GOOD ANIMALS IN BAD PLACES: EVALUATING LANDSCAPE ATTRIBUTES ASSOCIATED WITH ELK VULNERABILITY TO WOLF PREDATION

by

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ABSTRACT

Vulnerability of prey to predators is heavily influenced by their respective physical and behavioral characteristics; however their interactions with landscape, and climate, collectively termed "environmental vulnerability," may also assume considerable importance. Landscape or habitat-dependent prey vulnerability is well-studied in smaller taxa systems where environmental factors primarily influence encounter rates, however the impact of environmental vulnerability in large mammal systems, where the probability of a successful attack may be more important than encounter probability, is poorly understood. This study utilized 18 years of survival and mortality data for radio-collared elk (*Cervus elaphus*), in concert with abundance, distribution, and habitat use data prior to and following restoration of wolves (*Canis lupus*) to Yellowstone National Park to evaluate the relationship between environmental vulnerability and elk mortality. Logistic regression was used to model the odds of mortality for 108 elk in 1257 animal sample intervals from 1991-2009 across a range of environmental conditions and gradients of wolf predation risk to evaluate: 1) The relationship between landscape, habitat, and environmental attributes and elk vulnerability to wolf predation and 2) Changes in the attributes related to elk mortality before and after wolf colonization. In the absence of wolf predation, mortality risk for elk was primarily associated with physical attributes of elk due to age and condition, factors that are known to influence starvation mortality. Following wolf reintroduction mortality risk was related to these elk physical characteristics, but more so to characteristics of the landscape and climate within an animal's home range. These apparent environmental influences were strong enough to result in substantial changes in distribution and abundance of elk in the study system to the extent that by the end of the study elk almost exclusively utilized areas with high probability of wolf encounter, but also a high probability of escape due to the collective characteristics of the landscape promoting predation refuges. The strong influence of environmental vulnerability is likely to affect the abundance and distribution of elk and wolves across their range, and has broad applications to large mammal predator-prey dynamics in general.

INTRODUCTION

Predation is one of the fundamental interactions in nature that shapes communities and ecosystems through an array of direct and indirect effects on species (Kerfoot and Sih 1987, Abrams et al. 1996, Schmitz 1998, Preisser et al. 2005). Prey abundance and encounter rates strongly affect prey selection (Holling 1959), however a growing body of evidence indicates that the vulnerability of detected prey also influences the outcome of a predation attempt (Quinn et al. 2004, Caro 2005). Once encountered, vulnerability is influenced in part by individual differences in life history characteristics, sex, age, condition and behavior (Stephen and Krebs 1986), and thus is fundamental to the outcome of a predation event (Quinn et al. 2004, Caro 2005). In its most basic sense, vulnerability can be defined as susceptibility to getting killed, and in general can be categorized as physical, behavioral, or environmental vulnerability (Garrott et al. 2009a).

Vulnerability is typically considered in the physical context, where an animal's susceptibility is determined by such factors as species, age, size, sex, morphology, speed, body condition, and other variables relating to its physical state (Peckarsky 1984, Stephen and Krebs 1986, Sih 1987, Sinclair et al. 2003). Such a composite of factors relates to the doomed surplus idea behind compensatory mortality because large predators tend to select physically substandard individuals (Errington 1946, 1967) to reduce risk of injury or death from dangerous and physically larger prey (Mech and Peterson 2003, Smith et al. 2003, MacNulty et al. 2007, Garrott et al. 2007). In addition, how prey respond to the risk of predation is influenced by an array of potential behavioral responses such as vigilance, grouping, aggression, flight, the use of escape terrain, and migration or

dispersal, and whether they have physical defenses such antlers or horns (Stephen and Krebs 1986, Lima and Dill 1990, Caro 2005). Furthermore, both physical and behavioral attributes can interact, and vary fundamentally within and across species, sexes, individuals, and age classes (Fitzgibbon and Lazarus 1995).

While physical and behavioral characteristics are the best described factors affecting vulnerability, not all prey are substandard due to physical and behavioral attributes alone (Temple 1987). Various environmental factors can also influence vulnerability, and a rich literature demonstrates that predator-prey interactions can be dramatically influenced by habitat complexity (Grabowski and Powers 2004, Panzacchiet et al. 2009), landscape characteristics, (Lewis and Eby 2002, Hopcraft et al. 2005, Knapp et al. 2010), and environmental conditions such as light, temperature, turbidity, and snow pack (Christian and Tracy 1981, Clarke 1983, Gregory and Levings 1998). Such environmental factors can affect a predator's temporal and spatial patterns of foraging (Laundré and Hernández 2003, Hebblewhite et al. 2005, Bergman et al. 2006, Andruskiw et al. 2008, Schauber et al. 2009) and predation success such that landscape heterogeneity may result in certain attributes of the landscape serving as an effective prey refuge, whereas other areas may render prey more or less vulnerable to predation (Lima 1992, Lewis and Eby 2002, Hebblewhite et al. 2005, Knapp et al. 2010). Furthermore, the degree to which habitat complexity and landscape and environmental variables affect prey vulnerability likely depends on the hunting mode of the predator (Atwood et al. 2009), with the outcome of a predation attempt for a cursorial predator depending heavily on the type of terrain through which the pursuit takes place (Gorini et al. 2011).

Collectively, the interactions between landscape and climate variables and the behavioral and physical vulnerability of a prey individual define what we collectively term environmental vulnerability (Garrott et al. 2009a), and can also have significant effects on predator-prey dynamics and species persistence (Garrott et al. 2009b,c). The degree to which environmental vulnerability affects predator-prey dynamics likely differs on a site-specific basis, depending on the predator and prey assemblage and the characteristics of the environment (Hopcraft et al. 2005, Garrott et al. 2009a). The stability and persistence of predator-prey systems can then depend on variation in predation rates and prey vulnerability caused by landscape heterogeneity (Kareiva and Wennegren, 1995, Ellner et al. 2001) and the presence of prey refugia (Ruxton 1995, Berryman and Hawkins 2006). Thus, knowledge of how landscape and habitat features affect prey vulnerability and survival is critical to understanding predator-prey dynamics, and for implementing sound management and conservation strategies for populations and communities (Schauber et al. 2009). This can be important because in some places, the interactions of behavioral and physical vulnerability with characteristics of the environment may cause mortality that is additive by creating traps on the landscape for what could be considered otherwise healthy animals - the good animals in bad places concept (Garrott et al. 2009a,b,c).

