highest in Dome mountain, supporting the spatial predictions of the risk allocation hypothesis (Lima and Bednekoff 1999). Elk vigilance and movement levels attenuated within 3-5 weeks following the cessation of hunting by humans which supports the attenuation prediction and results of previous studies Wolff and Van Horn (2003). However, we saw no trade-off between increasing vigilance and grazing across any site (Figure 2). Grazing and vigilance behavior can easily be switched in the presence or absence of predation risk (Wolff and Van Horn 2003). In addition, we may not have been able to detect a change in grazing due to our sampling design. Elk could have been grazing more in timbered areas where we were not able to observe elk, or an increase in grazing could have occurred at night when we could not observe elk.

Elk vigilance was significantly greater at high risk (human and wolf) vs. moderate (human) and high (human and wolf) vs. low predation risk levels. Vigilance under moderate risk levels was only marginally significantly different in the human hunted

(North Hills) site when compared to the low risk site. Humans had a significant and higher impact on elk vigilance behavior than did wolves across our four sites, similar to recent results of other studies (Gude et al. 2006, Proffitt et al. 2009). Specifically, our results echoed those of Wolff and Van Horn (2003) that elk vigilance were highest in the highest predation risk areas of their study and areas devoid of predation risk had the lowest vigilance (Table 5). Contrary to predictions of the risk allocation hypothesis and our observations in Montana, Kloppers et al. (2005) observed a decrease in vigilance from ~13% to 7% following aversive conditioning in a habituated elk herd in Banff, Alberta. The contradictory results of Kloppers et al. (2005) could be attributed to a reduced anti-predator behavior as these elk were habituated and naïve to predation, which has also been observed in impala (Hunter and Skinner 1998). Regardless of this lone example, the remainders of studies on wild, non-habituated elk support our results showing how quickly elk can switch between behaviors given varying perceptions of predation risk.

Movement is another way in which animals mitigate predation risk. Movement occurs at multiple scales to avoid predation risk, from large scale migration (Hebblewhite and Merrill 2007), to local movements between habitat patches (Chapter 3), to flight response in the presence of perceived predation risk (Stankowich 2008). We observed how movement behavior of elk changed given different levels of predation risk. As predicted from the risk allocation hypothesis, we observed reduced movement behavior in the low risk site and declining movement levels following the removal of human predation risk in the moderate risk (human) site. These observational results were confirmed with GPS collar data that also showed increased movement rates during exposure to hunting (Chapter 3). Increased movement corresponded with a decline in vigilance following hunting season in the moderate risk (human) study site. However, the trend in declining movement behavior following the cessation of hunting as predicted by the risk allocation hypothesis was not observed in all study areas. Elk in the high risk study area showed constant and reduced movement behavior (Figure 4). In addition, the moderate risk (wolf) site started with reduced movement behavior but escalated over time. Elk in the high (human and wolf) and moderate risk (wolf) sites did not mitigate predation risk as expected under the risk allocation hypothesis considering elk behavior alone. Wolf kill rates usually increase in late winter (i.e., February and March, Smith et al. 2004) with increasing snow depths (Huggard 1993), resulting in increased predation risk by elk (Kauffman et al. 2007). This increase in predation risk in Yellowstone National Park in late winter likely explains the increase in movement behavior for elk in the moderate risk (wolf) study areas. This could also explain lower movement levels in the high risk area outside Yellowstone National Park where elk were also subject to wolf predation risk. It may be advantageous for the high risk group to reduce movement behavior as they were subjected to a lower wolf density outside of Yellowstone National Park than those elk inside the park (White and Garrott 2005).

There was substantial variation in elk behavior among and between sites in our study that was further hindered by logistical sampling issues. We were unable to sample behavior in the first three weeks following cessation of hunting in the high, moderate (wolf) and low risk study areas due to logistical constraints of access to some of the study sites. These gaps weaken the interpretation of our results, but our results are strengthened by their close correspondence to results from other regional studies (Table 5). The lack of direct measures of predation risk, specifically non-human predation risk, could explain some of the variation in response, for example, the sudden spike in week four vigilance in the moderate risk (human) study area (Figure 4). However, our failure to find an grazing cost to vigilance as predicted by the risk allocation hypothesis, suggests that vigilance, even as we stringently defined it, may not impart the energetic cost that is often assumed (Fortin et al. 2004). While our results showed elk increased vigilance levels under increasing risk, there was not a corresponding drop in foraging. This suggests vigilance may not necessarily be a good indicator of a costly trade-off, supporting the suggestions of Fortin et al. (2004). However, we did detect increases in movement levels and movement rates (Chapter 3) that do impart known energetic costs (Cook et al. 1996).

Increased movement and vigilance may combined to lead to increased energetic costs for elk under predation risk, especially when there is not an increase in foraging behavior to offset the energetic demands of moving (Bender et al. 2008). The impacts of increased movement rates could be especially important if movement behavior compromises grazing during late summer and fall during hunting (Cook et al. 1996). Predation risk by wolves and humans is also known to cause shifts in diet selection even though there may not be a decline in grazing (Morgantini and Hudson 1985, Christianson and Creel 2007). If ungulate foraging rates did not change, but forage quality or species composition did, then the combined changes in behavior we observed here with predation risk could have energetic and population consequences. These increases in energetic demand from increased movements and potential shifts in diet could in part explain potential declines in reproduction under high predation risk reported for elk in Montana (Creel et al. 2007) and moose in Alaska (Testa 2004).

Vigilance in the human-only predation risk system had the fastest attenuation time (3 weeks). Following this attenuation, vigilance did not rebound to high levels again as observed in Dome Mountain (Figure 3). The quick rebound of vigilance to high levels at Dome Mountain by week 5 may be attributed to increases in wolf predation risk following cessation of the human hunting season (Ruth et al. 2003, Berger 2007). In contrast, the North Hills lacked predators of adult female elk following hunting season, and we observed a more rapid and consistent attenuation of vigilance throughout the winter. In fact, vigilance attenuated to levels of habituated animals from the urban areas of Banff National Park (Kloppers et al. 2005). This suggests that the North Hills elk herd is exhibiting signs of habituation (Whittaker and Knight 1998). It also illustrates that even reduced hunting threat by humans when compared to Dome Mountain has a significant impact on anti-predator behavior.

Ecosystem dynamics of the Northern Range in Yellowstone National Park may be recovering following the re-introduction of wolves (Ripple et al. 2001), but in areas devoid of predation risk (i.e. the towns of Gardiner/Mammoth) the trophic effects of locally high density resident elk herd are likely still functioning. Elk in mammoth showed such consistently low vigilance and movement rates as to be consistent with almost zero exposure to predation risk from all predators (Ferrari et al. 2009). Thus, it is likely that human activity has disrupted normal predator-prey dynamics and potentially ecosystem dynamics such as grazing by elk in the Gardiner/Mammoth areas. To restore natural behavior in these areas, predation risk (humans or wolf, for example) could be returned to the landscape. Our results in the WUI of Missoula, Montana could be extended to attempt to restore ‘normal’ elk behavior in other WUI areas such as Gardiner/Mammoth. Park managers could adopt predator-resembling aversive conditioning tools (i.e., hazing and range riding) to de-habituate elk and restore more natural anti-predator behavior (Kloppers et al. 2005, Spaedtke 2009). Our results also suggest that an optimum reapplication frequency could be derived from our attenuation rate, and aversive conditioning could be applied every 3-5 weeks to discourage habituated behavior. Certainly, hunting may achieve quicker results than aversive conditioning, such as with dogs or humans on horseback (Spaedtke 2009). Given the complexities of national park management, and potential opposition to direct hunting in national parks, predator-resembling aversive conditioning could achieve similar ecological results (Spaedtke 2009).

The direct (lethal) effects of hunting are a well documented and widely used management tool for controlling ungulate populations. The lesser known and recognized indirect (non-lethal) effects of hunting may help managers better understand the process of habituation, and may improve the management of hunting in urban settings. The hunting season in Montana is currently structured such that hunting occurs in blocks of five weeks with occasional late season hunts lasting 4-8 weeks where populations or conflicts are high (MFWP 2008). In part, this strongly temporally structured hunting season has interacted spatially with private land refugia and risk allocation by elk to create growing problems of unmanageable elk populations (Burcham et al. 1999, Proffitt et al 2009). Our results suggest that one potential solution may be to consider restructuring hunting seasons to introduce predator-resembling hunting seasons. For example, given elk anti-predator behavior attenuated within 3-5 weeks, to restore normal elk movements and behavior, hunting seasons could consist of multiple, shorter hunts spaced out over a longer period of time. Increasing hunting pressure in these areas may also have a heightened and more prolonged effect on anti-predator behavior as illustrated by the significant difference in vigilance between Dome Mountain and the North Hills (Figure 3), and could help break the elk aggregation cycle facing western wildlife managers.

If managers do not try to modify habituated elk behavior, significant changes may occur on migration and movement patterns (Creel et al. 2005, Fortin et al. 2005), predator-prey dynamics (Hebblewhite et al. 2005), increased risk of disease transmission in predation refugia (Proffitt et al. 2009), reproductive rates (Phillips and Alldredge 2000, Shively et al. 2005, Creel et al. 2007), and vegetative communities (Hobbs 1996, Hebblewhite et al. 2005). In addition, direct human/wildlife conflict specifically in the urban setting may increase and result in decreased tolerance of elk (Kloppers et al. 2005, Snyder 2007). As human-caused habitat fragmentation continues to move into winter range the problem of urban elk populations will only expand. Waiting to respond to these issue leads to serious ecological and social problems

(Snyder 2007), and can lead to elk populations being out of managerial control (Haggerty and Travis 2006).

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Table 1. Predictions of the effect of spatial and temporal variation in human and non-human predation risk will have on grazing and vigilance behavior of elk following the end of hunting season October 2008 to March 2009. Plus signs (+) represent a predicted increase in a behavior, where as a negative sign (-) represents decrease in a behavior over time since the end of hunting season.

Study Area	Nonhuman Predation	Human Predation	Risk Level	Spatial Prediction	Temporal Prediction
Dome Mountain	Wolves	100 hunters/week	High	Grazing-Low Vigilance-High	Grazing (++) Vigilance (-)
North Hills	Limited	6 hunters/week	Moderate	Grazing-Moderate Vigilance-Moderate	Grazing (+) Vigilance (--)
Northern Range	Wolves	None	Moderate	Grazing-Moderate Vigilance-Moderate	Grazing Constant Vigilance Constant
Gardiner/Mammoth	Limited	Limited	Low	Grazing-Low Vigilance-Low	Grazing Constant Vigilance Constant

Table 2. Total sample size of elk behavioral observations collect from October 2008 to March 2009 by hunting season, time (weeks since the end of hunting seasons) and study area (High Risk (wolf and human) is the Dome Mountain Area, Montana, Moderate Risk (human) is the wildland-urban interface of Missoula, Montana, Moderate Risk (wolf), is the Northern Range of Yellowstone National Park in Montana and Wyoming, and Low risk is the towns of Gardiner, Montana and Mammoth, Wyoming, USA).

Study Area	Number of behavioral observations								Total
	Hunting Season	1	2	3	4	5	6	7	
High Risk	21	--	--	--	12	10	17	10	70
Moderate Risk (NH)	30	14	11	18	11	16	--	--	100
Moderate Risk (NR)	48	--	--	--	21	6	8	4	87
Low Risk	49	--	--	--	16	16	10	13	104

Table 3. Female elk behavioral responses to hunting predation risk in western Montana, from October 2008 to March 2009. Results of fixed-factorial ANOVA of the effects of time of day (time), Risk Level (High Risk (wolf and human) is the Dome Mountain Area, Montana, Moderate Risk (human) is the wildland-urban interface of Missoula, Montana, Moderate Risk (wolf), is the Northern Range of Yellowstone National Park in Montana and Wyoming, and Low risk is the towns of Gardiner, Montana and Mammoth, Wyoming, USA), Risk Level*Time, Time, position in the group (position), temperature, and group size has on female elk behavior.

