APPLYING RISK ALLOCATION THEORY IN A LARGE MAMMAL PREDATOR-PREY SYSTEM: ELK-WOLF BEHAVIORAL INTERACTIONS

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish & Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

March 2004

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of a thesis submitted by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

Financial support for this research was provided by an NSF Graduate Research Fellowship; the Montana Department of Fish, Wildlife, and Parks; the Sun Ranch; the Elk Meadows Ranch; and the Rocky Mountain Elk Foundation. The US Fish and Wildlife Service, the Turner Endangered Species Fund, and the Montana Department of Fish, Wildlife, and Parks provided wolf capture and marking support. Additional logistical support was provided by the community in the Madison valley. I especially thank the owners and residents of the CB Ranch, the Elkhorn Ranch, the Corral Creek Ranch, the Carroll Ranch, the Rising Sun Mountain Estates, the Sun Ranch, the High Valley Ranch, and the Elk Meadows Ranch for access to a large block of land, advice, countless cups of coffee, and many dinners. Thain Cook, Julie Fuller, John Salerno, Terra Scheer, and Renee Wulff aided in data collection under difficult winter conditions. I would like to thank my committee members for providing advice, input, and support throughout my graduate tenure. I owe a special thanks to Bob Garrott for many reasons, most notably for setting a superior example of professionalism. I also would like to thank my fellow graduate students, particularly Eric Bergman, Adam Messer, King Jones, Julie Fuller, Scott Powell, Katie Brown, and Darren Ireland. Of course, I would like to thank Patty Hernandez for help and support throughout the course of this work.

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ABSTRACT

Understanding the behaviorally-mediated indirect effects of predators in ecosystems requires knowledge of predator-prey behavioral interactions, and the risk allocation hypothesis can be used to make predictions about such interactions. In predator-ungulate-plant systems, empirical research quantifying how predators affect ungulate group sizes and distribution, in the context of other influential variables, is particularly needed. We determined non-predation variables that affect elk (*Cervus elaphus*) group sizes and distribution on a winter range in the Greater Yellowstone Ecosystem (GYE), using regression analyses of 1219 elk groups counted and mapped over 12 years prior to wolf (*Canis lupus*) recolonization. We next examined the relevance of these non-wolf-predation variables in the presence of wolves using logistic and linear regression on surveys of 513 1-km^2 areas conducted over 2 years. Using model selection techniques, we evaluated risk allocation and other *a priori* hypotheses of elk group size and distributional responses to wolf predation risk while accounting for influential non-wolf-predation variables. We found little evidence that wolves affect elk group sizes, which were strongly influenced by habitat type. Following predictions from the risk allocation hypothesis, wolves likely created a more dynamic elk distribution in areas that they frequently hunted, as elk tended to move during the period of safety following wolf encounters in those areas. We predict that this distributional response to wolf predation risk should decrease the spatial heterogeneity of elk impacts on grasslands in areas that wolves frequently hunt. We also predict that this response should decrease browsing pressure on heavily-browsed woody plant stands in certain areas, which is supported by recent research in the GYE. This research highlights the importance of predator-prey behavioral interactions in large mammal systems.

INTRODUCTION

How prey respond to predation risk is a central issue in ecosystem ecology. Predators can have indirect effects in food webs mediated by the behavioral responses of prey to predation risk (Lima 1998a, Schmitz et al. 2000). If herbivores change habitat use, movement, activity, or other behavioral patterns in response to predation risk, herbivore-plant interactions can be affected (Schmitz et al. 1997). Such behaviorally-mediated indirect interactions can be stronger than trophic cascades that are mediated through the demographic effects of predators on prey populations (Peacor and Werner 2001, Schmitz et al. 2004). While considerable research effort has focused on documenting trophic cascades (Pace et al. 1999), less attention has been given to delineating the behavioral mechanisms that are potentially responsible for such cascades. Empirical research quantifying prey responses to predation risk can provide a knowledge base for incorporating behavioral interactions into biologically sound models of the dynamics of multi-trophic systems (Polis et al. 2000, Schmitz et al. 2000, Werner and Peacor 2003).

Ungulates can modify and structure plant communities over vast areas through foraging pressure and nutrient inputs into soil (McNaughton 1985, Pastor and Naiman 1992, Hobbs 1996, Augustine and McNaughton 1998, Olff and Ritchie 1998, Bardgett and Wardle 2003). Predator-ungulate-plant systems might therefore offer insights into the indirect effects of predators in ecosystems. Two general aspects of ungulate ecology contribute to the impacts of ungulates on plant communities. First, the population size of ungulates in a particular area describes the total potential impact exerted on plant communities (Hobbs 1996). Predators can affect plant communities by influencing the population dynamics of ungulates (McLaren and Peterson 1994). Second, spatial concentrations of ungulates have the ability to affect plant community composition, plant productivity, and nutrient dynamics (McNaughton 1984, Augustine and McNaughton 1998). For a given ungulate population, behavioral decisions made by individual animals determine the amount of spatial concentration across a landscape.

Spatial concentrations in an ungulate population can be partitioned into two related variables: group sizes and distribution. If group sizes describe the number of ungulates in specific areas and distribution describes the location of ungulate groups, these two variables can together describe potential ungulate impacts on plant communities across a landscape at any point in time. Ungulate group sizes and distribution patterns are influenced by many variables, including weather (e.g. Merrill 1991, Turner et al. 1994, Skovlin et al. 2002), habitat type and habitat quality (e.g. Leuthold 1977, McNaughton 1988, Unsworth et al. 1998, Irwin 2002, Jones and Hudson 2002), population density (Vincent et al. 1995, Borkowski 2000), and season (e.g. migration: Irwin 2002, Skovlin et al. 2002). In combination with these causal factors, the feedback effects of herbivores on plant communities can lead to complex ungulate-plant interactions (Frank et al. 1998).

Animal group sizes and distribution patterns also respond to predation risk (Lima and Dill 1990, Lima 1998b). If ungulates respond to predation risk with changes in group sizes or distribution patterns, then predators may affect ungulate-plant interactions. In social ungulates, group sizes tend to be larger in open areas and smaller in forested areas, which has been interpreted as a behavioral response to how ungulates perceive predation risk in different habitat types (Leuthold 1977, Geist 2002). These observations assume that ungulates perceive a higher risk of predation in open habitats, and thus form larger groups in order to accrue the fitness benefits that larger groups confer (e.g. Hamilton 1971). Ungulates also may modify their distribution based on how they perceive predation risk in different habitat types or landscape features (Kotler et al. 1994). Such interpretations require questionable assumptions about how ungulates perceive predation risk, and direct measures of predation risk provide more reliable evidence for addressing ungulate responses to predators (Berger 1991).

Direct measures of predation risk have produced variable results concerning the effects of predators on ungulate group sizes and distribution patterns. Three issues likely contribute to this variability. First, analyses that only consider direct measures of predation risk may be confounded by other drivers of ungulate group sizes and distribution. Second, definitions of risky areas have been inconsistent in research examining how ungulates respond to spatial variation in predation risk. Some studies have treated the frequency of predator activity in different areas as a measure of risk (Ripple et al. 2001), while others have considered the distribution of kills made by predators to represent spatial variation in hunting pressure by predators (Prins and Iason 1989). Empirical research that addresses which measure of predation risk is more germane to large mammal systems is lacking. Third, predation risk varies not only spatially, but also temporally. In natural systems, predation risk is more consistent in some areas than in others, but the magnitude of risk in specific areas also varies across time at scales as short as minutes during encounters with predators (Sih 1992). Predation risk escalates dramatically when prey encounter predators, and then dissipates following an encounter. Prey animals might respond to either spatial or temporal variation in risk, or both, and recent research suggests that spatial and temporal variation in predation risk interact to affect prey behavior. The risk allocation hypothesis predicts differences in prey responses to temporal variation in predation risk in areas with different background frequencies of predation risk (Lima and Bednekoff 1999). Thus, ungulate responses to temporal variation in predation risk might depend on how common predation risk is. In areas with frequent predation risk, ungulates should make amplified behavioral changes during pulses of safety following recurring predator encounters. This is because pulses of safety are relatively infrequent in areas where predation risk is common. In areas typically devoid of predation risk, ungulates should make amplified behavioral changes during direct encounters with predators, which are less common than periods of safety.

We measured changes in elk (*Cervus elaphus*) group size and distribution patterns in response to spatial and temporal variation in predation risk from wolves (*Canis lupus*), on an elk winter range in the Greater Yellowstone Ecosystem (GYE). Plant population dynamics, productivity, and distribution patterns, as well as nutrient dynamics, are influenced by elk herbivory on winter ranges in the GYE (Frank 1998, Singer et al. 1998, Augustine and Frank 2001, Frank et al. 2002, Singer et al. 2003). For the majority of the previous century, humans were the major predators of elk in the region (Singer 1991). Dispersing wolves have recently recolonized most elk winter ranges in the GYE following their reintroduction in 1995-1996 (Smith et al. 2003, USFWS et al. 2004).

Because wolf predation in the GYE has focused on elk (Jaffe 2001, Smith et al. 2004), elk populations that were not exposed to wolves for almost a century are now faced with a source of predation risk that was absent for several generations. Research on one GYE elk winter range indicates that the reestablishment of wolf predation risk may indirectly affect deciduous tree communities (Ripple et al. 2001, Beschta 2003). While this indirect effect is likely due to behavioral interactions between wolves and elk (Beschta 2003), the behavioral mechanisms for this effect have not been quantified.