Understanding the role of environmental vulnerability in predator-prey dynamics of natural systems is challenging, and the majority of our knowledge of predator-prey dynamics comes from tractable systems of smaller taxa, where encounter rates are of primary importance and environmental factors primarily influence probability of detection (e.g. Stoner 2009). Studies of large mammal systems are lacking in this regard

and often hindered by ethical, financial, and logistical constraints imposed by the large scale of such investigations. However, such studies have the potential to yield significant insights given the substantial differences in life history characteristics and behavior between large predators and their prey and those from smaller taxa systems (Hobbs 1996, Garrott et al. 2007). For example, in aquatic systems, predator foraging generally varies inversely with habitat heterogeneity and prey often seek refuge in complex habitats where predation risk is lower, mainly due to lower encounter rates due to obstructive cover (Beukers and Jones 1997, Lewis and Eby 2002). Also, unlike systems of smaller taxa where prey typically rely on avoiding detection, large mammal systems differ in that prey species are often large, formidable, and exhibit a diverse array of defenses and behaviors once encountered (Carbyn et al. 1993, Garrott et al. 2007, MacNulty et al. 2007, Becker et al. 2009a). Furthermore, large intelligent predators with spatial memory often select for areas of high environmental vulnerability over areas of high prey density (Hopcraft et al. 2005, Bergman et al. 2006).

Consideration of environmental vulnerability is particularly important before restoring top carnivores to their historic ranges, especially when there are concerns that reintroduced predators will dramatically reduce prey populations (Treves and Karanth 2003). For example, in systems where certain native predators have been extirpated for generations, it is not known how site specific variables might affect the degree to which environmental vulnerability contributes to additive mortality of prey once the predators are restored (Garrott et al. 2009a). An excellent example of this concept is wolf reintroduction to Yellowstone National Park and central Idaho during 1995 through 1997. Though this restoration is considered one of the greatest conservation successes in the

last century (Smith et al. 2003), it is not without controversy. The abundance of elk, the primary prey of restored wolves (Becker et al. 2009a), decreased significantly following wolf restoration and these decreases were most pronounced (60-90%) in high elevation, deep snow environments such as Yellowstone National Park (Eberhardt et al. 2007, Garrott et al. 2009c, Hamlin et al. 2009). Several studies have explicitly linked variation in predation risk to habitat and landscape attributes in wolf-ungulate systems (Kunkel and Pletscher 2000, Hebblewhite et al. 2005, Bergman et al. 2006, Kauffman et al. 2007). However, much of this insight comes from kill site analyses and assumes where an elk dies equates to the risky place on the landscape. Though this assumption may generally be correct, it does not incorporate where the elk was encountered and where it typically spends its time, nor does it incorporate failed hunting attempts (Gorini et al. 2011), focusing only on where "successful" kills were made. Furthermore, animals typically have age- and sex-specific vital rates (Eberhardt 1985) but few, if any, studies have evaluated ungulate vulnerability while incorporating age, sex, and environmental characteristics associated with an individual's home range in the presence and absence of wolves.

Adequately evaluating the effects of environmental vulnerability on elk mortality risk is difficult and ideally requires data from long-term studies of known-age individuals both with and without wolf predation, conditions not typically possible in established wolf-elk systems throughout the greater Yellowstone ecosystem. However, the resident elk in the Madison headwaters area of Yellowstone National Park provided such an opportunity because intensive work was initiated in 1991 prior to wolf reintroduction and continued through 2009, well after the return of wolves to the area in 1997. The herd

remained at a relatively stable equilibrium (varying from 400 to 800 animals) prior to wolf reintroduction before decreasing in abundance by 90% by the end of the study due to wolf predation. Environmental vulnerability was thought to be a significant factor in this decrease (Garrott et al. 2009a,b,c; White et al. 2009a). Furthermore, while elk in the Madison headwaters area did not exhibit shifts in habitat use following wolf recolonization, the elk response was marked by a dramatic change in distribution across the area (White et al. 2009a). This change in distribution was due mostly to lower predation success in certain areas of the system and suggests a landscape level gradient of predation risk for elk exists across the study tract, with distinct areas potentially serving as a prey refuge where wolves have a difficult time making kills (White et al. 2009a).

A radio-collared study population of 8-35 adult (>1 year old) female elk was maintained throughout the 18-year study, allowing evaluation of vulnerability to death in relation to the characteristics of the home range each individual occupied prior to wolves and in the presence of wolf predation. The primary objective was to assess the extent to which certain landscape, habitat, and environmental attributes were related to elk vulnerability to wolf predation, and to spatially map predation risk to test the hypothesis that landscape attributes are related to elk mortality in the presence of wolves. Second, changes in the factors related to elk mortality before and after wolf colonization were evaluated to assess whether certain landscape attributes were related to vulnerability to death differently in pre-wolf years when mortality was primarily due to starvation versus post-wolf years when elk were most likely to die from predation by wolves (Garrott et al. 2009b,c). The odds of mortality were modeled separately in the presence and absence of wolves using logistic regression and 18 years of elk abundance, distribution, habitat use,

and survival/mortality data, both pre- and post-wolf from winter 1991-92 through winter 2008-09, and 12 years of wolf presence/abundance and spatial data from winters 1996-97 through 2008-09.

METHODS

Study Area

The Madison headwaters system encompasses 31,400 hectares and includes the Firehole, Gibbon, and Madison River drainages in the west-central portion of Yellowstone National Park (Figure 1). The landscape is primarily forested plateaus and river canyons with open grassy meadow complexes and sagebrush grassland in valley bottoms that run parallel to the three river drainages. The primary vegetation is a complex mosaic of lodgepole pine forests at varying stages of succession from the 1988 fires, which burned approximately 50% of the area, creating a patchwork of dead fallen trees and dense saplings. The area includes extensive geothermal areas varying in size and distribution which contributes additional habitat complexity and heterogeneity. Elevations range from 2150 m to 2800 m and snow water equivalent (SWE; amount of water in a column of snow) averages 35.75 cm, though there is substantial variability due to areas of reduced snow pack caused by geothermal heat (Watson et al. 2009a,b). The Madison, Gibbon, and Firehole rivers, and the river-sized Iron Spring in the Firehole River drainage, all remain ice free year-round due to a strong geothermal influence. The rivers differ in depth and width and, with the exception of the Madison, significant variations exist within each of the river channels.