	Grazing		Vigilant		Moving	
	F	*P*	*F*	*P*	*F*	*P*
1. Risk Level	8.25	**<0.0005**	1.77	0.1518	5.36	**0.0013**
2. Time	5.60	**<0.0005**	1.17	0.3222	3.29	**0.0021**
3. Risk Level*Time	4.27	**<0.0005**	2.46	**0.0076**	2.98	**0.0013**
4. Position	--	--	27.82	**<0.0005**	--	--
5. Time Period	13.85	**<0.0005**	2.60	0.076	11.04	**<0.0005**
6. Group Size	6.54	**0.011**	--	--	3.93	**0.0481**
7. Temperature	--	--	--	--	--	--

Table 4. Arcsine transformed vigilance levels as a function of threat level and categorical times of hunting season (HS) and weeks sense hunting season (1,2,3…) with standard errors (SE) by study area (High Risk (wolf and human) is the Dome Mountain Area, Montana, Moderate Risk (human) is the wildland-urban interface of Missoula, Montana, Moderate Risk (wolf), is the Northern Range of Yellowstone National Park in Montana and Wyoming, and Low risk is the towns of Gardiner, Montana and Mammoth, Wyoming, USA).

	Vigilance Levels															
	HS	SE	1	SE	2	SE	3	SE	4	SE	5	SE	6	SE	7	SE
High Risk (human and wolf)	0.27	0.04	--	--	--	--	--	--	0.12	0.04	0.18	0.04	0.25	0.04	0.22	0.05
Moderate Risk (human)	0.18	0.03	0.16	0.05	0.15	0.03	0.09	0.03	0.20	0.04	0.03	0.02				
Moderate Risk (wolf)	0.18	0.03	--	--	--	--	--	--	0.17	0.04	0.17	0.04	0.17	0.07	0.03	0.03
Low Risk	0.10	0.02	--	--	--	--	--	--	0.19	0.04	0.13	0.03	0.25	0.05	0.24	0.05

Table 5. Literature review of selected studies of vigilance levels of adult female elk in Montana that are subject to varying levels of predation risk. Vigilance percentage is the percentage of time that was reported in the study that adult female elk were vigilant given their sampling method.

Article	Adult Female Elk	Vigilance Percentage	Sampling Method	Risk Type	Study Area
Lung and Childress (2006)	Yes	18	Focal Species	Wolf	Yellowstone National Park
Childress and Lung (2003)	Yes	14.6	Focal Species	Wolf	Yellowstone National Park
Winnie and Creel (2007)	Yes	15.8	Scan Sampling	Wolf	Yellowstone National Park
Wolff and Van Horn (2003)	Yes	12	Scan Sampling	Wolf	Yellowstone National Park
	Yes	1	Scan Sampling	none	Rocky Mountain National Park
	Yes	1	Scan Sampling	none	Mammoth, Wyoming
Liley and Creel (2007)	Yes	22-32	Scan Sampling	Wolf	Yellowstone National Park
Cleveland Thesis	Yes	27	Scan Sampling	Wolf+Human	Dome Mountain, Montana
	Yes	18	Scan Sampling	Human	Missoula, Montana
	Yes	18	Scan Sampling	Wolf	Northern Range, Yellowstone National Park
	Yes	10	Scan Sampling	none	Gardiner, Montana, Mammoth, Wyoming

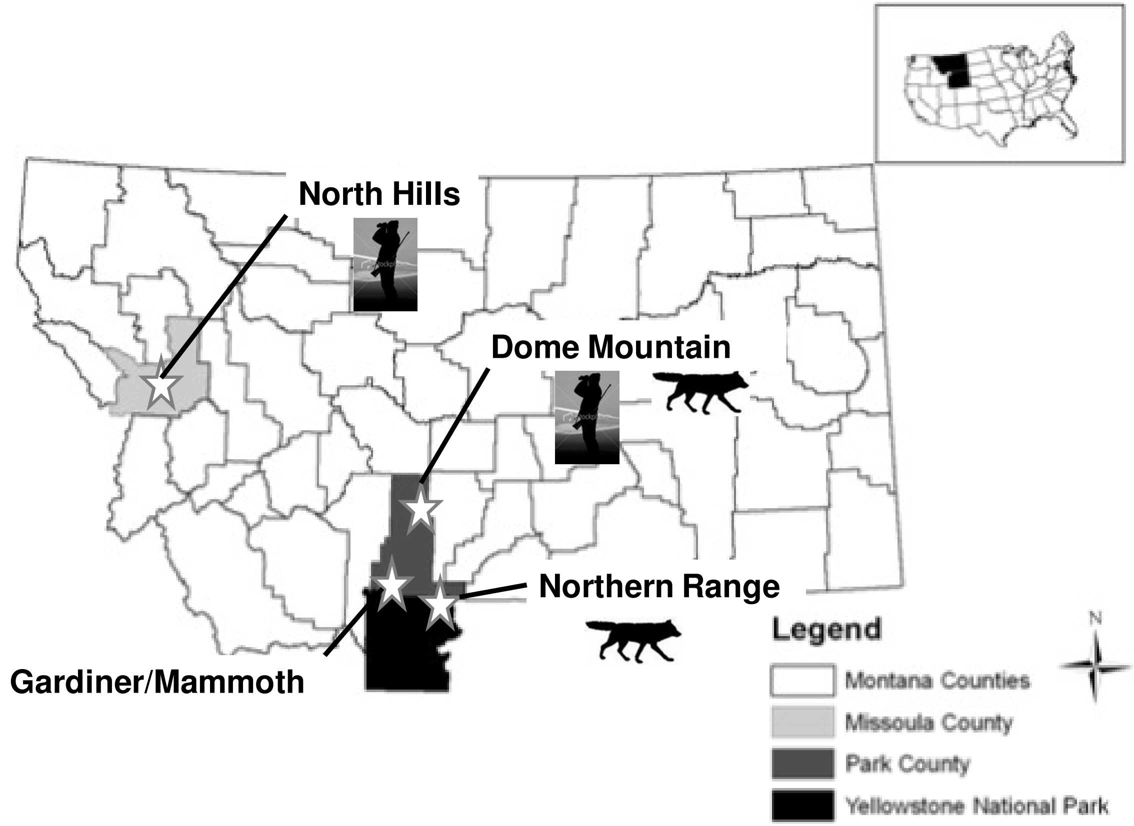

Figure 1. Geographic location of the four predation risk level study areas for testing the risk allocation hypothesis for female elk in western Montana and northern Wyoming. From the north, Missoula (moderate risk level, human only), Dome Mountain (high risk level, human and wolf), Gardiner/Mammoth (low risk level), and Northern Range (moderate risk level, wolf only).

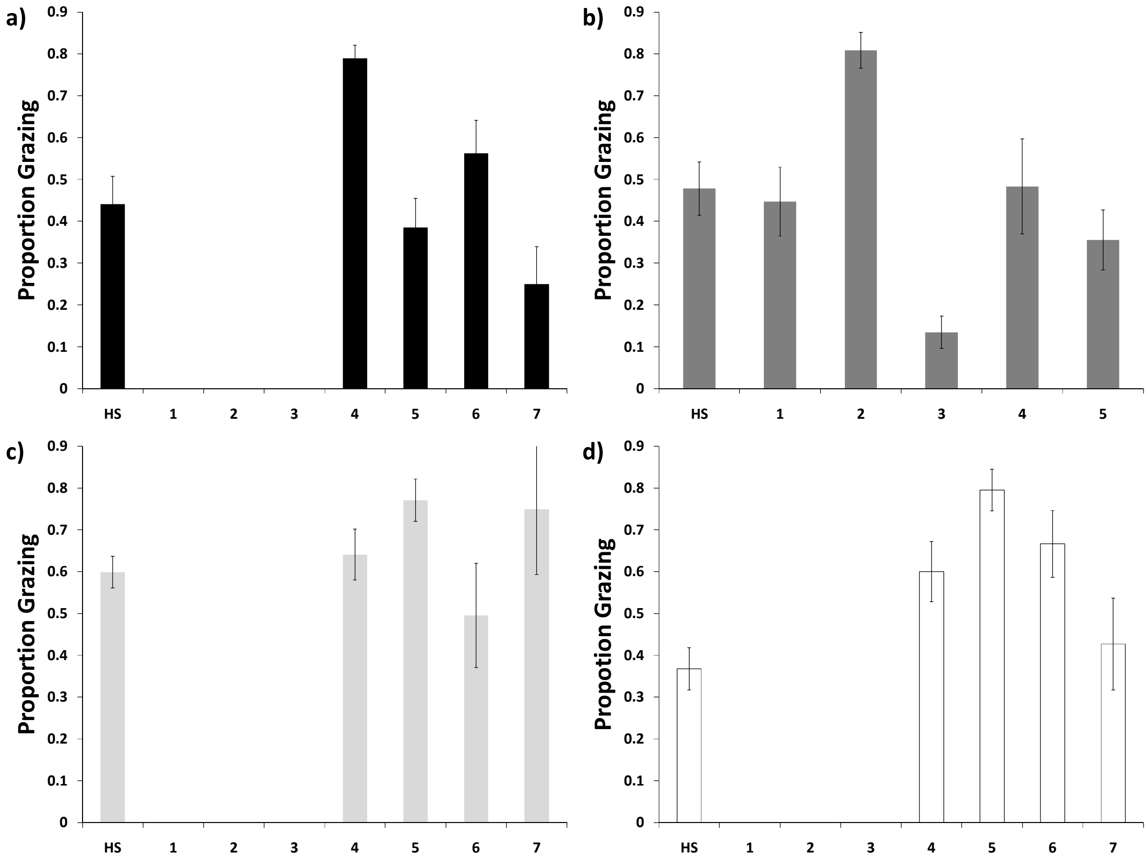

Figure 2**.** Elk grazing levels by predation risk level with standard errors as a function of time since hunting season from October 2008 to March 2009. HS is the grazing level during hunting season, 1 is one week post hunting season, 2 is two week post hunting season, etc. Figure a) is high risk (human and wolf, Dome Mountain area, Montana), b) is moderate risk (human, North Hills, Missoula, Montana), c) is moderate risk (wolf, Northern Range, Yellowstone National Park, Montana and Wyoming) d) is low risk (Gardiner, Montana and Mammoth, Wyoming).