Our research sheds light on mechanisms of elk-wolf behavioral interactions in two ways. First, we evaluate competing hypotheses for the effects of wolf predation risk on elk group sizes and distribution. We examine both wolf activity and wolf hunting pressure as measures of spatial variation in predation risk. We also compare risk allocative hypotheses of elk group size and distributional responses to wolf predation risk to hypotheses of elk responses to only spatial and temporal variation in wolf predation risk. Second, we evaluate these hypotheses in the context of other variables that influence elk group sizes and distribution, to accurately assess how wolves affect elk spatial concentrations during winter.

METHODS

Study Area

This research was conducted in the southern Madison River valley and the surrounding slopes in southwest Montana. The Madison valley is located 32 km west of YNP, between the Gravelly and Madison mountain ranges. The valley has cold winters, with daily minimum and maximum temperatures averaging -7.9 and 3.3 degrees Celsius during this study, respectively. Snow depth during winter was variable across the valley during this research. Standing snow depths in areas with woody vegetation often exceeded 40 cm while depths in grasslands rarely exceeded 10 cm, other than in cornices and snowbanks.

Data were collected on two adjacent sites separated by the Madison River. The East Madison Site is a 189 km^2 area primarily on private ranchlands to the east of the Madison River. The West Madison Site is 1.2 km westward, in a 106 km^2 area on both public and private lands. These sites are similar in elevation, which ranges from 1670-3064 m. They contain similar plant communities to those found in YNP (Despain 1990). Flat grassland, dominated by bunchgrasses (e.g. *Festuca idahoensis* and *Agropyron spicatum*) with occasional patches of sagebrush (*Artemisia sp.*), constitutes approximately 50% of the total area at both sites. Sagebrush steppe, grassland hills, and forested areas, including riparian and montane forest community types (Despain 1990) are the other major habitat types.

Elk numbers in the Madison valley have increased approximately 6-fold over the last 30 years, in concordance with management goals. The East and West Madison Sites have recently wintered approximately 4000 and 2500 migratory elk, respectively, based on aerial trend counts conducted by the Montana Department of Fish, Wildlife, and Parks. For the last 30 years, adult bull elk have usually constituted less than 5% of the population in both areas during classification surveys. Consequently there is little of the sexual segregation that is characteristic of other wintering elk populations (Geist 2002). Groups of elk observed in this research, therefore, were typically not influenced by the tendency for adult bulls to occur in smaller groups and in different habitats than other age-sex classes during winter. Approximately 100-300 mule deer (*Odocoileus hemionus*), 5-10 moose (*Alces alces*), 100-200 pronghorn antelope (*Antilcarpa americana*), and <100 white-tailed deer (*Odocoileus virginianis*) also spend at least a portion of the winter in each of the areas. During the winter of 1999-2000, wolves dispersing from YNP established a territory on the East Madison Site. One wolf pack has been present at the East Madison Site since that time. Dispersing wolves were sighted at the West Madison Site in the winter of 1998-1999, but resident wolves have not since been documented. Other wolf packs have become established outside of the East and West Madison Sites in the Madison valley and dispersing wolves have occasionally, but rarely, been sighted in both areas since 1998. Other ungulate predators in the areas during winter include mountain lions (*Felis concolor*), coyotes (*Canis latrans*), and humans.

Wolf Predation Risk

We collected data from January through April of 2002 and December through April of 2002-03 at the East Madison Site. One of two wolves from the single resident wolf pack was fitted with a VHF radio collar during the 2002 winter, and two of four wolves from the pack were fitted with VHF radio collars during the 2002-03 winter. Two locations of these wolves were triangulated daily at approximately 10-12 hour intervals in the morning and evening, as weather permitted. We defined wolf pack locations as the centroid of the polygon created by plotting three or more consecutive bearings on the VHF collars from pre-defined locations throughout the study area (White and Garrott 1990). The accuracy of this wolf location procedure was assessed by a naive observer triangulating the location of a total of 20 VHF radio collars placed at randomized points across 4 strata. Location error for the randomly placed collars was defined as the straight-line distance between estimated and true collar location.

Surveys for elk presence or absence and the sizes of elk groups were conducted in 1-km^2 square units surrounding estimated wolf locations. Survey units were defined using a stencil to draw a 1-km^2 area surrounding the location of interest on a 1:24000 scale topographic map to serve as a guide for observers. Surveys were most often conducted from a high point using a 10-40 power spotting scope to provide complete coverage of the area. When weather, rugged terrain, or thick vegetation precluded surveying the entire survey area from a distant point, a method analogous to area searching for avian communities was employed to detect and count elk groups (Ralph et al. 1993).

Surveys were conducted each day of the field season in 1-km^2 units surrounding wolf locations from that morning, the previous evening, and the previous morning. These surveys provided data in the range of 0 to 36 hours since the last known wolf presence in survey units. To ensure that wolves did not re-enter survey units during the lag time between the last known wolf presence and the time that each unit was surveyed, the general location of radio-collared wolves was monitored opportunistically throughout each day. To corroborate assessments of the amount of time since wolves departed each survey unit, telemetry was used to ensure that radio-marked wolves were not in a unit before each survey. To provide data for areas with more than 36 hours since wolf presence, 15 fixed 1-km^2 square survey units were placed throughout the East Madison Site. Using estimated wolf locations and daily monitoring of the general location of radio-marked wolves, we approximated the amount of time since wolves were located in the vicinity of each of these survey units on a daily basis. When time since wolf presence in fixed survey units exceeded 36 hours, they were opportunistically surveyed. If elk were flushed by observers using area searching techniques, survey units were not sampled again until wolves returned to the area in order to eliminate observer bias. Also, when two or more survey units were within five km of one another, data was only collected from the unit that wolves had most recently departed.

We considered spatial patterns in both wolf activity and hunting pressure as measures of spatial variation in wolf predation risk. Spatial variation in wolf activity was estimated using triangulated wolf pack locations. To estimate spatial variation in wolf hunting pressure, we used the location of wolf-killed ungulates. We employed daily snow tracking and searched the areas surrounding recent wolf pack locations to locate as many wolf-killed ungulates as possible (Jaffe 2001). When wind, snow, or temperature conditions eliminated wolf tracks, as much area as possible between and around consecutive locations was examined for scavenger activity and ungulate carcasses using 10-40 power optics. A necropsy was performed on all carcasses located in order to determine the cause and time of death. Subcutaneous hemorrhaging, puncture wounds, consumption patterns, and track patterns were used as criteria to differentiate definite and probable wolf-killed ungulates from those dying of other causes (Jaffe 2001).

Non-Wolf-Predation Effects

Factors other than wolf predation risk undoubtedly affect elk group sizes and distribution. As non-wolf-predation predictor variables, we identified seasons (Turner et al. 1994, Borkowski and Furubayashi 1998), temperature (Parker and Robbins 1984, Skovlin et al. 2002), falling snow (Skovlin et al 2002), snow depth (Peek 1998, Irwin 2002), habitat type (Unsworth et al. 1998, Jones and Hudson 2002, McCorquodale 2003), habitat openness (Leuthold 1977, Lagory 1986, Vincent el al. 1995, Thirgood 1996, Borkowski 2000), human elk-hunting (Millspaugh et al. 2000, Conner et al. 2001, Vieira et al. 2003), population size (Vincent et al. 1995, Borkowski 2000), time of day (Merrill 1991, Borkowski and Furubayashi 1998), and migration (Irwin 2002, Skovlin et al. 2002). To quantify the importance of these variables in the Madison valley in the absence of wolf predation risk, we used elk surveys conducted at the West Madison Site between the winters of 1986-87 and 1997-1998 (12 total winters prior to wolf recolonization). These surveys were conducted almost exclusively by the same Montana Department of Fish, Wildlife, and Parks professional throughout the time series. Surveys were conducted one to five times weekly between November and June from pre-defined locations that maximized visibility across the area. Surveys were completed between sunrise and three hours after sunrise, or three hours before sunset and sunset, coinciding with peak elk daytime activity periods. We assumed that elk would be most visible when active. Using 15-60 power optics, the observer noted the location and number of individuals in each visible elk group by drawing polygons on USGS 7.5 minute topographic maps. The elk population size for each survey was obtained by summing the number of elk in all visible groups, and the maximum elk population size for each winter was defined as the highest recorded population size for all surveys. The date, time, temperature, and precipitation conditions were recorded for each survey. At a later date, each elk group observation was associated with flat grassland, sagebrush steppe, grassland hills, montane forest, or riparian forest habitat types based on a digitized map of these habitats. Surveys were classified as falling into winter or spring seasons using snow water equivalent (SWE) data recorded at an automated SNOTEL site located southwest of the West Madison Site in the Gravelly Mountains at 2438 m elevation (NRCS 2004). The first day of spring for each year was defined as the last major peak in SWE accumulation, after which SWE only declined or increased briefly during spring storms. No human elk-hunting occurs at the West Madison Site during winter, and snow depth data from within the boundaries of the West Madison Site were unavailable, so we were not able to consider these potential drivers of elk spatial concentrations at the West Madison Site.