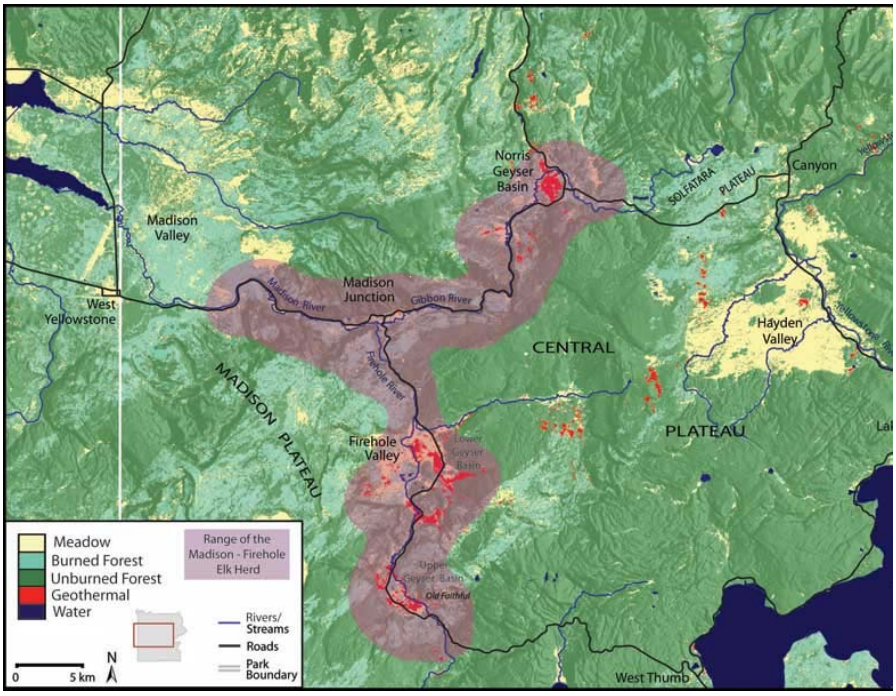


Figure 1: The central portion of Yellowstone National Park mapped using Landsat remote sensing data acquired on September 23, 2002, showing the primary vegetation types and the range of the Madison headwaters elk population (pink) (Newman and Watson 2009).

Elk and Wolf Monitoring

Field research began in December 1991 and continued for 18 consecutive years through April 2009. Throughout the duration of the study, 8-35 radio-collared female elk (approximately 4-10% of the population) were maintained per year (Garrott et al. 2009b). Elk were arbitrarily selected for capture while maintaining an even distribution and representative sample of individuals across the study area. Darting efforts took place in fall and late spring when all elk were congregated and highly visible in meadow areas, allowing for more unbiased selection of focal study animals.

Age of individual elk was determined via cementum annuli analyses from vestigial canine teeth (Hamlin et al. 2000). Radio collars were equipped with mortality sensors and each animal was located approximately 3-4 times per week following a stratified random sampling protocol from mid-November through the end of April (Garrott et al. 1996). Homing procedures described by White and Garrott (1990) were used to obtain accurate locations of collared individuals. Once the animal was sighted and collar positively identified (each individual had distinctive features on its radio-collar to facilitate identification) its location was recorded in Universal Transverse Mercator coordinates (UTM) using United States Geological Survey (USGS) quadrangle maps with the aid of a hand held Global Positioning System (GPS). Elk were not routinely located during summer months (May through mid-November), but radio signals were monitored monthly for mortality pulse rates. Collared elk mortalities were investigated immediately upon detection and causes of death were determined via field necropsies and thorough investigations of the surrounding areas for evidence of predators, blood trails, and/or signs of struggle (Becker et al. 2009a).

Wolves began colonizing the Madison headwaters area in winter 1996-97 with the appearance of several nomadic wolves, and a resident population became established in winter 1998-99 with the Nez Perce pack (Smith et al. 2009). Following establishment, the number of wolves and packs dramatically increased in subsequent years (by an average of 30% per year), peaking at approximately 45 wolves in five packs that used the study area in winter 2004-05 (Smith et al. 2009). The number and size of wolf packs using the study area were dynamic both within and among winters (Smith et al. 2009). Field crews detected and quantified the presence of wolves from November 15 to April

30 during the winters of 1996-97 through 2008-09. National Park Service biologists maintained 2–8 VHF radio collars on nearly all known wolf packs throughout the study. Telemetry data, intensive snow-tracking (Bergman et al. 2006), direct observations, and aerial counts during wolf tracking flights conducted by park biologists were used to estimate the daily presence and number of wolves within the study system (Smith et al. 2009), as well as to detect wolf predation on collared female elk (Garrott et al. 2009c).

Overview and Structure of the Statistical Analysis

I modeled the odds of dying for elk in the Madison headwaters area using logistic regression to evaluate the relative and collective importance of selected covariates. The data were split into pre- and post-wolf periods to compare and contrast the factors most important in influencing mortality in the presence and absence of wolves. Though itinerant wolves used the study area periodically beginning winter 1996-97, the Nez Perce pack became the first established wolf pack to use a portion of the study area (primarily the Firehole drainage) during 1998-99. However, wolves did not become established in the Gibbon and Madison drainages until later (2000-01 and 2001-02, respectively). Thus, the data were partitioned so that the pre-wolf period included the years 1991-92 through 1998-99, and the post-wolf period 1999-00 through 2008-09.