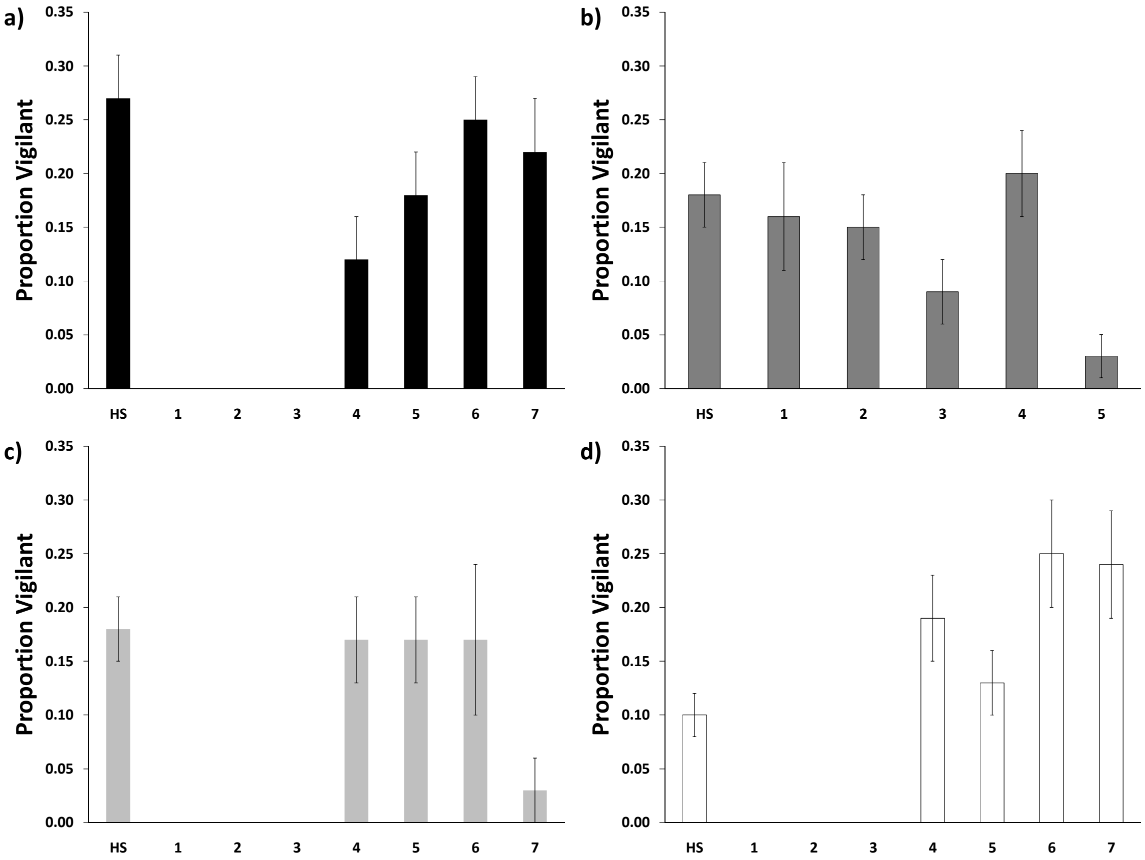

Figure 3. Elk vigilance levels by predation risk level with standard errors as a function of time since hunting season from October 2008 to March 2009. HS is the vigilance level during hunting season, 1 is one week post hunting season, 2 is two week post hunting season, etc. Figure a) is high risk (human and wolf, Dome Mountain area, Montana), b) is moderate risk (human, North Hills, Missoula, Montana), c) is moderate risk (wolf, Northern Range, Yellowstone National Park, Montana and Wyoming) d) is low risk (Gardiner, Montana and Mammoth, Wyoming).

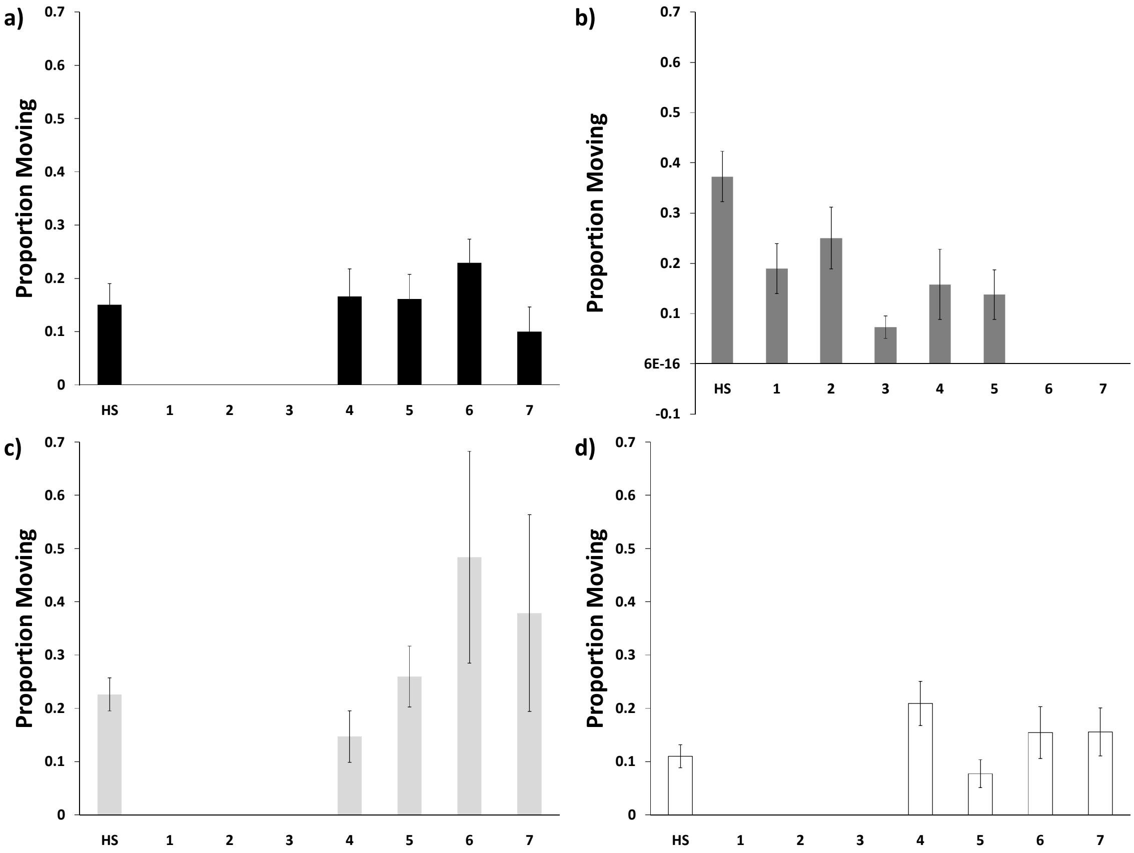

Figure 4. Elk movement levels by predation risk level with standard errors as a function of time since hunting season. HS is the movement level during hunting season, 1 is one week post hunting season, 2 is two week post hunting season, etc. Figure a) is high risk (human and wolf, Dome Mountain area, Montana), b) is moderate risk (human, North Hills, Missoula, Montana), c) is moderate risk (wolf, Northern Range, Yellowstone National Park, Montana and Wyoming) d) is low risk (Gardiner, Montana and Mammoth, Wyoming).

Chapter 3. Linking movement and resource selection of elk in a heterogeneous landscape

Introduction

Human activities can negatively affect animals through direct and indirect pathways (Gordon et al. 2004, 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 and destruction (Jules et al. 1999, Sawyer et al. 2006, Walker et al. 2007, Doherty et al. 2008). Through these direct and indirect effects in food webs, humans affect the balance animals must make between forage intake, energetic cost, and predation risk when selecting resources to maximize fitness (Altendorf et al. 2001, Creel et al. 2005, Lind and Cresswell 2005, Gude et al. 2006). Optimal foraging theory suggests that animals should spend most of their time in areas of high forage resources maximizing intake and minimizing energetic costs (Senft et al. 1987, Hobbs et al. 2003). However, animals are subject to more than just foraging constraints. Predation risk modifies animal resource selection and behavior (Nicholson et al. 1997, Rettie and Messier 2000, Creel et al. 2005, Dussault et al. 2005, Hebblewhite and Merrill 2009). For example, moose (*Alces alces*) calve in areas that grizzly bears (*Ursus arctos*) avoid, and select areas year-round with reduced predation risk (Bowyer et al. 1999, White and Berger 2001, Dussault et al. 2005). The influence of predation risk on resource selection can also vary by predator hunting mode and species. For example, sit-and-wait predators had larger effects on prey behavior than did coursing predators (Preisser et al. 2007, Schmitz 2008) such that the effects of predation risk often vary substantially between predator species, including humans.

Hunting by humans can often have dramatic direct effects on the demography and indirect effects on the behavior of large mammals (Gordon et al. 2004, Darimont et al. 2009, Gordon 2009). Unregulated direct human harvest can obviously cause population declines (Milner-Gulland et al. 2003), and can also result in subtle life-history and evolutionary changes of harvested species (Darimont et al. 2009). Under harvest by humans, wild boar (*Sus scrofa*) females made dramatic life history changes, investing more heavily in early reproduction at the cost of adult survival (Toigo et al. 2008). But even the mere risk of being killed by human hunters had a greater indirect effect on elk (*Cervus elaphus*) resource selection than did wolf (*Canis lupus*) presence (Gude et al. 2006). Under wolf and human predation risk, for example, elk selected refuge areas to avoid human predation risk in Montana (Burcham et al. 1999, Gude et al. 2006, Proffitt et al. 2009). Avoidance of human predation risk can even be strong enough to stop large-scale migratory behavior of elk (Boyce 1989;1991). These examples show that the risk of mortality from a predator, and in particular human predation risk, can cause animals to change resource selection strategies to avoid risk. How animals adjust their movement behavior in response to spatial and temporal variation in predation risk remains a neglected, but important, area of study in human-wildlife interactions (Lima and Bednekoff 1999).

Previous studies showed that movement rates of elk are influenced by predation risk and forage availability (Fortin et al. 2005a, Frair et al. 2005, Morales et al. 2005, Amo et al. 2007, Anderson et al. 2008). 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 have demonstrated changes in observational measures of anti-predator behavior, such as vigilance (Laundre et al. 2001, Liley and Creel 2008, Chapter 2), and found that ungulates modify vigilance in proportion to predation risk. Fewer studies have tested the resource selection and movement predictions of the 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 that 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, Kauffman et al. 2007), but from resource selection alone it is difficult to understand the mechanisms of risk avoidance such as whether animals adjust space use or movement behavior. Gude et al. (2006) showed that elk avoid human predation risk spatially more than areas of high wolf predation risk, but 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 (Fauchald and Tveraa 2003, Frair et al. 2005), provide novel approaches to test how spatio-temporal variation in predation risk influences the movement mechanisms of selection (Ferrari et al. 2009). For example, Frair et al. (2005) used first passage time to identify bedded, foraging, and movement behavior in elk that were differentially influenced by levels of forage resources and predation risk by wolves. Human activity in the form of forestry and oil and gas 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, Schmaljohann and Dierschke 2005). Thus, understanding the impacts 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 many ungulates (Toweill and Thomas 2002). The expansion of housing into ungulate winter range results in a complex matrix of land ownerships that vary spatially in human predation risk. In such landscapes, human predation risk varies from partial to complete exclusion, and is strongly temporally regulated with most hunting by humans restricted to mid-to-late fall. As habitat fragmentation encroaches on ungulate winter range, humans are increasing time in proximity to ungulates such as deer (*Odocoileus* spp.) and elk, potentially increasing the potential for habituation of wildlife to humans (Thompson and Henderson 1998, Haggerty and Travis 2006). Understanding the effects of predation risk and habitat fragmentation on elk movement and resource selection in these landscapes will provide managers information on avoiding human-wildlife conflict. Humans also use differing hunting modes, similar to coursing (rifle hunting) and sit-and-wait predators (archery hunting) that may also be expected to have different effects on risk allocation similar to the findings of recent experimental ecology studies (Preisser et al. 2007, Schmitz 2008). Thus, the winter range matrix of temporal and spatial variation in human predation risk and hunting modes provides an ideal and relevant setting to test the following predictions of the risk allocation hypotheses (Lima and Bednekoff 1999) as it pertains to elk movement and resource selection (see Chapter 2 for vigilance behavior): 1) first passage time for elk will be lower (i.e., faster movement rates) in areas that allow hunting than areas of refugia, and in hunted areas hiding cover will reduce movement rates; 2) elk will move faster in areas of rifle predation risk than 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 three 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, houses), and the influence of cover on first passage time and resource selection.