Each survey surrounding wolf locations and in fixed survey units at the East Madison Site was associated with the same non-wolf-predation predictor variables recorded at the West Madison Site. The montane and riparian forest habitat types at the East Madison Site were combined into one category based on pilot data analyses. Also, methods for obtaining elk population totals differed at the East Madison Site. The elk population size at the East Madison Site was estimated at two-week intervals using a stratified random sampling design and four-day sampling sessions. Flat grassland, sagebrush steppe, grassland hills, and forested habitats were used as sampling strata. Sampling units within these strata were defined based on features that permitted delineation of unit boundaries in the field. Ten-forty power optics were used to count all groups of elk present in each sampling unit, using a combination of observations from pre-specified high points and/or pre-specified walking routes that provided complete coverage of each unit in favorable weather conditions. Because winter weather often impeded our ability to completely sample units, we estimated the proportion of each sampling unit that was covered, using the categories 0%, 1-25%, 26-50%, 51-75%, 76-99%, and 100%. The midpoints of these categories were multiplied by the area of each sampling unit as a rudimentary method of determining the elk density in each unit, prior to extrapolating density estimates across the East Madison Site.

Data on human elk-hunting and snow depth were also recorded at the East Madison Site. The human elk-hunting season lasted for 16 total days in the month of

January during the 2002 winter. This 16-day season was divided into 4-day hunting periods interspersed with 3-day non-hunting periods. During the 2002-03 winter, the elk-hunting season lasted for 76 continuous days in the months of December though February. Surveys of elk group size and distribution patterns were classified as occurring during or outside of these hunting seasons, treating the entire month of January in 2002 as a hunting season.

Mean snow depth at the East Madison Site was estimated at two-week intervals using a stratified cluster design (Thompson 2002) and three-day sampling sessions. Twenty primary sampling units were equally allocated among flat grassland, sagebrush steppe, grassland hills, and forested habitats during the 2002 winter, and re-allocated to minimize variance estimates during the 2002-03 winter. Within each primary unit, snow depth samples were taken 30 meters in each cardinal direction from the center of the unit. In each direction, two snow depth measures were taken approximately ten meters apart, for a total of eight secondary units per primary unit.

Model Development

Estimated wolf pack locations and the locations of all definite and probable wolf-killed ungulates were used to estimate spatial variation in wolf activity and hunting pressure at the East Madison Site. In ArcView software (Animal Movement Extension, Hooge and Eichenlaub 1997), we used a fixed-width kernel density estimator to estimate these patterns, employing least-squares cross validation to determine the kernel bandwidth for each winter season (Seaman and Powell 1996). We defined the wolf core activity and core hunting areas as the 50% isopleths of wolf pack locations and wolf-killed ungulate locations for each winter, respectively. Correspondingly, the wolf pack territories and wolf hunting areas for each winter were defined as the 95% isopleths of wolf locations and wolf kill sites. The location of each 1-km^2 survey unit surrounding wolf locations and in fixed areas was assigned an indicator variable representing different frequencies of wolf activity and wolf hunting pressure. If a survey was conducted within the 50% isopleth of wolf activity or wolf hunting pressure, it was classified as falling within the wolf core activity or hunting area. If a survey was conducted within the 50-95% isopleth of wolf activity or wolf hunting pressure, it was classified as falling within the wolf medium activity or hunting area. If a survey was conducted outside of the 95% isopleths of wolf activity or wolf hunting pressure, it was classified as falling within the infrequent wolf activity or hunting area.

Using estimated patterns of spatial variation in wolf activity and hunting pressure, and the estimated amount of time elapsed since wolf presence in each 1-km^2 survey unit, we developed nine *a priori* statistical models for the effects of wolf predation risk on elk group size and distribution (Table 1). Other authors have proposed that elk respond to spatial variation in wolf predation risk (Ripple et al. 2001, Beschta 2003). We represented this hypothesis using models with coefficients for spatial variation in either wolf activity or hunting pressure. Our list also includes models with coefficients representing elk responses to temporal variability in wolf predation risk and models with combinations of elk responses to spatial and temporal variability in wolf predation risk.

Table 1. Nine *a priori* hypotheses and corresponding statistical models of wolf effects on elk group sizes and distribution.

		Aspect of wolf ecology that generates spatial variation in predation risk		Component(s) of wolf predation risk incorporated into hypothesis		
Verbal hypothesis	Statistical model†‡	activity	successful hunting	Spatial	Temporal	Risk allocation
elk group sizes and distribution are influenced by spatial patterns in wolf activity (WACT)	Y = WACT	Yes	No	Yes	No	No
elk group sizes and distribution are influenced by spatial patterns in wolf hunting pressure (WHUNT)	Y = WHUNT	No	Yes	Yes	No	No
elk group sizes and distribution are influenced by wolf encounters and following safety periods (time since wolf presence in survey units = TIME)	Y = TIME	N/A	N/A	No	Yes	No
elk group sizes and distribution are influenced by spatial patterns in wolf activity and the amount of time since wolf presence in survey units	Y = WACT + TIME	Yes	No	Yes	Yes	No
elk group sizes and distribution are influenced by spatial patterns in wolf hunting pressure and the amount of time since wolf presence in survey units	Y = WHUNT + TIME	No	Yes	Yes	Yes	No
elk group sizes and distribution are influenced by the amount of time since wolf presence in survey units, and elk responses are more pronounced in areas with more wolf activity (WAC*TIME interactions)	Y = TIME + (WACT*TIME)	Yes	No	Yes	Yes	Yes

Table 1. Continued.

elk group sizes and distribution are influenced by the amount of time since wolf presence in survey units, and elk responses are more pronounced in areas with more wolf hunting pressure (WHUNT*TIME interactions)	Y = TIME + (WHUNT*TIME)	No	Yes	Yes	Yes	Yes
elk group sizes and distribution are influenced by spatial patterns in wolf activity and the amount of time since wolf presence in survey units, and elk responses are more pronounced in areas with more wolf activity	Y = WACT + TIME + (WACT*TIME)	Yes	No	Yes	Yes	Yes
elk group sizes and distribution are influenced by spatial patterns in wolf hunting pressure and the amount of time since wolf presence in survey units, and elk responses are more pronounced in areas with more wolf hunting pressure	Y = WHUNT + TIME + (WHUNT*TIME)	No	Yes	Yes	Yes	Yes

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† Response variable (Y) modeled with a log link for analyses of of elk group sizes and a logistic link for analyses of elk distribution patterns

‡ Both WACT and WHUNT contain three indicator variables describing the location of survey units in relation to infrequent, medium, and core wolf activity or hunting pressure areas

To develop *a priori* models representing risk allocation hypotheses, we noted that wolves tend to move throughout their winter ranges (Jedrzejewski et al. 2001), and their movement paths tend to continue in a particular direction (Bergman et al. in review). For elk located along wolf travel routes, this implies that encounters with wolves should bepreceded and followed by periods of safety. This is because wolves tend to enter and leave particular areas due to their directional movements. We also noted that the risk allocation hypothesis can be used to make predictions about the behavior of prey animals that are exposed to a background frequency of predation risk or prey animals that are not typically exposed to predation risk (Lima and Bednekoff 1999). Wolf presence is constant during winter at the East Madison Site and both wolves and elk (Turner et al. 1994, Messer 2003) move throughout their winter ranges. These two conditions imply that all elk wintering on the East Madison Site are exposed to wolf predation risk through encounters with wolves and/or movements into areas used by wolves. So, we assumed that our elk-wolf system could only provide information on the behavior of prey animals exposed to a background frequency of predation risk. Prey activity levels should be highest during pulses of safety in such situations (Sih and McCarthy 2002). This implies that changes in elk group sizes or distribution should occur during pulses of safety that ensue when wolves vacate encounter sites, coinciding with the time frame in which we conducted our surveys in 1-km^2 units surrounding wolf locations and in fixed areas. Because background frequencies of predation risk should be highest in wolf core activity or hunting areas, we based *a priori* models representing risk allocative hypotheses on the notion that elk responses when wolves vacate encounter sites should be amplified in wolf core activity or hunting areas.

In order to accurately evaluate *a priori* hypotheses of elk responses to wolf predation risk, we had to account for non-wolf-predation effects. Because we had no *a priori* hypotheses about how these non-wolf predation effects might act in concert with one another, we identified important non-wolf-predation predictor variables using a two-step exploratory model building exercise. For the first step, we used data from the West Madison Site to pare down our list of non-wolf-predation predictor variables. For these analyses, we divided predictor variables into four groups. These groups included predictors related to weather (season, temperature, and precipitation conditions), habitat (categorical habitat effect, a linear effect across flat grassland, sagebrush steppe, grassland hills, riparian forest, and montane forest habitat types, as well as a binomial measure of habitat openness), population size (current population sizes and the maximum population size for each winter), and time. The time group included mechanistic predictors (migration, which was represented by a curvilinear effect of month, and time of day) and predictors that tried to capture variability that was not explained by biologically-meaningful mechanisms (an individual survey effect, categorical and linear effects of months, and a year effect). Within each group, we constructed all possible additive linear subset models using elk group sizes as a response variable. We used the results of this analysis to identify predictors that likely influence both elk group sizes and distribution patterns in the presence of wolf predation risk at the East Madison Site. The available literature in which both group sizes and distribution patterns of ungulates were simultaneously considered identified the same predictors as influences on both measures of spatial concentrations (Vincent et al. 1995, Thirgood 1996, Borkowski 2000). For the second step, non-wolf-predation predictors identified as important in analyses of the West Madison Site data, as well as data on human elk-hunting and snow depth, were used in analyses of data collected at the East Madison Site. For these analyses, all possible additive linear subsets of this pared-down set of non-wolf-predation predictors were constructed, using both elk group sizes and elk distribution as response variables.