For the analysis, I partitioned each winter into three approximately 8-week periods representing early (Nov. 15 – Jan. 10), middle (Jan. 11 – March 6), and late winter (March 7 – April 30) to account for the temporal variation in wolf presence, snow pack, and elk distribution within the study area each winter (Garrott et al. 2009a,b, Becker et al. 2009a). A dichotomous response variable was used corresponding to

whether an individual collared elk was alive (0) or dead (1) at the end of each winter period. A record for the fate of an individual collared elk was included for each of the three time periods across all years for which the individual was alive and available for monitoring at the start of the period. Because radio-collaring occurred throughout the study, the analysis followed a staggered entry design, with each individual's first entry beginning at the time period following collaring. The observation for a period was removed (censored) if a collar failed prematurely or if the animal permanently dispersed from the study area (Gower et al. 2009), resulting in all zeros for those individuals. Likewise, if the animal died during the summer months the animal received a "0" (alive) for the preceding late winter period and was thereafter censored.

Cougar and grizzly bear predation and unknown mortalities were included as deaths in the initial analysis. However, to explore potential differences in landscape effects between predators, I censored these mortalities (i.e., only the observation/data for the period in which the animal died was removed) in post-hoc exploratory analysis and compared the strength of the coefficient estimates from each. Previous studies conducted in the Madison headwaters area demonstrated that a small percentage of elk responded to increased wolf presence by permanently dispersing out of the study area, presumably in an attempt to decrease their predation risk (Gower et al. 2009). I explored this hypothesis further by coding dispersal events as mortalities during post-hoc exploratory analysis; considering dispersal a response to vulnerability to wolf predation that resulted in the loss of animals from the study population.

To evaluate factors potentially related to elk vulnerability in the presence of wolves, I considered diverse prey, predator, snow pack, and landscape variables. These covariates were chosen based on knowledge of the system and variables reported to influence prey vulnerability in previous studies and other systems. Values for each covariate were estimated for each approximately 8-week winter period in each year. Some covariates had values that were specific to an individual animal and/or winter period, whereas others were shared across animals and/or periods (see below).

Non-Landscape Covariates

Prey Age and Predator Presence

Wolf presence was measured in wolf days - one wolf day was assigned for every wolf in the study area for each day of the sampling period. Wolf days were accumulated for each of the three approximately 8-week winter periods to obtain the primary wolf covariate ($WOLF_{days}$). This covariate was used to account for variations in wolf abundance and predation pressure and their influence on the odds of dying for elk. Rather than using a spatially explicit metric (i.e., drainage), I used a study area-wide metric for accumulated wolf days because wolves could have used any portion of the study area - wolf packs frequently utilized all three drainages to varying degrees of success, perhaps due to differing landscape characteristics resulting in some areas rendering elk more or less vulnerable to predation (Bergman et al. 2006, Garrott et al. 2009a). Previous demographic studies in the Madison headwaters area found age to be an important predictor of female elk survival both pre- and post-wolf (Garrott et al. 2009b,c). Thus, I considered a continuous covariate (AGE), representing the age of elk

in years for each winter period, to account for age-related variations in adult female survival.

Snow Pack

Accumulation and duration of snow can have a long-term weakening effect on ungulates that can ultimately lead to starvation in severe winters (Sæther 1997, Jedrzejewski et al. 1992, Garrott et al. 2003, White et al. 2009b). Snow pack can also substantially increase the vulnerability of ungulates to wolf predation by impeding mobility, and reduced body condition may also influence their ability to successfully escape predation (Nelson and Mech 1986, Becker et al. 2009a). The spatially-explicit Langur snow pack model, developed and validated for the Yellowstone area, was used to generate two snow pack covariates (Watson et al. 2009b). The snow pack covariate (SWE_{mean}) was developed using mean snow-water equivalents and used as an index for escape difficulty and to account for temporal variation in snow pack and its effect on the odds of mortality for elk. SWE is the amount of water in a column of snow and more accurately represents important snow pack attributes such as density, crust conditions, and layers than measurements of snow depth alone (Garrott et al. 2003). SWE_{mean} was estimated daily, study area-wide for each 8-week winter period across all years. A metric of the severity and duration of snow pack (SWE_{acc}) was calculated by accumulating daily SWE_{mean} values beginning at the start of each winter (October 1) through the end of each 8-week winter period, and used to index the extent of physiological weakening due to the energetic deficit caused by decreased forage accessibility and increased locomotion costs (Sæther 1997, Jedrzejewski et al. 1992, Garrott et al. 2003, White et al. 2009b).

Landscape Covariates

To quantify landscape attributes associated with areas occupied by each radio collared elk, I approximated a circular home range for each animal for each of the three winter periods (see Figure 1A, Appendix A). The centroid of each home range was defined as the arithmetic mean of all X and Y coordinates of all locations for each collared elk during a given winter period. However, single locations were censored if they were >10 km from the median centroid point to avoid distortion of the mean centroid due to a single non-typical movement. The area, or size of the circle encompassing the centroid point, was determined by calculating the appropriate radius based on the relationship between mean annual 95% fixed kernel elk home range area and the total number of wolf days in the study area as demonstrated by previous research conducted in the Madison headwaters area (Gower et al. 2009, home range size = 16.909 + 0.004*$WOLF_{days}$ (see Figure 2A, Appendix A)). Thus, the size of each home range circle varied by year (i.e. was the same size for winter periods within a year) depending on total annual wolf days, with average home range size increasing with increasing wolf days (Gower et al. 2009).

GIS data developed specifically for the study area and described in Newman and Watson (2009) and Watson et al. (2009a,b), were used to quantify landscape attributes within each elk home range. A vegetation map created using Landsat satellite imagery was used to calculate the proportion of each elk's home range circle that was burned forest (BF), unburned forest (UF), and meadow (MEAD) habitats (Newman and Watson 2009). Geothermal influences within the Madison Headwaters study area have been

demonstrated to have effects on elk spatial dynamics and distribution across the landscape, in addition to physiological and predation risk effects (Messer et al. 2009, Bergmann et al. 2006, White et al. 2009b). Thus, a map of geothermal heat flux, derived from remotely sensed data as described in Watson et al. (2009a), was used to quantify the proportion of each home range circle that was geothermally influenced (THERM).