Study area

Our study area focused on the montane winter range for elk living in the North Hills of Missoula, Montana, USA (Figure 1) from 2007-2009. During the study, the herd ranged from 300-350 elk and showed an intrinsic growth rate of 11% from 1990-2007 with the population remaining stable from 2007-2009 (Montana Fish, Wildlife and Parks, unpublished survey data). The winter range was a matrix of subdivisions, private agricultural lands, National Forest, and the Rattlesnake Wilderness along the northern boundary of the study area. Land use was a mix of cattle ranching and recreation (i.e., hiking, biking, hunting). This matrix of land ownership exposes elk to varying intensity, duration, and modes (i.e., archery, rifle) of hunting pressure (Table 1, see methods). Northern slopes are dominated by mixed conifer forest, primarily Douglas fir (*Pseudosuga menziesii*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*P. contorta*). Southern slopes are composed of ponderosa pine stands and mixed bunchgrass communities dominated by native grasses: blue-bunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca scabrella*), green needlegrass (*Stipa viridula*), needle-and-thread grass (*S. comata*), timothy (*Phleum pratense*), and non-native Kentucky bluegrass (*Poa pratensis*), and cheat grass (*Bromus tactorum*). The dominant native forbs are arrowleaf balsamroot (*Balsamorhiza sagittata*) and lupine (*Lupinus* spp.) and the dominant exotic forbs are spotted knapweed (*Centaurea maculosa*), cinquefoil (*Potentilla* spp.), and leafy spurge (*Euphorbia esula*). Elevation ranges from 1,100 to 1,500 m, with the lowest elevation at the southern boundary of the study area gaining in elevation northward. Topography is characterized by rolling hills with slopes from 0-60%. The primary aspect is to the south and west. The average annual precipitation was ~35 cm based on data from the National Oceanic and Atmospheric Administration (http://www.wrh.noaa.gov/mso/climfacts.php). Precipitation primarily falls in the spring and autumn as rain, and snow and rain in the winter. The average summer temperature is 29 C° and the average winter temperature is -9 C°. White-tailed deer (*O.virginianus*) and mule deer (*O. hemionus*) are 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 radio-collared elk was hunting, compared to 9% non-hunting mortality, n=3 mortalities, S. M. Cleveland, unpublished data). 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 (Lima and Dill 1990). During periods where hunting is illegal (out of season) or not allowed (e.g., private land, close to residential houses), predation risk was defined as 0.

Methods

We trapped and radiocollared adult female elk with 4400M Global Positioning System (GPS) Lotek© (Ontario, Canada) during winter in 2007, 2008, and 2009. We captured elk using clover traps (Clover 1954, Thompson et al. 1989), a corral trap, and aerial helicopter darting in accordance with approved animal use protocol (International Animal Care and Use Committee 058-06MHECS-122706, University of Montana, USA). We used six hour location data from nine GPS collared elk for movement and resource selection function analyses to test predictions of the risk allocation hypothesis. GPS collar fix-rates were high (mean fix rate > 95%) enough to ignore potential habitat induced bias in movement or resource selection analyses (Frair et al. 2010 *In Press*). Human predation risk on elk, as expressed in the number of huntable days (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 ~ 30% by the state Fish and Wildlife manager (MFWP, unpublished data) in human predation risk with the goal of curbing wildland-urban interface (WUI) elk population growth (MFWP, unpublished data, Table 1). This manipulation provided 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 slow down in areas and at times with high forage value and speed up in areas and times of high predation risk (Lima and Bednekoff 1999, Ferrari et al. 2009). The interplay between spatial and temporal responses, however, means that one cannot address only one dimension (time or space) of risk allocation. Consider the hypothesis that humans have a greater impact on elk resource selection (and thus indirectly on populations) than do wolves (Hebblewhite et al. 2005, Gude et al. 2006). Consider the example in Figure 2 of equal numbers of used elk locations in habitat A (moderate human predation risk and high resource value) and B (moderate wolf predation risk and high resource value) and the habitat patches are equally available (Figure 2). Under standard resource selection analysis the risk allocation hypothesis would not be supported as selection was equal for patches A and B, so wolves and humans have equal effect on resource selection**.** However, instead of only adjusting time spent in a patch, elk could change movement strategies in response to the spatio-temporal variation in predation risk. For example, under the risk allocation hypothesis one would expect a reduction in the proportion of foraging bouts and an increase in exploratory movement in riskier landscapes (Lima and Bednekoff 1999). Animals could either become sedentary moving between patches only once, or move back and forth between A and B between foraging and resting bouts to reduce predictability (Figure 2, Ferrari et al. 2009). The optimal strategy depends on the relative spatial and temporal variance in predation risk and whether movement itself is risky (Lima and Bednekoff 1999, Ferrari et al. 2009). In Figure 2b, considering movement would support the hypothesis of the effects of humans on elk being greater than effect of wolves. We tested the predictions of the risk allocation hypothesis for elk using analysis of first passage time 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 processes by which animals make behavioral decisions to select resources in space and time (Turchin 1998, Moorcroft and Barnett 2008). Animal movement can be thought of a series of biological ‘moves’ between foraging, resting or safe ‘patches’. Recent movement analyses such as first passage time incorporate step length, turning angles, and tortuosity to determine the amount of time it takes an animal to leave a patch (Fauchald and Tveraa 2003). This is an important improvement as our sampling of steps and turns does not necessarily represent the biologically relevant move, whereas first passage time can help identify the relevant scale of biological moves (Turchin 1998, Morales et al. 2005). Understanding the scale of behavioral switching between foraging and movement states can help explain how animals make resource selection trade-offs.

We tested the effects of spatial and temporal variation in hunting pressure on first passage time and movement behaviors of GPS collared adult female elk. First passage time calculates the time it takes an animal to leave a patch of a specified radius (Fauchald and Tveraa 2003). By examining the circle that maximizes variance in first passage time, ecologists can discriminate area-restricted search behavior, such as foraging and resting, from long-distance movement between foraging patches (Figure 3). We measured the first passage time of GPS collared elk forward and backward across the radius (*t(r)*), excluding the first location as the previous location was unknown, 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 first passage time *(S(r)*) that distinguishes area restricted search from directed movement (Fauchald and Tveraa 2003, Pinaud 2008). Circles of radii between 25-100 and 100-2,500 m were applied to each location, increasing in 25 and 100 m increments respectively to determine the threshold where variation in area restricted search was maximized, thus defining the decision space in which elk move. First passage time was calculated using the Hawthtools extension in ArcGIS 9.3.1 (ESRI).

We next tested whether human hunting seasons and modes changed the way in which elk perceived their landscape and transitioned between foraging and exploratory states by evaluating the time spent in the identified radii for elk. Under the risk allocation hypothesis, we predicted first passage time to decrease during the hunting season and to increase outside of the hunting season. We also predicted that rifle hunters (coursing) would decrease first passage time when compared to archery hunters (sit-and-wait) (Table 2). Finally, because predation risk increased 30% from 2007 to 2009, we also predicted an annual decrease in first passage time. We tested these predictions on first passage time with two complimentary analyses. First, we conducted simple descriptive one-way analyses of variance (ANOVA) across the four hunting seasons (i.e., non-hunted, archery, rifle, game damage, Table 1), hunting mode (i.e., archery, rifle), and time (i.e., year, month) (Zar 1999). We used simple post-hoc tests to test for differences in simple one-way ANOVA's.

Next, we tested how spatial and temporal covariates influenced first passage time at the area restricted search threshold we identified in the first step 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 (McCullough and Nelder 1989, Bolker et al. 2009) of first passage time fit to a function of hunting and landscape covariates using the following equation:

$$\text{First passage time}_{i} = \beta_0 + \gamma_{0i} + \beta_{1i}\,X_{1\ldots\ldots} + \beta_{ni}\,X_n + \epsilon \qquad \textit{(Equation 1)}$$

Where β_o is the intercept or base, γ_{0i} is the random effect for individual elk i, β_x is the individual selection for resource X, and ϵ is the residual variation unexplained by the model. We added a random effect (γ_{0i}) for each individual elk to account for individual variation in elk movement behavior (Gillies et al. 2006). We predicted that elk movement will be exploratory (low first passage time) outside of refugia to avoid human predation risk during the hunting season. Within the hunting refugia, we predicted that movement will be reduced to a foraging state (Morales et al. 2004). If movement rates outside of refugia decreased following the cessation of hunting resulting in increased selection for previously hunted areas, then the prediction that elk are selecting for refuge during hunting season would be upheld. We expected other factors such as topography, vegetation cover, and proximity to humans to also potentially influence first passage time 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 be expected to 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). A resource selection function is any statistical function that is proportional to the probability of use by an organism (Manly et al. 2002). We developed resource selection models for elk resource selection as a function of human predation risk on their winter home range 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 (also known as conditional logistic regression) to evaluate the effect of landscape covariates on elk resource selection. We generated two locations from the empirical step length and turning angle distribution of the movement pathways (Hosmer and Lemeshow 2000, Compton et al. 2002). Matched-case control designs appropriately use an animal's biological movements to define a biologically meaningful measure of availability (Compton et al. 2002, Whittington et al. 2005). We conducted a two-staged modeling where we estimated a matched-case logistic regression for each elk and then averaged among individuals (Sawyer et al. 2006, Fieberg et al. 2009, Fieberg et al. 2010 *In Press*). 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 normally do not have an intercept (Hosmer and Lemeshow 2000, Fieberg et al. 2009, Fieberg et al. 2010 *In Press*). We estimated individual elk resource selection along movement paths using fixed-effects conditional logistic regression for each individual elk (i) using:

$$w(x)_i = (\beta_{1i} X_{1\ldots..} + \beta_{ni} X_n + \epsilon)/(1 + \beta_{1i} X_{1\ldots..} + \beta_{ni} X_n + \epsilon) \qquad \textit{(Equation 2)}$$

where (i) is the individual elk, β is the individual selection for resource covariate X_n, and ϵ is the residual variation unexplained by the model. The probability in equation 2, $w(x)_i$, is a relative probability because of the problem of defining availability in use-availability resource selection designs (Keating and Cherry 2004, Johnson et al. 2006). Regardless, $w(x)_i$ can still be interpreted as a valid relative probability and the coefficients from conditional logistic regression interpreted in terms of their effects on the relative or ranked selection by elk (Keating and Cherry 2004, Johnson et al. 2006).

Covariates influencing first passage time and resource selection

We used spatial measures of hunter accessibility, distance from trails, roads, and houses (m), housing density (# houses/km^2), distance to streams, Normalized Difference Vegetation Index (NDVI), elevation, slope, hillshade and landcover variables to develop a-priori models of elk resource selection (Anderson et al. 2000, Burnham and Anderson 2001). Spatial data for hunter access, trails, roads, houses, streams, and a digital elevation model were all obtained from Montana Cadastral Mapping (http://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 (MFWP unpublished data), and by following legal hunting district boundaries (MFWP Hunting Regulations 2007, 2008, 2009). As a surrogate for spatial human predation, we estimated human activity as function distance from known human use areas (trails, roads, houses) (Merrill et al. 1999) in the Spatial Analyst Extension of ArcGIS 9.2 (Olympia, WA, USA). We measured housing density by measuring the centroid point of individual landowner parcel data. We then screened the data to insure a house was in the parcel, and then calculated the number of houses per km^2 in ArcGIS 9.2. We obtained 30m pixel resolution digital elevation model, slope, and aspect covariates, and calculated hillshade using the default value in ArcGIS 9.3 (NE 315 degrees) to obtain a continuous variable where high variables represent warm southwest hillsides. We measured changes in primary productivity using NDVI data from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite at a 250m^2 resolution (Huete et al. 2002, Pettorelli et al. 2005). We included two measures of NDVI measured in winter (NDVI_W) and summer (NDVI_S) to represent the seasonal transition from high forage biomass in the fall to spring green up. We defined fall 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 30m pixel resolution United States Department of Agriculture Forest Service's Northern Region Vegetation Mapping Project (VMAP) landcover map to determine available landcover components (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) as suggested for elk by Creel et al. (2005).

We predicted landscape covariates (distance to houses, trails, and roads) that decreased first passage time 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 first passage time and increasing the signal for resource selection. Hiding cover, as represented by percent canopy cover, was expected to increase first passage time, as would steeper slopes that reduce movement rates (Fortin et al. 2005b). 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 first passage time 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 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 if elk were selecting for intermediate distances to these variable (Hosmer and Lemeshow 2000).

First passage time and resource selection model selection and analyses

We tested the predictions of the resource allocation hypothesis (Table 2) for both first passage time and resource selection in a stepwise model selection procedure following recommendations from Hosmer and Lemeshow (2000). We first screened explanatory variables for collinearity (using a correlation coefficient, r ~= 0.50) using univariate analysis while accounting for confounded variables (Hosmer and Lemeshow 2000). We then manually built three different suites of models using mechanical stepwise model selection following Hosmer and Lemeshow (2000) that considered only human-only covariates, environmental-only covariates, and a combined model. We selected the top first passage time or resource selection model from either human, environmental, or combined models using Akaike’s Information Criteria (AIC) (Burnham and Anderson 2004). We chose this ‘hybrid’ model selection form to avoid allowing collinear or confounded variables in the same models and because our study was inherently observational and not experimental (Stephens et al. 2005).