Model Fitting and Inferences

Linear regression was used to model natural-log transformed elk group sizes for both the West and East Madison Site data. Logistic regression was used to model the presence of elk groups in survey units as a measure of elk distribution at the East Madison Site. All models were fit and model diagnostics were checked using PROC GLM, PROC LOGISTIC, and PROC REG in SAS (SAS 1999) and/or the linear modeling and generalized linear modeling procedures in R (Dalgaard 2002).

For each group of West Madison Site predictors, AIC_c weight values were determined for each model, and these values were summed across models containing each individual predictor to determine its variable importance (VI) value (Burnham and Anderson 1998). We defined important non-wolf-predation predictors as those with VI ≥ 0.50. Because AIC_c weight values in a model selection analysis sum to one, this cutoff value signifies that, within each group, models containing important predictors garnered at least half of the support available in the data.

We made inferences based on models fit to the East Madison Site data in the following manner. First, we used model fit statistics and estimated coefficient values of non-wolf-predation models to determine the strongest non-wolf-predation influences on elk group sizes and distribution. We then combined the most supported non-wolf-predation effects with the nine *a priori* models of elk responses to wolf predation risk, with consideration taken to minimize the number of coefficients in the models relative to sample sizes. We used fit statistics and estimated coefficient values for these wolf models to delineate likely mechanisms of elk responses to wolf predation risk. To determine if wolves modify elk group sizes and distribution, we compared the fit and estimated coefficient values of well-supported wolf models to those of well-supported non-wolf-predation models.

For the East Madison Site data, the overall fit of elk group size models was assessed using R^2 values, and the overall fit of the most general model of elk distribution was assessed with the Hosmer-Lemeshow (H-L) goodness of fit test (Hosmer and Lemeshow 2000). If the most general model in a model comparison analysis is determined to fit the data, AIC-related model selection procedures will not provide support for a less general model that does not fit the data (Burnham and Anderson 1998). The relative fit of East Madison Site models was compared using ΔAIC_c and AIC_c weights. AIC_c weights were summed for all models containing particular variables and/or various statistical representations of a particular hypothesis. Because AIC_c weights sum to one within a model comparison analysis, these summed values represent the proportion of support in the data for each individual variable or hypothesis (Burnham and Anderson 1998).

RESULTS

We sampled 513 1-km^2 survey units around triangulated wolf pack locations and in fixed survey units at the East Madison Site, and 143 survey units contained elk groups. Based on the estimated locations of randomly placed VHF collars, our mean triangulation error was 0.44 km (SE= 0.065 km). If our triangulation error was zero km, the 1-km^2 survey units would result in an approximately 0.56 km distance in any direction from a triangulated location being sampled. Our mean triangulation error signifies that we actually conducted surveys in areas ranging from approximately 0 to 1 km away from triangulated wolf pack locations (i.e. the expected 0.56 km distance + 0.44 km).

Non-Wolf-Predation Effects

In total, 181 surveys were conducted and 1219 groups of elk were counted and mapped at the West Madison Site. Because the habitat and population size variable groups contained predictors with high collinearity, we constructed one-predictor models rather than all subset combinations to determine the VI of predictors within these groups. We identified seasons (VI= 0.58), temperature (VI= 0.90), habitat categories (VI= 1.0), population size (VI= 1.0), migration (VI= 0.66), time of day (VI= 0.64), and a year effect (VI= 0.61) as non-wolf-predation predictors to be considered along with human elk-hunting and snow depth in analyses of data collected at the East Madison Site. The year effect had little intrinsic biological significance, but suggested that different biological mechanisms operate in different years to affect elk spatial concentrations. We thus modeled elk group sizes and distribution patterns separately for the two years of data collected at the East Madison Site. Also, based on the 1.0 VI of habitat categories, and field observations, we hypothesized post-hoc that some non-wolf-predation predictors affect elk group size and distribution patterns differently in different habitat types. We therefore considered non-wolf-predation models with interactions among habitat type and human elk-hunting, snow depth, elk population size, and time of day, and all additive linear subsets of non-wolf-predation predictors, in analyses of East Madison Site data.

Three non-wolf-predation predictors showed marked variation between 2002 and 2002-03 at the East Madison Site. First, the different structure of the human elk-hunting season increased the known elk harvest from 86 elk in 2002 to 135 elk in 2002-03. Second, estimated elk population dynamics differed between the two winters. Estimated elk population totals ranged from 2700-5341 during the 2002 winter, with elk reaching peak numbers in early April. During the 2002-03 winter, estimated elk numbers ranged from 873-4939, with numbers peaking in late January. Third, while estimated mean snow depths were similar between the two winters at 11 cm and 14 cm, respectively, snow accumulation patterns differed. During the 2002 winter, mean snow depth estimates peaked in late January at 25 cm, and then slowly declined until spring meltout. During the 2002-03 winter, mean snow depth steadily increased until reaching a peak in early March at 23 cm, and then rapidly declined during the spring meltout period.

For the 2002 data, all non-wolf-predation models of elk group sizes that contained a habitat type effect had R^2 values >0.50 (Table 2a). The coefficient estimates in the most supported non-wolf-predation model also showed that elk groups were generally smaller during the human elk-hunting season and in the spring, and showed a convex pattern in relation to the early-mid-late winter period (following elk migratory patterns) (Table 2a). The most substantial effect in this model was habitat type, and every elk group size model that had an AIC_c weight >0.01 in 2002 included habitat type. On average, groups of elk were 135 times larger in flat grasslands than in forested areas during 2002 (Figure 1). For the 2002-03 data, the two most supported non-wolf-predation models of elk group sizes had R^2 values >0.35 (Table 2b). These models were separated by <1 AIC_c unit, indicating poor differentiation among the processes described by their coefficient estimates. The most supported non-wolf-predation model of elk group sizes for 2002-03 contained a poorly-estimated effect of snow depth on elk group sizes that differed between habitat types. In the flat grasslands, grassland hills, and sagebrush steppe habitats, the 95% CI's for the effects of snow depth on elk group sizes included values ranging from positive to negative over the range of estimated snow depths (1.9-23.4 cm). In forested areas, the 95% CI for the effect of increasing snow depth ranged from a 46% to a 290-fold decrease in elk group sizes. Based on the second most supported non-wolf-predation model of elk group sizes for the 2002-03 winter, human elk-hunting affected the sizes of elk groups in different habitats (Figure 1). This model also contained a poorly-estimated snow depth coefficient, with 95% CI's that included values ranging from positive to negative effects for the range of estimated snow depths.

The most parameterized model of elk distribution in 2002 contained 13 parameters and had questionable fit (H-L statistic= 14.46, df= 8, P= 0.07). Therefore, we used the H-L test to assess the overall fit of well-supported models for 2002. The common feature of all well-supported non-wolf-predation models in 2002 was an effect

Table 2. Model selection results for analyses of factors affecting elk group sizes at the East Madison Site during the 2002 (a) and 2002-03 (b) winters. The three top non-wolf-predation models and wolf models are shown for each winter.

a

				Within-suite comparison		Between-suite comparison	
	Model[†]	R^2	K[‡]	ΔAIC_c	w_i[¥]	ΔAIC_c	w_i[§]
non-wolf-predation suite	HAB + MIGR + SEAS + HHUNT	0.58	9	0.00	0.19	6.35	0.03
	HAB	0.51	5	1.47	0.09	7.83	0.01
	HAB + MIGR + HHUNT	0.55	8	1.52	0.09	7.87	0.01
wolf suite	HAB + WHUNT	0.58	7	0.00	0.66	0.00	0.68
	HAB + WHUNT + TIME	0.58	8	2.41	0.20	2.41	0.20
	HAB + WACT	0.56	7	4.70	0.06	4.70	0.06

b

non-wolf-predation suite	HAB + SD + (HAB*SD)	0.36	9	0.00	0.20	0.00	0.34
	HAB + HHUNT + (HAB*HHUNT) + SD	0.38	10	0.49	0.15	0.49	0.27
	HAB + SD	0.26	6	1.91	0.08	1.91	0.13
wolf suite	HAB + TIME + (WACT*TIME)	0.32	8	0.00	0.46	1.51	0.16
	HAB + WACT	0.27	7	2.05	0.16	3.55	0.06
	HAB + TIME	0.33	6	3.22	0.09	4.73	0.03

[†] HAB = habitat type; MIGR = elk migration; SEAS = season; HHUNT = human elk-hunting season; SD = mean snow depth; TIME = time since wolf presence; WACT = wolf activity level; WHUNT = wolf hunting pressure level

[‡] number of model parameters

[¥] AIC_c weights for within-suite comparisons of all models considered during each year

[§] AIC_c weights for between-suite comparisons of the three top models within each suite for each year