Previous work by Bergman et al. (2006) found that elk were more vulnerable to wolf predation near habitat edges creating structural changes in the environment that could impede an elk's movement when being pursued by wolves. Such hard edges included transitions into burned forest, with dense tree regrowth and tangles of burned downfall, as well as boundaries between meadows and unburned forests due to difference in snow pack caused by interception of snow fall by forest canopy (Bergman et al. 2006). Thus, an index of hard edges in each home range was calculated by estimating the linear meters (rescaled to 100 kilometers – 10^5 meters) of habitat boundaries within each home range circle (EDGE).

In contrast, the presence of deep water is a landscape attribute that may enhance survival of elk when pursued by wolves. Ungulates use rivers, lakes, and ponds as escape terrain when attacked by wolves (Carbyn 1974, Nelson and Mech 1981) and observations in the Madison headwaters area supported this behavioral response (Garrott et al. 2009a, White et al. 2009a). However, river characteristics and their subsequent efficacy as refuges varied throughout the study area. Thus, the suitability of river-ways as potential refuges was described based on flow, depth, and drainage area. Categorization was based on our collective knowledge of river depth from 18 years of crossing study area rivers, observations of elk successfully (and unsuccessfully) avoiding predation by using rivers

throughout the study system, kill sites of elk in waterways, and knowledge of wolf height, river depth, and current, given that wolf predation was less successful in deep flowing water necessitating swimming. A map of watershed area was generated and projected onto a stream map as a proxy for water flow to delineate those sections of rivers considered potential escape terrain for elk when pursued by wolves (see Figure 3A, Appendix A). From this map, two categories of waterways were designated: deep river at greater than 500 km^2 (watershed area) and thus considered potentially viable escape terrain for elk, and shallow river at less than 500 km^2 and not considered deep enough to serve as viable escape terrain. If any section of river considered deep (RivDeep) fell within a home range circle, the total number of linear meters (rescaled to hectometers – 10^2 meters) of river within the home range circle was recorded for the value of the covariate. Lastly, due to significant topographic variation in elevation and slope across the Madison headwaters study area, a USGS digital elevation model at a spatial resolution of (28.5 m) was used to estimate average elevation (ELEV) in meters (rescaled to hectometers – 10^2 meters) and average slope in degrees (SLOPE) for each HR circle (Newman and Watson 2009).

Overview of Model Development

I began constructing models using the post-wolf data to allow for model building using a multi-step procedure where models were built up by evaluating the importance of landscape covariates through model selection (procedure explained in more detail below). Before I could begin evaluating landscape covariates, however, I needed to account for the non-landscape covariates already shown to be important factors in elk vulnerability

and mortality from previous studies in the Madison headwaters study area (Becker et al. 2009a, Garrott et al. 2009b,c). Thus, my first step was to build competing *a priori* candidate base models for the post-wolf data using various combinations of non-landscape/non-home range-specific covariates, including AGE, SWE_{acc}, and $WOLF_{days}$. The top base model then served as the null for all landscape models, representing the combination of non home-range specific covariates that best explained variation in elk mortality in the presence of wolves before considering landscape attributes. Next, I employed the multi-step modeling process to build models and evaluate each of the landscape covariates with the post-wolf data. Thus, increasingly complex landscape models were developed from the base model and evaluated with the data using this iterative procedure (see below).

Following construction and evaluation of the full suite of landscape models using the post-wolf data, the same suite of landscape models excluding $WOLF_{days}$, and using an *a priori* base/null model comprised of the covariates AGE and SWE_{acc}, was then fit to the pre-wolf data to test the hypothesis that landscape attributes would be related to vulnerability to death differently in the pre-wolf versus post-wolf years. Though the methods are presented in the order in which analyses were performed, the results are presented in the order of timing of events to match the chronology of the pre- and post-wolf periods.

Base Model Development Using Non-Landscape Covariates

In large herbivores, prime-age adult females typically have high annual survival rates, which are followed by a period of senescence where survival probability declines

for the oldest age classes (Eberhardt 1985, Loison et al. 1999). Furthermore, wolves often select for certain age classes of prey such as older animals that are physiologically compromised or young-of-the-year (Mech et al. 1995, Jaffe 2001, Smith et al. 2004, Becker et al. 2009a). Previous demographic studies in the Madison headwaters area found age to be an important predictor of female elk survival before and after wolf restoration (Garrott et al. 2009b,c). Thus, I considered AGE in our candidate base models and predicted the odds of mortality for elk would increase with age before and after wolf restoration, with a stronger relationship pre-wolf.

Wolf presence ($WOLF_{days}$) and snow pack (SWE_{acc}) covariates were considered in candidate base models to account for variations in wolf predation pressure and snow pack within and among years. Snow depth and density increase the vulnerability of elk in the Madison headwaters to wolf predation by impeding their mobility (Becker et al. 2009a). Thus, I predicted the odds of mortality would increase with increasing mean SWE before and after wolf restoration. However, the long-term negative effects of snow pack on ungulates are thought to be better measured by accumulated snow pack (SWE_{acc}) (Becker et al. 2009a). Thus, I also predicted a positive association between accumulated snow pack and the odds of elk dying before and after wolf restoration, with a stronger pre-wolf relationship. The snow pack metrics were highly collinear and, thus, I only considered SWE_{acc} for the initial analysis. However, SWE_{acc} was replaced with SWE_{mean} in the top model during exploratory analysis to determine if model fit improved.

Though previous studies in the Madison headwaters area demonstrated increased wolf presence (predation pressure) was associated with a decrease in per capita kill rates, likely due to elk behavioral responses and competition (Becker et al. 2009b), increasing

wolf presence still resulted in increasing elk predation (Garrott et al. 2009c). Thus, I predicted the odds of mortality for elk would increase with increasing wolf presence. Previous studies demonstrated that the winter survival of female elk before wolf restoration was dependent on age and snow pack severity, with a more pronounced snow pack effect in older-age classes. In contrast, post-wolf data supported an age only model (Garrott et al. 2009b,c). Thus, I considered interactions between AGE, SWE_{acc}, and $WOLF_{days}$ in the candidate base models.