The fit of first passage time GLMM's was evaluated with the coefficient of determination. We evaluated model fit for conditional logistic resource selection models using a modified version of k-folds cross validation adapted for matched-case control designs. K-folds cross validation is an approach to evaluate predictive model fit in resource selection models (Boyce et al. 2002) and 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 and averaged across elk to evaluate predictive capacity for the population (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 Texas, USA) (Johnson et al. 2006).

Results

We obtained 39,000 GPS telemetry locations of nine GPS collared elk during the focal sampling period (September to March of each year) over the three years of the study (2007-2009). The variance in area restricted search was maximized at 1,600m radii, although there was also a lower peak at very small radii that is likely due to GPS error (Figure 4, Frair et al. 2005). Using this threshold of 1,600m to discriminate movements between patches, first passage time varied as a function of year, month, hunting season, and hunting mode (Figure 5). Focusing first on the effect of changing hunting season, first passage time decreased as hunting pressure increased (Table 1) during the hunting season from 2007 (p-value 0.093), 2008 (p-value 0.031), and 2009, but was not significantly different during the non-hunting periods. In addition, first passage time of hunted elk was not significantly different from non-hunted elk in 2007, but first passage time was significantly lower in 2008 (p-value <0.0001) and 2009 (p-value 0.0008), supporting the hypothesis that hunting decreased first passage time. First passage time was significantly lower between the archery and rifle hunt than non-hunted periods (p-values < 0.011; Figure 2), yet multiple comparisons revealed first passage time during archery was not different than during non-hunting times. Monthly variation in first passage time was lowest during September, peaking in December, and dropping again in February (Figure 2). First passage time during hunting season was significantly lower than non-hunted times for all months except September and November, (Figure 5).

The top first passage time model combined human and environmental factors (Table 3). Individual variation in first passage time was substantial (var = 0.235) in the top model, confirming the need for a random effect for individual elk. Human related covariates (access, year, mode) caused the biggest reductions in first passage time, and hence greatest increases in movement rates (Table 4). Elk first passage time showed a quadratic relationship with distance to houses (Table 4), with first passage time increasing until elk were ~750m from homes and then declining thereafter (Figure 6). Important environmental covariates that increased first passage time were distance (in meters) to streams (β= 0.0002) and hillshade (β= 0.00017); whereas first passage time declined in areas of highcover (β= -0.09, Table 4). Distance to streams was highly correlated with distances to roads in our analysis (correlation coefficient= 0.50) and as such can be thought of as a human related variable.

The top model describing adult female elk resource selection was also the combined human and environmental model (r^2= 0.83, Table 3). Distance to houses and distance to trails were the only human variables that had significant influence on resource selection. Elk selected for intermediate distances from both houses and human trails. Elk resource selection peaked at 1200m from human activity, whereas their selection peaked from trails. Hunter access was statistically insignificant in the model (p-value= 0.34) but was retained regardless to test Prediction 1 (Table 4). Elk selected for high NDVI values during winter months (β= 16.19), which we interpreted as selection for tree cover because NDVI was highest in closed forests in our study area. Conversely, during fall, elk avoided high NDVI values (β= -16.26, Table 4), suggesting elk selected for hiding cover during high risk times and selecting for high forage biomass during less risky time supporting the risk allocation hypothesis. 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 spatial and temporal variation in human predation risk drove patterns of elk movement, but not necessarily resource selection, in a heterogeneous wildland urban interface landscape. As expected under the risk allocation hypothesis, elk first passage time declined where and when they were exposed to more human predation risk, except when hiding 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, elk resource selection was not driven by hunting access, instead, resource selection was driven more 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 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 wildland urban interface would have been much poorer.

How animals move is influenced by landscape heterogeneity and predation risk (Morales et al. 2005, Anderson et al. 2008). These movement decisions are made at a biologically relevant spatial scale (decision space) which can defined where the variance in movement is maximized (Fauchald and Tveraa 2003). The threshold of elk movements between foraging and movement scales was maximized at 1600m similar to elk in Frair et al. (2005) study in a wolf predation system, but much larger than Le Corre et al. (2008) study of roe deer (*Capreolus capreolus*) (area restricted search <100m). This suggests that elk were making decisions at a similar spatial scale under predation risk of wolves (Frair et al. 2005) and humans (this thesis), although humans had a larger impact on resources selection that do wolves in another study in Montana (Gude et al. 2006). We also observed a peak in variance in first passage time at very small radii that may be because of small-scale foraging decisions or GPS-induced error in apparent movement (Frair et al. 2010).

However, within this threshold of movement behavior (1,600m), we did see a significant change in first passage time as a function of increased predation risk by year (Figure 6), by differing hunting modes, and by season type (Figure 2). During every year of the study, management agencies increased hunting pressure and we documented a corresponding decrease in first passage time, as expect under prediction 3. The mode of predation with the largest negative influence on first passage time was rifle hunting, which we identified as a coursing predation type, which supported Prediction 2. However, this finding is contrary to the effect seen by Preisser et al. (2007) and 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 their prey species (Darimont et al. 2009), or that we did not have enough archery hunters to illicit a response. Interestingly, season structure, whether archery, focused on the herd (Game Damage Rifle Season) or the general rifle season (MFWP, unpublished data), had a significant impact on first passage time (Figure 2)(Wildlife-Division 2004). First passage time of elk did not differ during the non-hunting and archery seasons. However, the first passage time of two rifle hunting seasons differed significantly (General Rifle Season vs. Game Damage Rifle Season). The significant decline in first passage time as a function of hunting season structure illustrates that focused hunting has a significant impact on elk movement patterns over a more general hunting season structure that is designed to control regional elk populations. The relationship of first passage time declining as function of focused vs general was also evident in monthly first passage time as first passage time of hunted elk decreased from October and November (General Rifle Season) to January and February (Game Damage Rifle Season) (Figure 2). Thus, wildlife managers seeking to manage ungulates in the WUI and other fragmented landscapes might need to make a trade-off between the direct and indirect effects of human harvest on elk.

Accessibility to hunters (which decreased first passage time) and distance to streams (increased first passage time) were the primary drivers of first passage time in our top model (Table 4). In contrast, human related variables (access, distance to streams, houses, trials, and housing density) had less of an impact on resource selection, which was more driven by environmental variables (forage, open habitats, and slope). For example, hunter access had little impact on resource selection (p-value= 0.3350) in the top resource selection model, contrary to other studies (Gude et al. 2006, Proffitt et al. 2009). Humans were still influencing the system with non-linear relationship of distance to trails and distance to houses (Figure 7). In addition, elk selected for areas farther from streams (and, because of the correlation in our area of 0.5 between then, roads) which is well support in the literature (Lyon 1979, Rost and Bailey 1979, Rowland et al. 2000, Long et al. 2008). Elk selected for forested areas during winter as indicated by NDVI_W values (high NDVI values represented forested landscapes, Table 4), and selected for open grass lands in the fall given our NDVI_S values (Table 4). These results were similar to Creel et al. (2005) and Gude et al. (2006) that showed elk selected for areas of forage availability in the absence of predation risk.

The results of this study might have been limited by a small 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. However, it is worth noting that only adult female elk were collared and application of our results to adult male elk is limited, although male elk did use the WUI. One 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. Regardless, few wildlife management agencies are able to track the numbers of hunters on the landscape, and so our results that showed a significant effect of increasing hunting season length on elk movement and resource selection should be even more valuable to developing management strategies to address elk harvest in fragmented landscapes.

We believe that the general application of these results will be helpful in understanding how elk and other ungulates mitigate heterogeneous temporal and spatial predation risk. Under the common assumption that time spent in an area equals preference for these areas, one would assume that hunter access is not an important factor influencing elk behavior in the WUI. By combining first passage time and resource selection analyses we were better able to understand the influence of human predation risk on elk behavior and how elk move through a heterogeneous threat matrix. Understanding that elk first passage time is decreasing in areas closer to humans suggests that elk are still viewing humans as a predation risk and that hunting is having an effect on habituation concerns voiced by Thompson and Henderson (1998). We were able to identify that when elk are accessible to hunters they greatly reduce the amount of time spent in these areas and spend more time in (select for) areas that represent refugia.

Management implications

By understanding that elk avoid houses at intermediate distances (750m) and move quickly through areas closer to humans, managers know that humans are still viewed as a potential predation risk, but their willingness to be close to a potential predator (humans) suggest they are showing signs of habituation (Frid and Dill 2002). These highly orchestrated hunts are reducing the risk of habituation, an import credibility challenge to wildlife managers (Thompson and Henderson 1998). One primary concern of wildlife managers is the effectiveness of these highly orchestrated hunts. These data support the efficacy of these highly focused and orchestrated hunts' ability to impact elk movement, as the focused Game Damage Rifle Season had the greatest reduction in first passage time.

The mode of hunting was also important to the success of elk management in heterogeneous landscapes. Archery had little effect on movement and resource selection. If moving elk around is important to management objectives to make them more vulnerable to additional hunting pressure, then more effort should be put into implementing rifle seasons in these areas. It has been suggested that movement increases the chance of encounter of elk by wolves and thus increases predator success (Hebblewhite and Merrill 2007). If this holds true for human hunting pressure, than increasing access to increase elk movement may result in population level reduction in elk populations in the WUI. To answer these questions, more comparative work on human and non-human predators is needed.

In our study area, elk selected areas 1600m from houses and started to slow down at 750m from houses (Figure 6). 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 750m from homes. Knowing that elk will move quickly through areas 750m from houses suggests a minimum of 1,500m buffer between subdivisions to insure movement corridors remain functional. Maintaining migratory behavior of elk population is imperative to the maintenance of ecosystem function (White et al. 1998, Hebblewhite et al. 2005), as resident elk population degrade range condition (Baker et al. 1997, Snyder 2007). In addition, migration of this elk herd allows elk to move through more public land rather than being sequestered on the winter range which is predominately private. The 1,500m buffer zones provide conservation organizations guideline by which to prioritize conservation easements in the WUI to insure continued migration of WUI elk populations.

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Table 1. Elk hunting season structure by 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	September 15-November 25	Rifle	71
	Archery	September 1-October 14	Archery	44
	General Season	October 21-November 25	Rifle	35
	National Wildlife Federation	No Hunt	Archery	0
	Game Damage	December 15-February 15	Rifle	61
			Total	211
2008-2009	Rattlesnake Wilderness	September 15-November 30	Rifle	76
	Archery	September 6-October 19	Archery	43
	General Season	October 26-November 30	Rifle	35
	National Wildlife Federation	September 6-October 19 October 26-November30	Archery	78
	Game Damage	January 3-February 13	Rifle	41
			Total	273

Table 2. The predicted effect selected covariates on first passage time (FPT) and resource selection of nine 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	--	-
NDVI	++	++
Highcover	neutral	-
Distance to roads	+	+

Table 3. Competing model selection results for first passage time mixed-effects models and resource selection functions from two-stage mixed-effect conditional logistic regression based from nine GPS collared elk in the wildland-urban interface of Missoula, Montana, USA. Models in bold were selected as the top model based on Akaike Information Criteria (AIC) scores.

Model	Obs	ll(model)	df	ΔAIC
First Passage Time				
Top Human	39151	-13172.6	10	1122.09
Top Environmental	39151	-14745.9	10	4763.22
Top Combined	**39151**	**-12607.5**	**10**	**0**
Matched Case Control Resource Selection Functions				
Top Human	117453	-38852	72	63128.64
Top Environmental	117453	-7610.33	54	609.33
Top Combined	**117453**	**-7251.66**	**108**	**0**

Table 4. The highest ranked first passage time (FPT) and resource selection function models from based Akaike Information Criteria (AIC) values of competing models from nine GPS 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 kilometer squared.