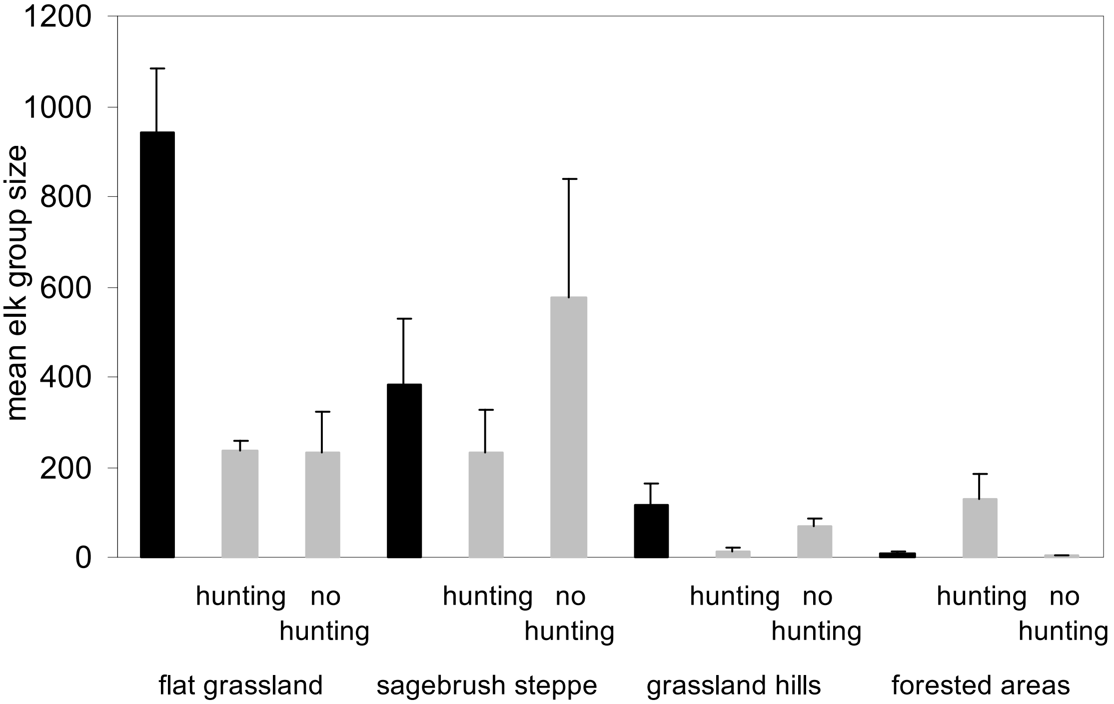

Figure 1. Effect of habitat type on elk group sizes at the East Madison Site during the 2002 winter (black bars), and the effects of habitat type and human elk-hunting on elk group sizes during the 2002-03 winter (gray bars). Error bars represent 1 SE.

of habitat type (Table 3a). Based on the most supported model, which had adequate fit (H-L statistic=0.01, df= 2, P= 0.99), the estimated probability of elk presence in survey units was highest in the grassland hills (0.35, 95%CI= 0.25-0.46) and flat grassland (0.29, 95% CI=0.20-0.39) habitats, and lowest in the forested (0.17, 95% CI= 0.07-0.32) and sagebrush steppe (0.13, 95% CI= 0.06-0.24) habitats. For the 2002-03 data, the most general model of elk distribution contained 15 parameters and had adequate fit (H-L statistic= 4.82, df= 8, P= 0.78). For this winter, a model containing snow depth and a habitat type effect that interacted with human elk-hunting was clearly the most supported non-wolf-predation model (Table 3b). Outside of the human elk-hunting season, the

Table 3. Model selection results for analyses of factors affecting elk distribution at the East Madison Site during the 2002 (a) and 2002-03 (b) winters. The three top non-wolf-predation models and wolf models are shown for each winter.

a

			Within-suite comparison		Between-suite comparison	
	Model[†]	K[‡]	ΔAIC_c	w_i[¥]	ΔAIC_c	w_i[§]
non-wolf-predation suite	HAB	5	0.00	0.24	8.86	0.01
	HAB + TOD + TEMP + SEAS + SD	9	1.31	0.12	10.17	0.00
	HAB + POP + (HAB*POP)	9	2.24	0.08	11.10	0.00
wolf suite	HAB + WHUNT + TIME + (WHUNT*TIME)	10	0.00	0.32	0.00	0.44
	HAB + TIME + (WHUNT*TIME)	8	0.90	0.20	0.90	0.28
	HAB + WACT	7	1.05	0.19	1.05	0.26

b

non-wolf-predation suite	HAB + HHUNT + (HAB*HHUNT) + SD	10	0.00	0.82	0.00	0.43
	HAB + HHUNT + (HAB*HHUNT)	9	4.12	0.10	4.12	0.05
	MIGR + POP	5	5.58	0.05	5.58	0.03
wolf suite	HAB + HHUNT + (HAB*HHUNT) + SD + TIME + (WHUNT*TIME)	13	0.00	0.40	0.82	0.28
	HAB + HHUNT + (HAB*HHUNT) + SD + TIME	11	0.94	0.25	2.14	0.15
	HAB + HHUNT + (HAB*HHUNT) + SD + WHUNT	12	2.85	0.09	3.69	0.07

[†] HAB = habitat type; TOD = time of day; TEMP = temperature; SEAS = season; SD = mean snow depth; POP = elk population size; HHUNT = human elk-hunting season; MIGR = elk migration; WHUNT = wolf hunting pressure level; TIME = time since wolf presence; WACT = wolf activity level

[‡] number of model parameters

[¥] AIC_c weights for within-suite comparisons of all models considered during each year

[§] AIC_c weights for between-suite comparisons of the three top models within each suite for each year coefficient estimates for the effects of habitat type on elk distribution were almost identical to the pattern observed in 2002, with the exception of a poorly estimated snow depth coefficient. Over the range of estimated snow depths, estimates for the effect of snow depth on the probability of elk presence in survey units had 95% CI's spanning positive and negative values in each habitat type. During the human elk-hunting season, the coefficient estimates for the effect of habitat type in this model changed. The estimated probability of elk presence in survey units became highest in forested areas (0.30, 95% CI = 0.16-0.49) and sagebrush steppe (0.17, 95% CI = 0.09-0.31), and lowest in grassland hills (0.08, 95% CI = 0.02-0.29) and flat grasslands (0.07, 95% CI = 0.02-0.24).

In summary, habitat type was the most important non-wolf-predation influence on elk group sizes during both 2002 and 2002-03 at the East Madison Site (Figure 1). Snow depth may have influenced elk group sizes during 2002-03, but snow depth coefficients were poorly estimated. Human elk-hunting had a well-supported effect on the sizes of elk groups in different habitat types during the 2002-03 winter (Figure 1). However, sample sizes for analyses of factors affecting elk group sizes were limited to 73 and 70 groups of elk observed in survey units in 2002 and 2002-03, respectively. We thus chose to analyze wolf effects on elk group sizes by building *a priori* models into the effect of habitat type for both winters. A habitat type effect was contained in every well-supported non-wolf-predation model of elk group sizes during 2002 and 2002-03 (Table 2) (Figure 1). We felt that this approach would maximize the amount of data available to estimate coefficients representing wolf effects after accounting for non-wolf-predation effects.

Habitat type also had a strong influence on elk distribution during 2002 and 2002-03. During 2002-03, human elk-hunting affected the distribution of elk in different habitat types as well. Snow depth may have affected elk distribution in 2002-03, but snow depth coefficients were poorly estimated. We felt that there was ample data available to estimate both wolf effect and non-wolf-predation effect coefficients in the same models of elk distribution (253 survey units for 2002 and 260 survey units in 2002-03). We thus conducted analyses of wolf effects on elk distribution by building *a priori* models into the most supported non-wolf-predation models for each winter.

Wolf Predation Risk

We triangulated 267 wolf pack locations and found 23 definite and probable wolf kills during 2002, and we triangulated 301 locations and found 54 wolf kills during 2002-03. Based on estimation methods described elsewhere (Borkowski et al. in review), the wolf kills that we located represented approximately 70% of all kills made by wolves during each winter. Elk constituted 80% of these kills, indicating that wolf predation was focused on elk. Patterns of spatial variation in wolf activity were similar during the two winters (Figure 2). Patterns of spatial variation in wolf hunting pressure differed substantially between the two winters (Figure 2). Spatial variation in wolf hunting pressure also differed noticeably from spatial variation in wolf activity during both winters.