Evaluating Landscape Covariates

I developed a set of models including the top base model plus one of each of the seven landscape covariates and appropriate interactions based on *a priori* knowledge of the system and previous studies (see Landscape Covariate Predictions and Interactions section below). Each model in the set included only one of the seven landscape covariates and corresponding interactions, in addition to the top base model. The top model from that suite was then used as the base or starting model in the next suite (or step), and to which we added one of each of the remaining landscape covariates and corresponding interactions to create the new suite of models to be evaluated. I repeated this multi-step process, each time including the new top model as the base (null) model in the suite, plus any other additional landscape covariates, until all appropriate combinations of landscape covariates were evaluated and adding additional covariates to models no longer improved results. This process was driven by strong *a priori* thinking about each covariate, appropriate interactions, and potential collinearity among covariates. Only covariates that I *a priori* predicted to be related to elk

vulnerability/mortality in the presence of wolves based on previous research and knowledge of the study system were included in the model building. Likewise, only realistic and appropriate interactions were included, and covariates that were known to be highly collinear (see discussion on collinearity below) were not included together in models. All covariates that were excluded from models due to collinearity, were later substituted back into all well-supported models containing the corresponding collinear covariate, and models then re-evaluated. All models were then combined into one AIC_c table to provide a cleaner and simpler presentation of results for both the pre- and post-wolf analyses.

Landscape Covariate Predictions and Interactions

Geothermal heat prevents snow accumulation in many places throughout Yellowstone National Park during winter months (Watson et al. 2009a). How geothermal areas influence elk survival in the Madison headwaters area likely depends on characteristics such as the size and extent of geothermal patches, snow pack, and whether wolves are present in the system (Messer et al. 2009, Garrott et al. 2009c). This absence of snow (or low snow) as a result of geothermal influence enables herbivores to access photosynthesizing forage year-round, providing an ecological niche for elk in an otherwise harsh winter environment (Garrott et al. 2009b, White et al. 2009b). Previous studies in this system demonstrated that elk strongly selected for geothermal areas both pre- and post-wolf, likely for increased access to forage (Garrott et al. 2009b, Messer et al. 2009). However, in post-wolf years geothermal patches surrounded by deep snow likely served as environmental traps acting as hard edges impeding effective escape as

elk attempted to flee to avoid predation (Bergman et al. 2006, White et al. 2009a). Thus, I predicted the relationship between geothermal area (THERM) and the odds of mortality for elk would be negative during pre-wolf winters, but positive after wolves became established in the system (or with increasing wolf presence) (see Table 1A, Appendix A for covariate descriptions and predicted relationships with the odds of mortality). Large interconnected meadows may provide a modest refuge effect for elk (Bergman et al. 2006, Garrott et al. 2009a), especially in low snow pack conditions. Thus, I predicted a negative relationship between proportion of meadow area (MEAD) and the odds of mortality in the presence of wolves, with little or no relationship before wolves.

A patchwork of complex structured forests with downed timber and dense regeneration covers a large portion (~50%) of the Madison headwaters area (Newman and Watson 2009). These burned forest areas combined with deep snow pack likely serve as hard edges or traps hindering movement and escape of ungulates in the event of an attack (Bergman et al. 2006). Fleeing elk are likely impeded by the complex structure of burned regenerating forests resulting in most kills occurring along burned forest edges (Bergman et al. 2006). Thus, I predicted a positive relationship between proportion of burned forest area (BF) and the odds of mortality for elk in the presence of wolves, but little or no relationship before wolves. In contrast, the less dense stand structure and more open understory characteristic of unburned or old growth forests may serve as a partial refuge where ungulates can seek cover while still being able to move/flee/escape in the event of an attack. This idea is supported by previous work demonstrating that ungulates often seek conifer cover and its associated structure to reduce attack rates by wolves and that ungulate prey are often safer when they are nearer to, or within areas

sheltered by large trees (Stephens and Peterson 1984, Kunkel and Pletscher 2000, Creel et al. 2005). Thus, I predicted a negative relationship between unburned forest area (UF) and the odds of mortality for elk in the presence of wolves, but no relationship before wolves. I predicted a strong negative relationship between the odds of mortality and the amount of deep river (RivDeep**)** within an elk's home range in the presence of wolves, but no relationship before wolves. Lastly, I predicted a positive relationship between edge (EDGE) and the odds of mortality in the presence of wolves, but no relationship before wolves.

Topography, habitat and elevation can have a strong influence on snow pack attributes, including snow pack heterogeneity (i.e., spatial variability of the snow pack) (Messer et al. 2009, Watson et al. 2009a,b). For example, the presence of geothermal features in the Madison headwaters area resulted in extreme snow pack heterogeneity and some refuges from severe snow pack (Watson et al. 2009a,b). Previous research in the system found that elk were more likely to occupy areas with increased snow pack heterogeneity (Messer et al. 2009). Thus, I considered interactions between snow pack (SWE_{acc}) and both elevation (ELEV**)** and geothermal area (THERM) covariates to generally capture the spatial variability of snow pack across the study area. Furthermore, I predicted the relationship between snow pack and the odds of mortality would vary (or interact) with geothermal area by either creating areas with less snow and enabling increased access to forage or by creating terrain traps in the presence of wolves. In addition, interactions between (SWE_{acc}) and edge (EDGE) and burned forest (BF) habitat were considered due to the resulting edge effect created by the abrupt change in snow pack due to the interception of snow fall by forest canopy. Furthermore, I predicted the

effect of MEAD would depend on SWE_{acc}, in that at high levels of accumulated mean SWE the proportion of meadow area would be positively related to the odds of elk dying, and therefore I considered the interaction MEAD * SWE_{acc}. Also, an interaction term for $WOLF_{days}$ and each of the landscape covariates were included to allow for predicted relationships between landscape attributes to vary depending on the number of wolves present in the system.

Slope (SLOPE) was included in post-hoc exploratory analyses as an additional covariate in the best supported model, due to its potential to influence predation encounter probability. Studies have found that ungulate prey are encountered less by predators such as wolves and coyotes on steep slopes; possibly due to low hunting success in these areas as a result of prey detecting approaching predators from vantage points and then moving to higher ground (Bergerud et al. 1984, Bowyer et al. 1999). Thus, I predicted a negative relationship between slope and the odds of mortality for elk.