	First Passage Time			Resource Selection Functions		
Variables	β	*SE*	*p*	β	*SE*	*p*
Access	-0.29	0.007	<0.0005	-0.11	-0.037	**0.3350**
Distance to streams	0.0002	4E-06	<0.0005	0.0007	0.00022	0.0334
Distance to houses	0.0002	2E-05	<0.0005	0.003	0.0011	0.0047
Distance to houses2	-1E-07	1E-08	<0.0005	-2E-06	-5E-07	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	--	--	--	-3E-07	-9E-08	0.0065
Housing density	--	--	--	-0.006	-0.0020	**0.1507**
Hillshade	0.0002	6.13E-05	0.0070	-0.003	-0.0010	**0.1022**
Highcover	-0.09	0.005	<0.0005	--	--	--
Lowcover	--	--	--	-9.25	-3.085	0.0298
NDVI_W	--	--	--	16.2	5.41	<0.0001
NDVI_S	--	--	--	-16.3	-5.42	<0.0001
Slope	--	--	--	0.014	0.0046	**0.8104**
Constant	103.17	3.788	<0.0005	--	--	--

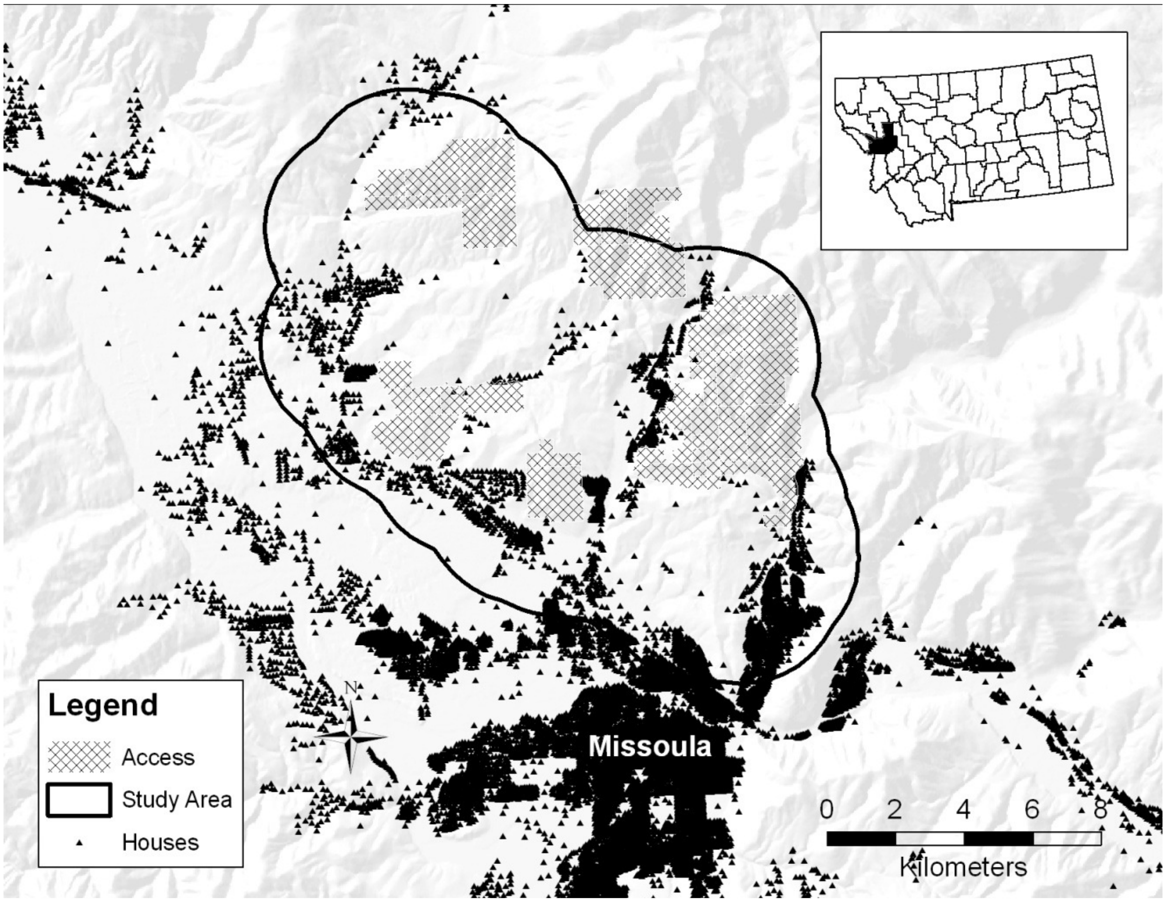


Figure 1. The location of the study in Missoula County, in the wildland-urban interface of Missoula, Montana, USA. The study area was defined by the location data from nine GPS collared elk within the winter range of an urban elk herd in the North Hills of Missoula, Montana. The cross-hatched grids (Access) are the areas where human hunters had access to elk hunting during the course of the study (2007-2009).

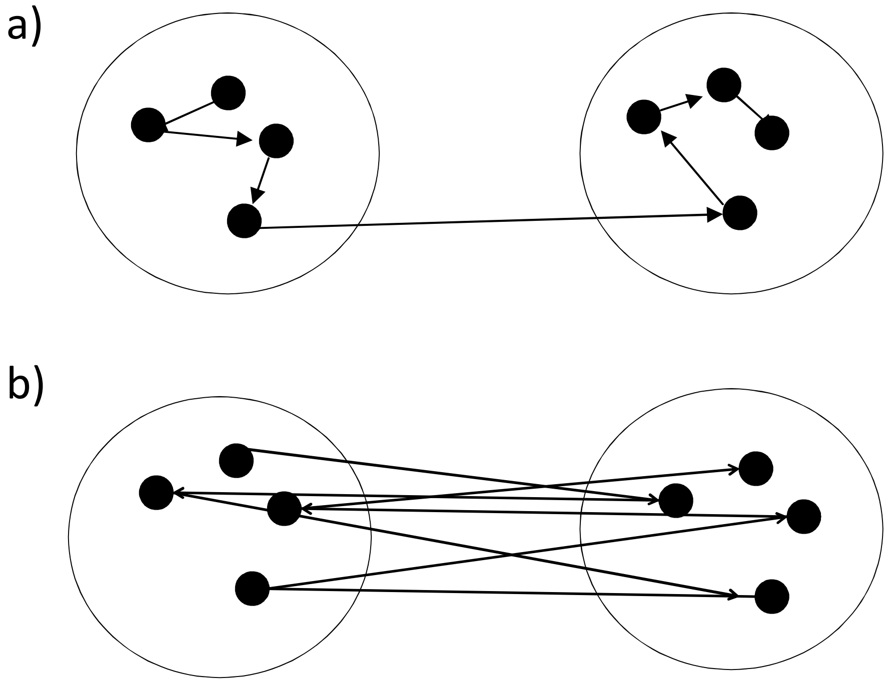


Figure 2. Conceptual representation of different anti-predator movement strategies that result in the same resource selection pattern in both a and b (animal locations sampled at regular intervals such as with GPS telemetry are represented by the black dots). Resource selection analyses alone would fail to recognize the different movement strategies employed in both examples. In a) animals are sedentary in the two habitat patches with only one move between patches, whereas in b) the animal is continuously moving between the habitat patches. Without combining analysis of movement and resource selection, conclusions drawn about the selection behavior of this animal would be misleading.

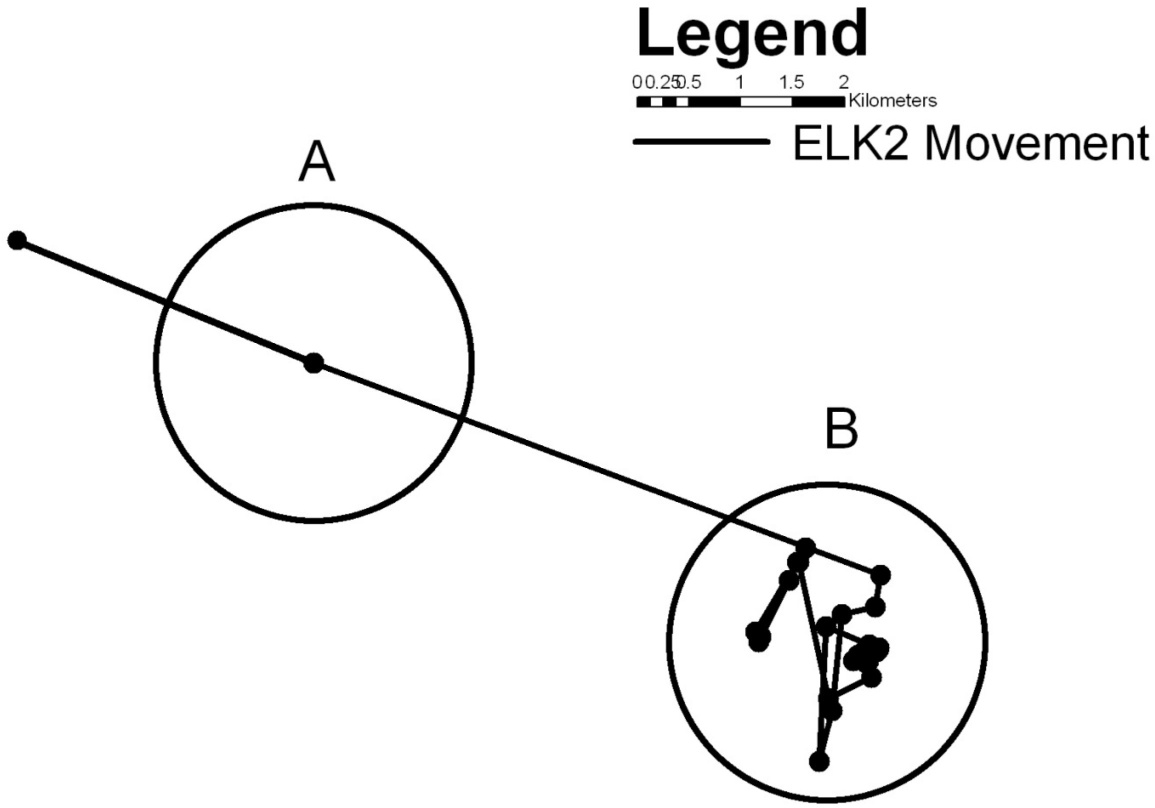


Figure 3. An example of first passage time (FPT) from a GPS collared adult female elk (Elk2) from the wildland-urban interface of Missoula, Montana, USA. Both circles have a radii of 1,600m (drawn to scale) A) represents a low FPT B) represent a high FPT respectively.