For the 2002 data, wolf models of elk group sizes were the most supported models overall (Table 2a). However, the most supported wolf model was the only wolf

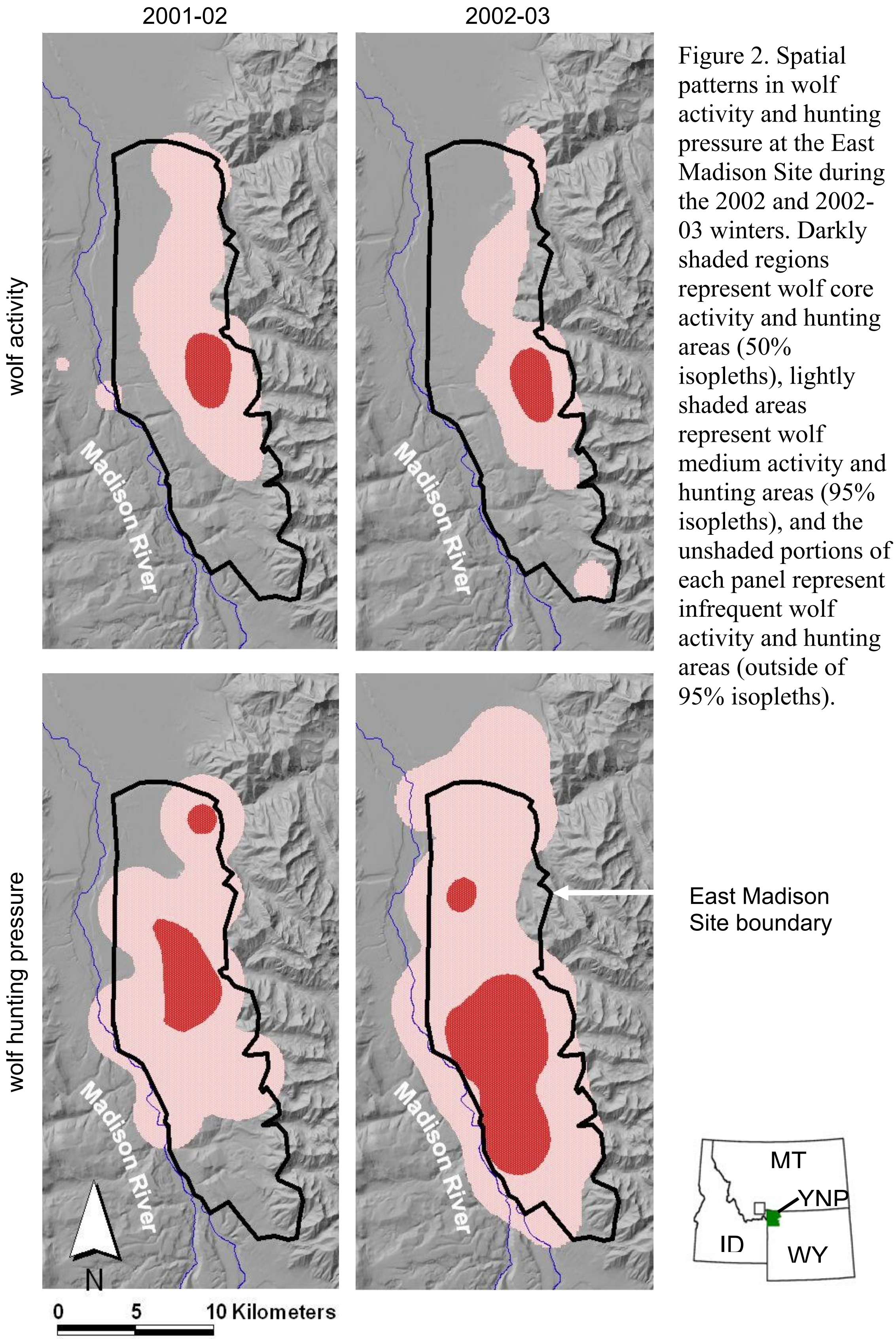

Figure 2. Spatial patterns in wolf activity and hunting pressure at the East Madison Site during the 2002 and 2002-03 winters. Darkly shaded regions represent wolf core activity and hunting areas (50% isopleths), lightly shaded areas represent wolf medium activity and hunting areas (95% isopleths), and the unshaded portions of each panel represent infrequent wolf activity and hunting areas (outside of 95% isopleths).

model for 2002 that contained at least one estimated wolf effect coefficient with a 95% CI that did not span zero. This model ostensibly included an elk response to spatial variation in wolf hunting pressure, after accounting for the effect of habitat type on elk group sizes. Estimated coefficients for this model revealed that elk groups present in survey units falling within the wolf medium hunting area were 7.4 times larger than elk groups observed in the wolf infrequent hunting area and 2.1 times larger than elk groups observed in the wolf core hunting area. This pattern is not easily explainable with a simple biological mechanism, and could indicate that the effects of spatial variation in wolf hunting pressure were confounded with other, unaccounted for influences on elk group sizes. Further, this model resulted in a <1 unit increase in R^2 from the most supported non-wolf-predation model (Table 2a). For the 2002-03 data, wolf models of elk group sizes were not as well supported as non-wolf-predation models (Table 2b). All wolf models for this year also contained estimated wolf effect coefficients with 95% CI's that spanned zero, and did not improve R^2 values from the most supported non-wolf-predation models. We therefore had little evidence that wolf predation risk influenced elk group sizes in either 2002 or 2002-03.

For the 2002 data, the two most supported wolf models of elk distribution obtained over 50% of the support in the data when compared to non-wolf-predation models (Table 3a). Both of these models had adequate fit (H-L statistics= 9.92 and 1.90, df= 8 and 8, and P= 0.27 and 0.98, respectively), and they both contained a risk allocative effect of wolf hunting pressure on elk distribution, after accounting for elk preferences for grassland hill and flat grassland habitats. Coefficient estimates revealed a pattern of elk vacating survey units as time since wolf presence in survey units increased. This pattern was amplified in the wolf core hunting area, consistent with the risk allocation hypothesis (Figure 3). The most supported of these models contained a larger estimated intercept value for the core wolf hunting area, indicating a high probability of elk presence close in time to wolf presence in survey units falling within that area (Figure 3). For the 2002-03 data, the most supported wolf model of elk distribution was separated from the most supported non-wolf-predation model by <1 ΔAIC_c unit, indicating similar support for both models (Table 3b). The coefficient estimates for this model suggested a risk allocative elk distributional response to spatial variation in wolf hunting pressure, similar to that observed in 2002 (Figure 4). Therefore, both the 2002 and 2002-03 data provided support for a risk allocative elk distributional response to spatial variation in wolf hunting pressure.

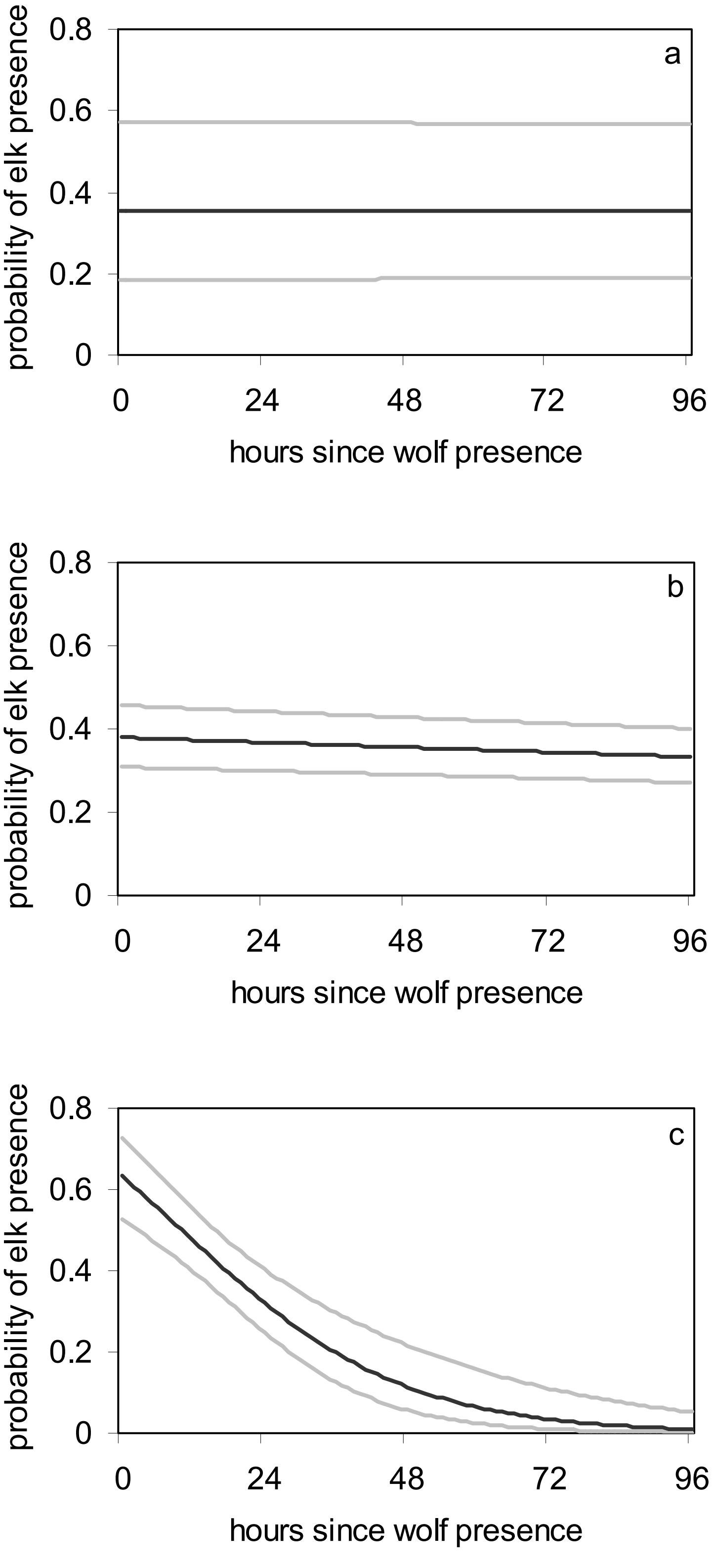

Figure 3. The effect of wolves on elk distribution in the grassland hills, as depicted by the most supported wolf model of elk distribution during 2002 ($\ln\left[\frac{\Pr(\text{elkpresence})}{1-\Pr(\text{elkpresence})}\right]$ = HAB + WHUNT + TIME + (WHUNT* TIME), see Table 1 for variable definitions). The estimated probabilities of elk presence in survey units in wolf infrequent (a), medium (b), and core (c) hunting areas +/- 1 SE are shown. Based on this model, intercept terms are adjusted for other habitat types, but the slope terms are the same for all habitats.