It is important to consider possible relationships among landscape attributes within our study area and the inherent limitations to what can be learned as a result. Though highly correlated covariates were not included together in models, virtually all landscape covariates were correlated to some extent. The landscape attributes predicted to be important/related to risk of mortality are aggregated by drainage and across the landscape, making it difficult, if not impossible, to capture the relative effects of different landscape attributes. For example, deep river exists primarily in the Madison drainage, which is also the lowest in elevation (and therefore has less snow), and has little or no geothermal influence (see Figures 1B – 8B in Appendix B for plots of each of the landscape covariates by drainage). Unlike the Madison drainage, the Gibbon River is

shallow and narrow in its entirety and the drainage is higher in elevation (deeper snow pack) with a substantial amount of geothermal influence (creating heterogeneity in snow pack and terrain traps). The Firehole River shares many characteristics of the Gibbon River, but also contains small segments deep and wide enough to serve as potential escape terrain. Also, the Firehole drainage has several large, interconnected, thermally influenced basins with reduced snow pack that potentially allow for fleeing elk to effectively escape from wolf attacks. Thus, the Gibbon and Madison drainages are characterized by landscape attributes that collectively and independently are predicted to be related the odds of elk mortality in a positive or negative way, respectively.

As a result, I focused on assessing whether landscape matters in the presence or absence of wolves, focusing more on the collective attributes of the landscape rather than the relative effects of individual landscape attributes. However, during post-hoc exploratory analyses, model suites were constructed for each landscape covariate to evaluate whether the particular landscape attribute was related to the odds of elk mortality in the presence of wolves, without the influence of collinear covariates. Single landscape covariate model suites included the post-wolf base model as the null model ($BM = AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$) and single landscape models comprised of the base model, the landscape covariate, and any appropriate *a priori* interactions.

Overall, I predicted that landscape attributes associated with each elk's home range, interacting with snow pack and wolf presence, would be strongly related to elk mortality following wolf establishment. However, I predicted that age of elk and snow pack would be most important before wolves were established in the system, with

landscape attributes having little or no relationship with the odds of mortality for elk during this time.

Model Selection

I developed competing hypotheses expressed as *a priori* candidate models for the analysis and used Akaike's information criterion adjusted for small sample size (AIC_c) to rank models and compare the relative ability of each to explain variation in the data. Akaike model weights (w_{ic}) were used to address model selection uncertainty and well-supported models were considered those within four ΔAIC_c of the top model (Burnham and Anderson 2002). Models were nested in many cases and I considered parameters uninformative if their inclusion resulted in ΔAIC_c scores close to the maximum penalty of adding one (2 AIC units) or two (4 AIC units) additional parameter(s) to the model and had 95% confidence intervals for the respective covariate coefficients that spanned zero (Arnold 2010).

Potential collinearity between covariates was assessed through inspection of pairwise plots in combination with the corresponding correlation coefficients and variance inflation factors for those covariates with linear relationships. Covariates determined to be highly collinear and not included together in models were SWE_{mean} and SWE_{acc}, EDGE and both UF and BF**,** and THERM and RivDeep (see Figure 4A in Appendix A for matrix of pairwise plots of all covariates). Data were modeled in R version 2.11.1 (R Development Core Team 2010) using generalized linear models with a logit link and binomial error structure (logistic regression). Profile likelihood 95% confidence intervals based on the log-likelihood function were computed in program R

(using the ‘confint’ function in the MASS package (Venables and Ripley 2002)). The delta method, using a first-order Taylor series expansion, was used for calculating appropriate standard errors and corresponding 95% confidence intervals for the odds ratios using the function ‘deltaMethod’ in the R package ‘alr3’ (Weisberg 2005) to account for the covariance among parameters used to calculate the odds ratios (Cooch and White 2009).

To aid in the interpretation of important interactions and help interpret the biological significance of the results, plots were constructed showing predicted relative mortality as a function of selected covariates based on coefficient estimates from top models from both pre- and post-wolf suites. Predictive plots were made for various combinations of the covariates to incorporate the interactive effects, using only combinations of covariates values for which data were observed - thus staying within the appropriate inference space. For example, when examining how the odds of mortality changed as a function of changes in elevation and the amount of deep river habitat, only elevation levels at which deep river existed were used.

Geographic Information System (GIS) techniques were used to create landscape vulnerability maps representing areas of relative vulnerability or risk across the study area for pre- and post-wolf periods based on coefficient estimates from the top pre- and post-wolf models. Specifically, the maps of risk were created by obtaining predictions from the logistic regression model at the spatial covariate values given to each grid cell from maps of each of the spatial covariates. Each covariate map was obtained by starting with an original map of covariate values mapped at a 28.5 m pixel resolution, and then creating a new map that effectively blurred the spatial resolution to be consistent with the

median elk home range radius (2571 m). Pixel values in the blurred maps represented the average of all pixel values from the original map within a 2571 m radius. The original ELEV map was obtained from standard USGS raster products, while the original THERM map was obtained from Watson et al. (2009a). The original EDGE map was derived from the land cover map described by Newman and Watson (2009), processed to yield a map where each pixel value was half the total length of all included edge types bounding that pixel (the values were halved, since each edge was represented by two adjacent pixels). The original RivDeep map was obtained from a standard USGS vector product, subset to include only streams in the study area with watershed area greater than 500 km^2 (i.e., streams hypothesized to be large enough to provide a refuge for elk). The maps were used to illustrate the estimated relationship and interaction between wolf presence and landscape vulnerability for various levels of SWE_{acc} and were later supplemented with figures illustrating current elk abundance and distribution estimates obtained from the latest mark-resight survey results (Garrott et al. 2009c,b).