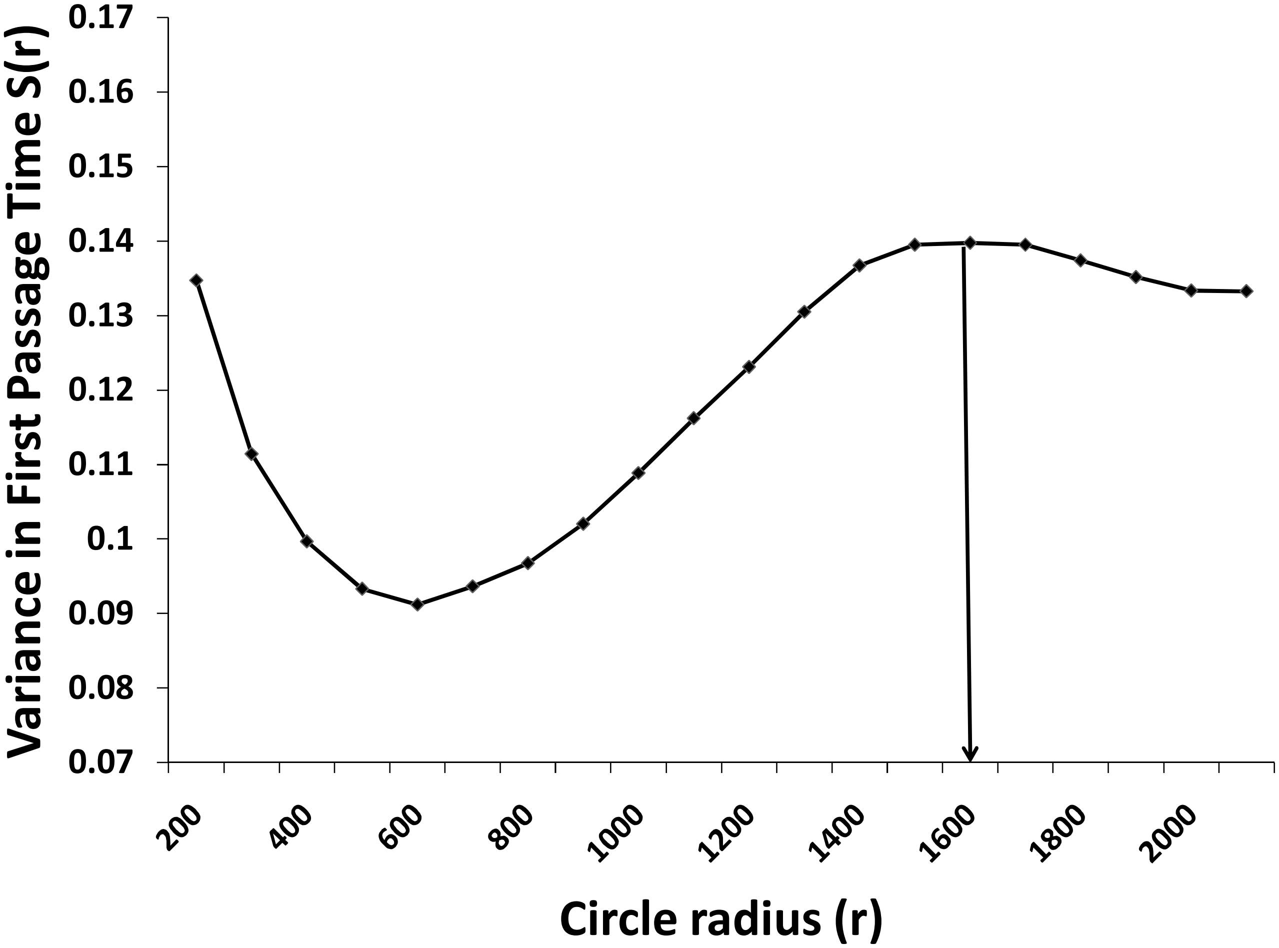


Figure 4. The variance in log first passage time S(r) as a function of area to define area restricted search (ARS), given an increasing circle radius (r), for elk in the wildland-urban interface of Missoula, Montana, USA. ARS is maximized at a radii of 1,600m.

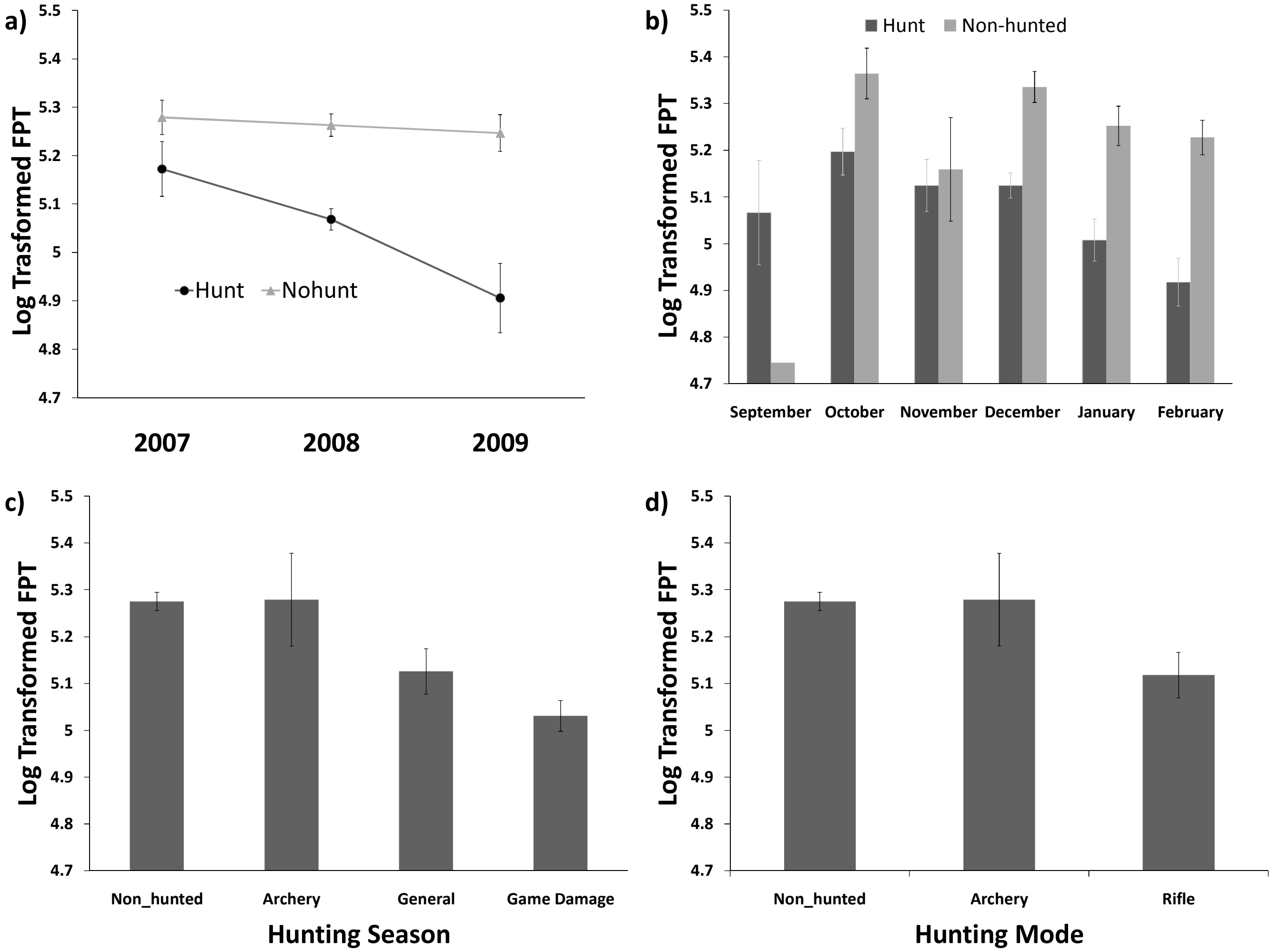


Figure 5. Log transformed first passage time values with standard errors from nine GPS collared adult female elk in the wildland-urban interface of Missoula, Montana, USA as a function of a) year b) month across all years (2007-2009) c) hunting season across all (2007-2009) d) hunting mode across all year (2007-2009). Year 2007 represents the lowest human predation risk increasing with risk increasing in 2008, and 2009.

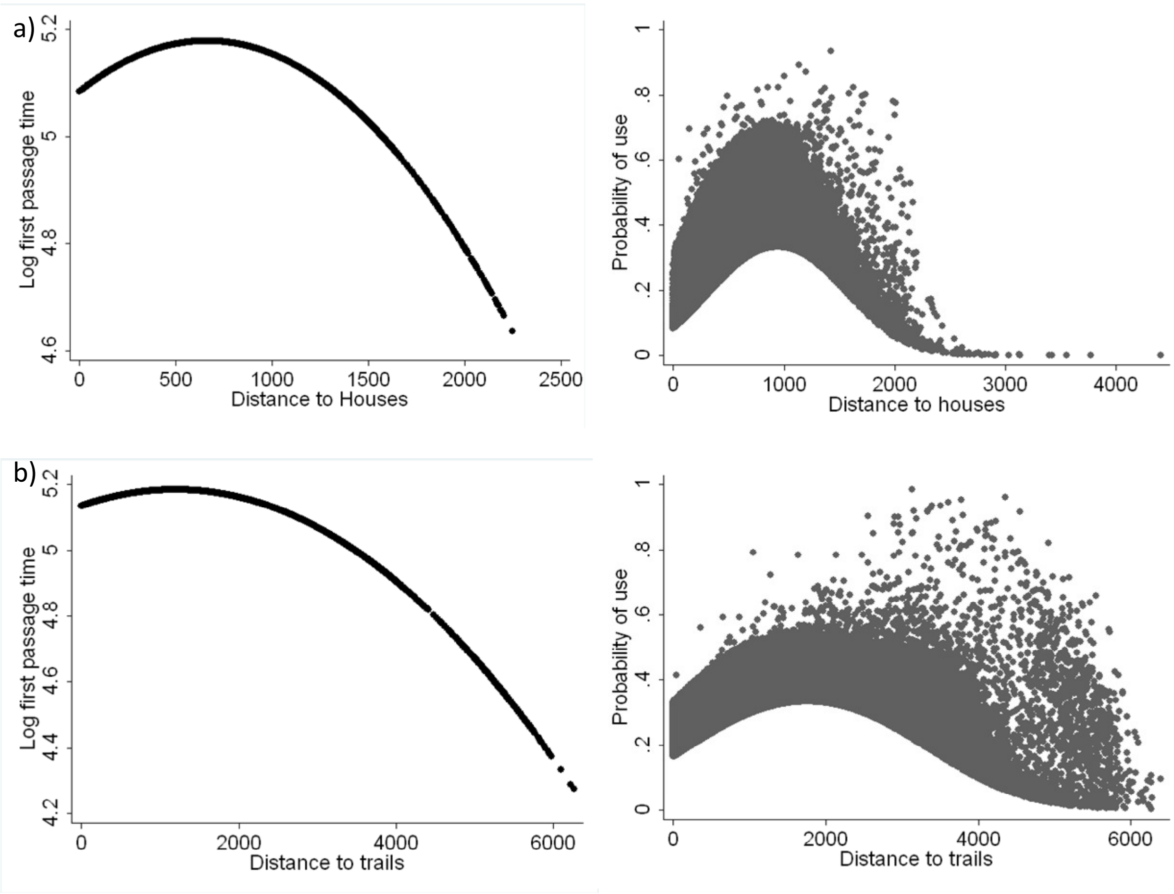
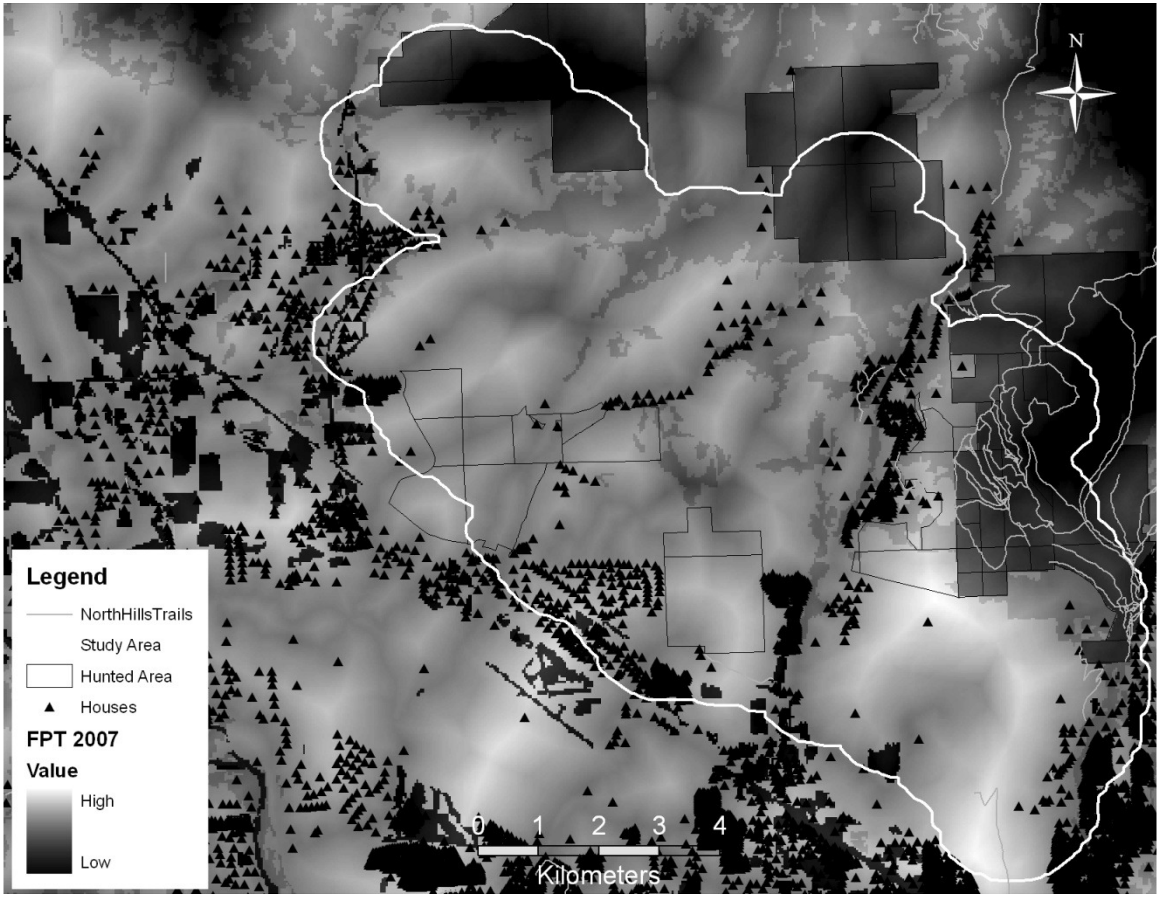