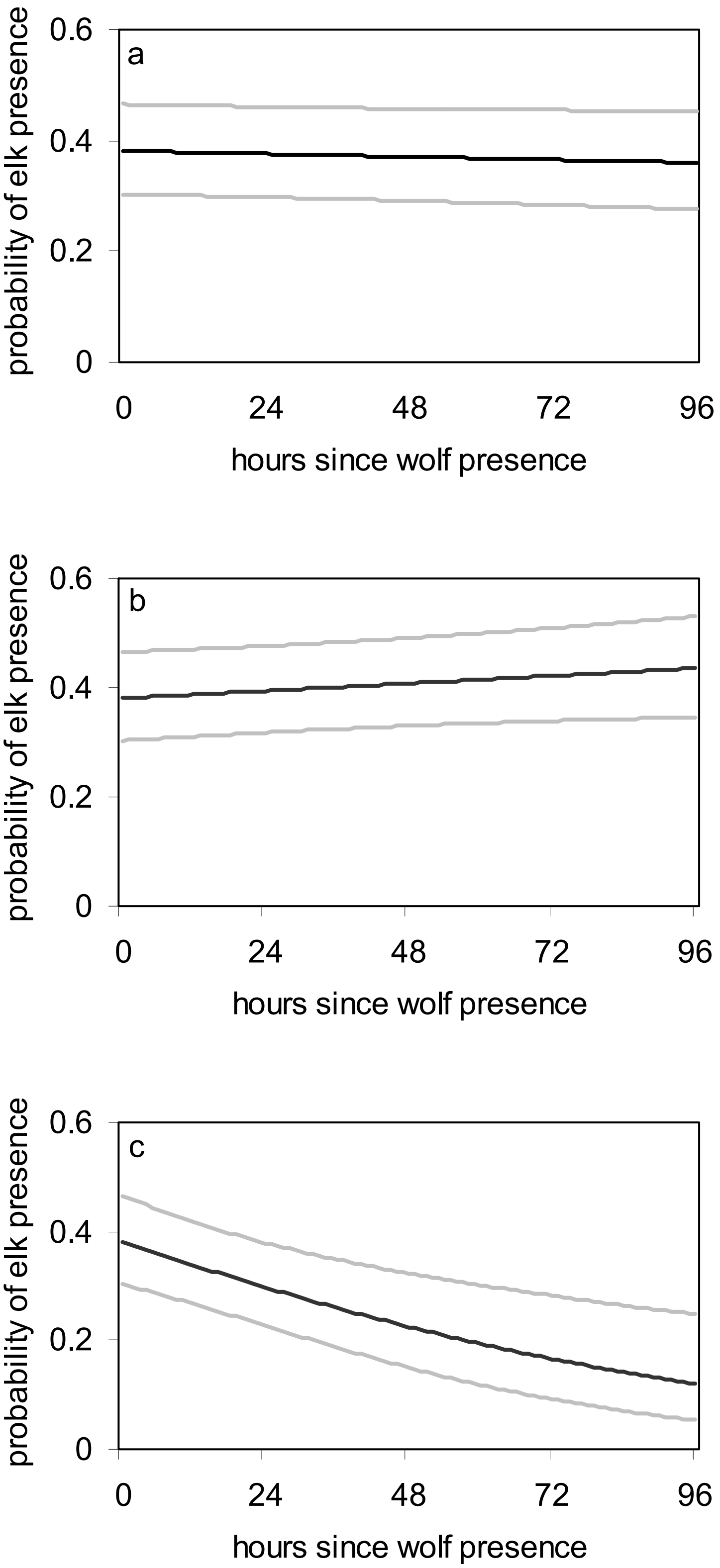

Figure 4. The effect of wolves on elk distribution in the grassland hills outside of the human elk-hunting season, as depicted by the most supported wolf model of elk distribution during 2002-03 ($\ln\left[\frac{\Pr(\text{elkpresence})}{1-\Pr(\text{elkpresence})}\right]$ = HAB + HHUNT + (HAB* HHUNT) + SD + TIME + (WHUNT* TIME), see Table 1 for variable definitions). The estimated probabilities of elk presence in survey units in wolf infrequent (a), medium (b), and core (c) hunting areas +/- 1 SE are shown for the mean snow depth observed in 2002-03 (14 cm). Based on this model, intercept terms are adjusted for other habitat types and the human elk-hunting season. The slope terms are the same for all habitats and both during and outside of the human elk-hunting season.

DISCUSSION

The effects of ungulate behavior on plant communities are currently not understood well enough to be incorporated into models of grazing ecosystems (Hobbs 1996). Ungulate behavioral responses to predation risk constitute a particular knowledge gap that precludes incorporating ungulate behavior into such models (Augustine and McNaughton 1998). In GYE elk-wolf systems, this issue is one of the most important and least understood impacts of the recent gray wolf reintroduction (Smith et al. 2003). In these analyses we evaluated several hypotheses of elk behavioral responses to wolf predation risk in a GYE system, and we evaluated these hypotheses in the context of other influences on elk behavior. Our analyses include an empirical evaluation of the risk allocation hypothesis in a natural system. To our knowledge, all previous empirical evaluations of this hypothesis were conducted using laboratory microcosms (Hamilton and Heithaus 2001, Sih and McCarthy 2002, Van Buskirk et al. 2002, Koivisto and Pusenius 2003, Pecor and Hazlett 2003). The elk behaviors that we focused on, group sizes and distribution, are related to elk impacts on plant communities because together they define elk spatial concentrations. Below, we summarize mechanisms of elk behavioral responses to wolf predation risk to generate hypotheses concerning the behaviorally-mediated effects of wolves on plant communities.

It appeared that wolves had little effect on the sizes of elk groups at the East Madison Site. Due to limited sample sizes for elk group size analyses, however, we may not have been able to detect smaller wolf effects. The dominant non-wolf-predation effects on elk group sizes were habitat type and human elk-hunting. During the 2002 winter, elk groups were larger in flat grasslands than in any other habitat type (Figure 1). We believe that this trend does not necessarily represent an elk response to higher perceived predation risk in open habitats, as others have hypothesized (Leuthold 1977, Geist 2002). Elk groups were smaller in other habitats with high visibility during 2002, such as sagebrush steppe and grassland hills (Figure 1). Further, elk groups were generally larger in these habitats outside of the human elk-hunting season in 2002-03 (Figure 1), when predation risk from humans was reduced. Other processes might also influence this trend. For example, spatial concentrations in ungulates often track the available forage biomass (Frank et al. 1998), and the diet of elk during winter consists primarily of grasses (DelGiudice et al. 2001). Due to clumped woody vegetation, patches of grass are smaller in forested and sagebrush steppe habitats than in flat grasslands. Also, deep snow accumulations and snow drifts limit the size of grass patches in the grassland hills, forested areas, and sagebrush steppe habitats during winter. In flat grasslands, wind tends to remove snow to expose relatively large patches of grass. We argue that flat grasslands contain higher forage biomass and provide better access to forage that other habitat types, and are therefore able to support larger elk groups during winter.

During the 2002-03 winter, the change in structure and magnitude of the human elk-hunting season had a well-supported effect on elk group sizes in different habitat types (Table 2b) (Figure 1). We speculate that this pattern can be explained in part by the proximity of these habitat types to roads and consequently hunter access and activity. Road access is correlated with the vulnerability of elk to hunting mortality

(McCorquodale et al. 2003), and elk often select areas further from roads during hunting seasons (Unsworth et al. 1998). Grassland hills and flat grasslands are immediately adjacent to roads throughout the East Madison Site, and high visibility in these habitat types makes large elk groups conspicuous and prone to human hunting pressure. When the human elk-hunting season was liberalized in 2002-03, elk groups were on average two times smaller in grassland hills and four times smaller in flat grasslands than elk groups observed in the same habitats in 2002 (Figure 1). Forested areas and sagebrush steppe are typically further from roads and hunter access points in the East Madison Site. The larger elk groups observed in forested areas during the hunting season might represent large elk groups from flat grassland and grassland hill habitats seeking refuge from human hunting pressure. While it appeared that elk groups were smaller in the sagebrush steppe habitat during the hunting season, this difference was not well estimated due to high variability in elk group sizes (Figure 1). Large groups of elk also may have split up upon entering sagebrush steppe habitat, as the probability of elk group observations in both forested area and sagebrush steppe survey units increased during the human elk-hunting season in 2002-03. Similar habitat use shifts to areas less accessible to hunters have also been reported in other areas (Millspaugh et al. 2000, Conner et al. 2001, Vieira et al. 2003).