Figure 6. The distance (m) to houses (a) and trails (b) where first passage time and the relative probability of resource selection was maximized from generalized linear models developed from nine GPS collared adult female elk. The data was collected from 2007-2009 in the wildland-urban interface of Missoula, Montana, USA.

a)


N
Legend
NorthHillsTrails
Study Area
Hunted Area
Houses
FPT 2007
Value
High
Low
0
1
2
3
4
Kilometers

b)

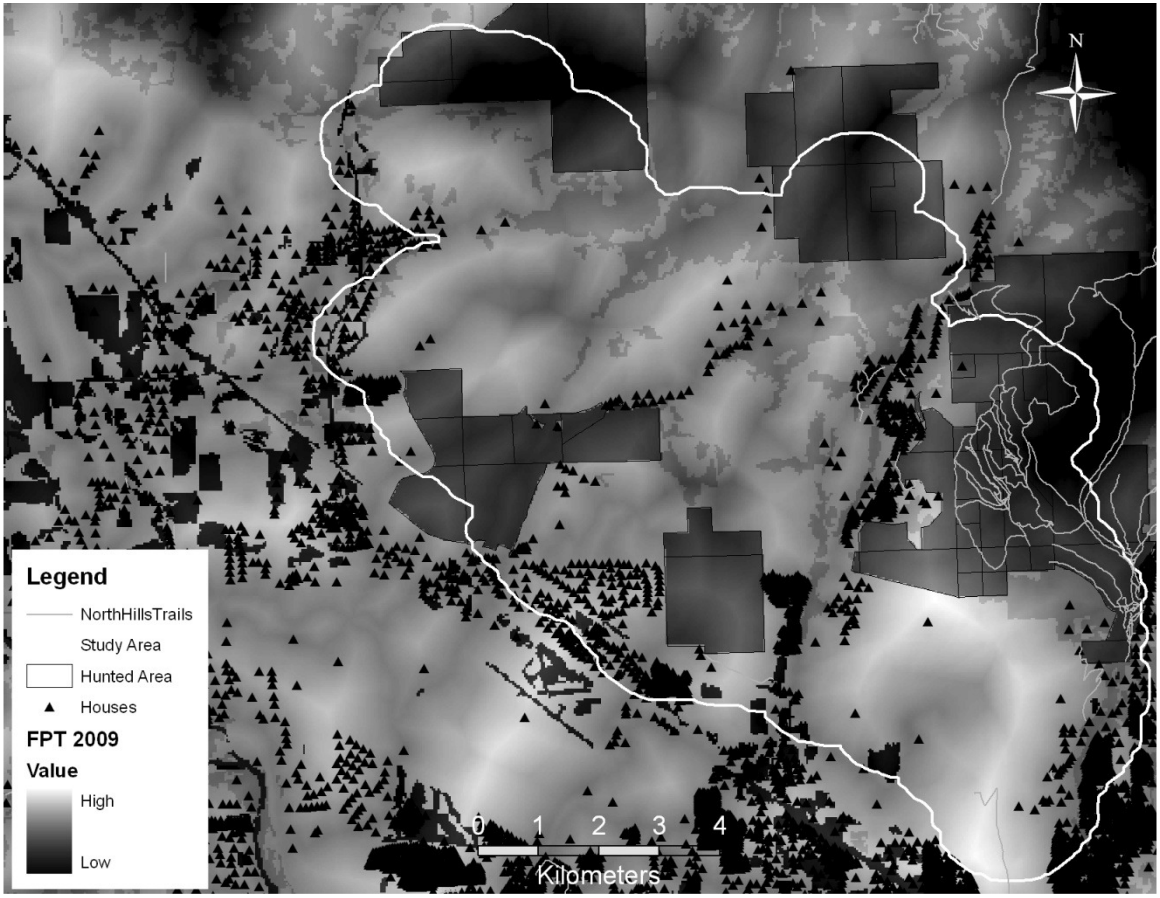


Figure 7. Map of predicted first passage time (FPT) from the combined generalized linear mixed model (GLMM) model for female elk in the North Hills of Missoula, Montana, as a function of human predation risk (access) and years 2007 (a) and 2009 (b). Notice that FPT in a) has less access (access is outline but no hunting occurred) than b), and there is a corresponding decrease in FPT on accessible land from 2007 to 2009. High FPT values represent increased time spent in that area.

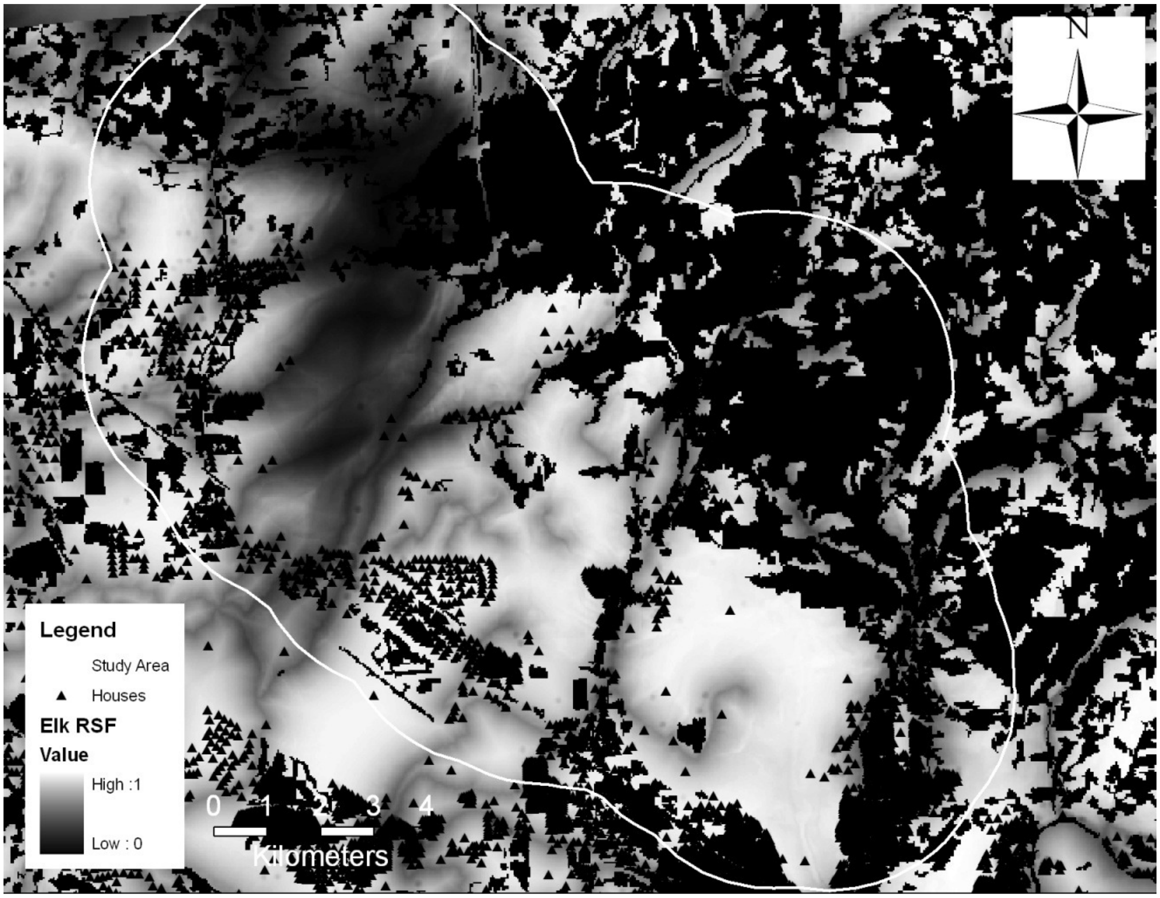


Figure 8. Spatial predictions of the relative probability of use from the top RSF model from GPS collared elk (n=9) in the wildland-urban interface of Missoula, Montana, USA (2007-2009). Darker colors represent lower relative probability of use, where as lighter colors represent higher relative probability of use.

APPENDIX A

Behavioral responses – Bedded

Elk bedded more mid-day than during other times of day. Lamar bedded statistically more than did all other groups. Missoula elk bedded less during hunting season than during the following weeks except week 4**.**

Behavioral responses –Standing

Elk stood least in the morning than other times of day. Missoula elk stood less than all other study areas. Elk stood more in Missoula during weeks 2, 3, and 4 post hunting season

Table 1. Results of fixed-factorial ANOVA of the effects of time of day (time), Risk Level, Risk Level*Time, Time, position in the group (position), temperature, and group size has on female elk behavior.

	Bedded		Standing	
	F	*P*	*F*	*P*
1. Risk Level	5.88	**0.0006**	6.59	0.0002
2. Time	3.43	**0.0015**	1.01	0.4257
3. Risk Level*Time	3.36	**0.0004**	1.44	0.1594
4. Position	4.46	**0.0356**	8.05	0.0048
5. Time Period	9.72	**0.0001**	11.62	**<0.0005**
6. Group Size	--	--	--	--
7. Temperature	0.50	0.4805	--	--

APPENDIX B

Table 1. The known fate of collared adult female elk in the North Hills, Missoula, Montana, USA from 2007-2009. Harvested animals were legally taken by elk hunters.

Elk ID	Frequency	Collar Type	Month	Year	Known Fate	Month	Year	Comments
A	150.8392	VHF	March	2007	Deceased	February	2008	Harvested
B	150.1390	VHF	March	2007	Alive	April	2009	
C	150.1179	VHF	March	2007	Alive	April	2009	
D	150.1280	VHF	March	2007	Deceased	February	2008	Harvested
E	150.0973	VHF	March	2007	Alive	April	2009	
F	150.1080	VHF	March	2007	Deceased	September	2008	Black bear
G	150.0485	VHF	March	2007	Alive	April	2009	
I	150.4240	VHF	February	2008	Alive	April	2009	
J	150.2190	VHF	March	2008	Alive	April	2009	
L	150.2990	VHF	April	2008	Alive	April	2009	
Blue 1	150.1500	VHF	March	2008	Alive	April	2009	
Blue 2	150.8600	VHF	March	2008	Alive	April	2009	
1230	149.0464	GPS	February	2007	Alive	April	2009	
1231	150.5780	GPS	March	2007	Alive	April	2009	
1232	149.3950	GPS	March	2007	Deceased	January	2008	Harvested
1232	149.3950	GPS	February	2008	Alive	February	2008	
1233	149.6477	GPS	February	2007	Deceased	March	2007	Unknown
1233	149.6477	GPS	March	2007	Alive	April	2009	
1314	150.7988	GPS	March	2007	Alive	April	2009	
1315	150.8694	GPS	March	2007	Alive	April	2009	
1316	150.9400	GPS	March	2007	Deceased	January	2009	Harvested
1317	151.3581	GPS	March	2007	Alive	April	2009	