We hypothesize that declines in human hunting pressure lead to elk distributional responses that occur over even shorter time scales than we deciphered here. This could explain the lack of an elk distributional response to human elk-hunting in our 2002 data. Elk may have responded to human hunters during the 4-day hunting periods in 2002, but changes in elk distribution during the 3-day non-hunting (safety) periods would make such a response difficult to detect. Because we did not anticipate the change in the structure of the human elk-hunting season in 2002-03, we did not structure data collection during 2002 in a manner that would highlight such a response. We also suspect that elk may respond to decreases in hunting pressure from humans with changes in distribution during the nighttime hours, but our focus on data collection during the daylight hours prevented us from detecting such an effect. These hypothesized elk responses to human hunting pressure follow predictions of risk allocation theory for areas with a background frequency of predation risk, in that they occur during periods of safety. We do note that mechanisms of elk responses to human hunting pressure may differ from responses to wolf hunting pressure, because wolves are more mobile and are not as limited by access points and roads. This difference is represented in the results of our analyses. We uncovered evidence that elk avoided habitats adjacent to roads during the human elk-hunting season. Conversely, we had little evidence that elk avoided portions of the East Madison Site with frequent wolf activity or hunting pressure.

Despite a large effect of human hunting on elk distribution in 2002-03, the data provided support for a wolf model after accounting for elk responses to humans (Table 3b). The wolf effect coefficients in this model indicate that elk likely responded to spatial variation in wolf hunting pressure with risk allocative changes in distribution (Figure 4). This effect was similar to the well-supported wolf effect on elk distribution in 2002 (Figure 3). The general pattern during both winters was that elk eventually, but not immediately, leave wolf encounter sites in the wolf core hunting area. Wolves are coursing predators that hunt by inducing movement in prey animals (Mech 1970). Immediate movement away from wolf encounter sites might be dangerous for elk, and it is often difficult for prey to determine if predators have left an area (Sih 1992). Wolves have well-developed spatial memories and learning abilities (Mech 1970). Failing to leave wolf encounter sites might be dangerous for elk because wolves might return to hunt again. Research in other systems has shown that wolves do return to different portions of their territories at periodic intervals (Jedrzejewski et al. 2001). Remaining on the move makes exact locations less predictable, which is a successful strategy for prey that live in herds to abate predation risk from mobile predators with spatial memories (Mitchell and Lima 2002). A dynamic elk distributional response to wolf encounters may have been profitable in the wolf core hunting area, where encounters with wolves were the most dangerous. The risk of fatal wolf encounters for elk was reduced in the medium and infrequent hunting areas, perhaps negating the need for such repeated elk movements.

Wolves also may seek out groups of elk in their core hunting area. This is indicated by the larger intercept value for the core hunting area in 2001-02 (Figure 3), which portrays a high probability of elk presence close in time to wolf presence in survey units falling within that area. In fact, if the 1 km^2 units that we sampled close in time to wolf presence in the core hunting area were located in areas frequented by elk, while units sampled farther in time from wolf presence were not, a pattern similar to that observed in this study would emerge, regardless of elk responses to wolf predation risk (Figure 3) (Figure 4). However, both the area covered by the 1 km^2 units that we sampled close in time to wolf presence and the area covered by the units that we sampled farther in time from wolf presence blanketed the wolf core hunting area during both 2002 and 2002-03. It is therefore unlikely that wolf movements alone can explain the pattern we observed in the data. An elk distributional response following wolf encounters in the core hunting area is likely the major factor driving the observed pattern.

This likely elk response to wolf encounters was amplified in areas with elevated wolf hunting pressure, not wolf activity. This implies that elk have the ability to discern areas with high predation pressure from areas with frequent predator activity. The logic of this finding is corroborated by observations of elk spatial avoidance of roads and other hunter access points during hunting seasons, but not outside of hunting seasons (Unsworth et al. 1998), as well as elk responses to human activity on refuges. In refuges with no hunting and significant human activity, even elk that are hunted by humans during certain seasons do not avoid human activity or roads (Wolfe et al. 2002). After the end of the human elk-hunting season in 2003 during this study, elk used habitats that were dangerous during the hunting season, despite the presence of a number of year-round human residents.

In terms of mechanisms of behaviorally-mediated wolf effects on plant communities, wolves likely created a more even spread of ungulate foraging in their core hunting area by making elk distribution more dynamic. This response should decrease the amount of time that elk groups spend at any one foraging site. The implications for this mechanism might not be uniform across the wolf core hunting area because the reported impacts of ungulate foraging on plant communities in the GYE differ between grassland

and woody community types (Singer et al. 2003). During both winters in which we detected evidence of this mechanism, wolf core hunting areas were large (21 km^2 in 2002 and 56 km^2 in 2002-03) and contained all four major habitat types. During both 2002 and 2002-03, the core hunting area was dominated by flat grassland and grassland hills (81% and 68% during the two winters, respectively). All forested areas constituted 13% and 17% of the core hunting areas in the two winters, and riparian forests constituted 5% and 11% of the core hunting areas. Sagebrush steppe made up 6% and 15% of the core hunting areas in 2002 and 2002-03, respectively.

The impacts of ungulate winter grazing in GYE grassland communities include increases in aboveground annual net primary productivity (ANPP), belowground ANPP, nitrogen cycling rates, and spatial variation in nitrogen concentration (Frank 1998, Augustine and Frank 2001, Frank et al. 2002, Singer et al. 2003). These effects are due primarily to impacts associated with foraging pressure, such as hoof action, release of shading competition, and fertilizer deposition (Frank 1998, Frank et al 2002, Singer et al. 2003). We hypothesize that the major effect of a more dynamic elk distribution in wolf core hunting areas in grassland habitats will lie with the spatial dilution of these foraging-related impacts. This should decrease heterogeneity in ungulate effects on grasslands in some areas in the GYE, making ungulate impacts more uniform spatially.

The impacts of ungulate winter browsing on woody plant communities reported in the GYE, including low-elevation sagebrush steppe, riparian and other wetland deciduous forests, and aspen (*Populus tremuloides*) stands, consist of decreased plant density and height, decreases in recruitment, and decreases in stand size (NRC 2002, Beschta 2003, Singer et al. 2003). These effects are due primarily to excessive browsing pressure (Singer et al. 2003). We hypothesize that the impact of a more dynamic elk distribution in wolf core hunting areas in these habitat types will lie with a more even spread of browsing pressure and thus decreased pressure in heavily browsed stands. Such a mechanism should alleviate the effects of ungulate browsing on woody plants in some heavily-browsed areas, a hypothesis that is consistent with recent observations in some deciduous tree stands in the GYE (Ripple et al. 2001, Beschta 2003, Smith et al. 2003).

Many factors other than ungulate foraging pressure influence the dynamics of plant communities in the GYE (Singer et al. 1998). The potential effects of wolves on plant communities therefore will not occur in isolation, and our hypotheses for the potential behaviorally-mediated effects of wolves are accompanied by four major caveats. First, human hunters showed a marked ability to provide a top-down influence on elk spatial concentrations under the more liberal hunting season structure observed in 2002-03. Human elk-hunting occurs on the majority of elk winter ranges in the GYE (Singer 1991). The magnitude of behaviorally-mediated wolf impacts on plant communities will likely be influenced by human hunters on elk winter ranges, depending on season and harvest structures. Second, the East Madison Site, like most elk winter ranges in the GYE, is used for cattle grazing during the summer months. The effects of ungulates on plant communities described above depend largely on seasonal rest from ungulate foraging (Frank 1998). When ungulates and cattle share the same range in different seasons, the effects of wild ungulate foraging can be more substantial and different (Hobbs et al. 1996). The impact of behaviorally-mediated wolf effects on plant communities will therefore likely also depend on summer cattle grazing regimes. Third, the density of wolves observed in this study was low and the density of elk was high for the GYE region. The behaviorally-mediated trophic effects of predators can differ over ranges of both predator and prey densities (Werner and Peacor 2003). Behaviorally-mediated wolf impacts on plant communities in the GYE might differ across space and time with predator and prey densities. Lastly, we expect the behavioral responses of elk to wolf predation risk to differ in general across the GYE. Elk winter ranges occur in vastly different landscapes in the GYE, and we suspect that successful strategies for elk on one winter range may not apply on all winter ranges, regardless of animal densities.

Using mechanisms of predator-prey behavioral interactions to make predictions about trophic dynamics is the first step towards developing biologically sound models of ecosystems that incorporate animal behavior (Werner and Peacor 2003). Continued research will permit the evaluation of the hypotheses generated in this paper. In any case, our research program provides support for the notion that behaviorally-mediated indirect interactions can be important in ecosystem dynamics, perhaps even more important than demographic interactions in some cases (Peacor and Werner 2001, Schmitz et al. 2004). We uncovered elk behavioral responses to wolf predation risk, but the demographic impacts of wolves on the elk population at the East Madison Site have been minute (J. A. Gude and R. A. Garrott unpublished data). Under this scenario, any indirect effects of wolves on plant communities that are elucidated in future research in this system will result from predator-prey behavioral interactions. This highlights the need to understand animal behavioral interactions across landscapes (Lima and Zollner 1996). In systems like the GYE where large mammals are abundant and natural resource management is often contentious and scrutinized by the public, such knowledge will be invaluable in the development of effective management strategies.

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