Investigation of Potential Violations of Assumptions

My primary objective was to understand how mortality risk varied across different values of landscape (e.g., RivDeep), environmental (e.g., SWE_{acc}), and wolf presence covariates. These covariates varied by winter period across time, and therefore I focused the analysis at the level of a single binary event defined by whether a cow survives or dies in a given winter period rather than at the level of the individual female with a time to death (i.e., survival) analysis. Thus, a single female in a single winter period was considered a "trial". The binary logistic regression strategy allowed covariate

values to vary by winter period and by female because each trial was treated as an independent observation. The appropriate use of logistic regression in this context requires assuming homogeneity in probabilities of mortality across individual females and across years after accounting for individual differences captured by the covariates. In general, this was assumed to be a reasonable assumption given that most elk in this system respond to the threat of predation in a similar manner (i.e. by fleeing and/or utilizing escape terrain) and that carefully selected covariates accounted for the other factors potentially related to the probability of mortality. In addition, I assumed that observations from the same female in different time periods, as well as observations from different females within the same time period, are independent. Potential lack of independence due to repeated measures on the same females across time and possible dependence among cows included in the same winter period was a serious concern, as well as complications in the study design that affected the ability to estimate the probability (or odds) of elk mortality.

My original intent was to use logistic regression to model the probability or odds of mortality for an elk as a function of temporally and spatially varying covariates. I assumed that each trial (a single female in a single winter period) provided independent information useful in the estimation of the probability of a female dying in a given winter period. Without considering other variables (i.e., covariates), the probability of an event is based on the baseline log(odds) of occurrence or β_o (i.e., the intercept), while β_1 for example, reflects the linear increase/decrease in the log(odds) attributed to a one unit change in a given variable. However, there are several aspects of the study design that led me to question the appropriateness of the above assumption including: radio-collaring

occurred throughout the study resulting in a staggered entry design, individuals entered the study at different ages (versus as a cohort), and the same individuals were used repeatedly over time. This design created a problem with estimating probabilities similar to that commonly associated with retrospective study designs and therefore limiting potential inferences to estimation of odds ratios (Ramsey and Schafer 2002). For example, the number of observations that an individual elk was recorded as alive before dying depended not only on the probability of dying, but also on when and at what age the animal happened to enter the study. In other words, the relative number of 0's (alives) and 1's (deads) in the data set was somewhat arbitrary in that a female collared by chance two years earlier or two years later, would have had a different number of 0's in the data set, but the same number of 1's. Thus, the same true probability of dying could be accompanied by data with differing relative numbers of 0's and 1's, which would then lead to different estimates of the probability of death/mortality. For example, suppose a female lived 19 winter periods, which in truth provides 19 failures and 1 success. If the female was collared in the first winter period of the study, all failures and the success would be included. However, if the female was collared in winter period 10, only 9 failures contributed with 1 success. Clearly these two situations lead to different estimates of the probability of death for fixed values of the covariates. Furthermore, retrospectively adding zeros for time periods for which we knew individual elk were alive was not possible without measured covariate values for those given time periods. In the context of logistic regression this corresponds to biased intercept estimates (β_o) and thus potentially misleading estimates of the probability or odds of mortality as a function of covariate values. Though it may be inappropriate to interpret the odds (or probability)

of mortality at a specific set of covariate values, it is still meaningful to compare the odds of mortality under two different values of a covariate using odds ratios, because the intercept cancels out in the calculation (Ramsey and Schafer 2002). Additionally, many cows had only zeroes recorded if the collar malfunctioned, if they permanently dispersed from the study area, if they died during the summer, or if they lived until the end of the study.

To investigate the extent of potential bias due to the staggered entry design and repeated measures (i.e. lack of independence and/or heterogeneity in probabilities), I simulated realistic data incorporating the characteristics of concern in program R version 2.11.1 (R Development Core Team 2010), under fixed and known true values of the coefficients and then assessed the ability of binary logistic regression (under the previously described assumptions) to recover the true values. Binary survival data were simulated for pre- and post-wolf realizations under realistic scenarios, with females entering and leaving the study at time periods consistent with that seen in the real data (i.e., staggered entry). I began the simulation procedure by first obtaining coefficient estimates from logistic regression using the actual/real pre- and post-wolf data for the covariates SWE_{acc} and SWE_{acc} + RivDeep respectively. I then created a matrix of probabilities (p(death)) varying by female (based on actual mean RivDeep values) and through time (based on SWE_{acc}), using the covariate values from the actual pre- and post-wolf data and the logistic regression model. Thus, for each time period a cow was known to be alive (ages taken from real data set), each cow received a p(death) based on the covariate values that were associated with her (i.e. RivDeep) and the time period (SWE_{acc}). I then randomly drew from the Bernoulli distribution either a '0' (survives) or

‘1’ (death) with probability of success equal to the p(death) associated with each trial. This was repeated for each cow (51 total cows for pre-wolf, 84 total cows for post-wolf) giving us a series of 0’s (survives) or 1’s (death) for each. Because a cow can only die once, all zeroes were removed after the first ‘1’ in the sequence. The zeroes were removed for time periods the cow was alive but not yet collared to reflect the staggered entry design. Furthermore, a percentage of females were randomly assigned only zero values using the actual proportion of cows in the real data that had only zeros due to collar malfunction, censoring, or were still alive at the end of the study (i.e. each cow had a 42% chance of having only zeros). The “1” was removed for these cows, along with a random number of the “0”s. Then, I treated all 0’s and 1’s remaining (from all cows) as a single simulated data set and ran binary logistic regression on this generated data to estimate the coefficients. This was done 5,000 times to quantify the bias and variability in the coefficient estimates (compared to true coefficient values used to generate the probabilities of death for each trial). Actual coverage of 95 % confidence intervals was also calculated.

As expected, the simulation results showed bias, and substantial variability, in estimates of the intercept parameter. The average bias for estimating the intercept over 5000 simulations was -0.47 for the pre-wolf data, with 0.025 and 0.975 quantiles of -2.10 and 0.71, respectively (see Figure 1C in Appendix C). Likewise, the average bias for estimating the intercept was -0.19 for the post-wolf data, with 0.025 and 0.975 quantiles of -1.28 and 0.84, respectively (see Figure 3C in Appendix C). The biased intercept estimates translated into biased and substantially variable probability estimates as well (see Figures 2C and 4C in Appendix C), and therefore I was uncomfortable with

reporting these quantities. However, the simulations demonstrated the ability of the model to accurately estimate coefficients associated with the covariates (Figures 1C and 3C in Appendix C) and, therefore, the relationship between odds of elk dying and changes in covariate values were described using odds ratios. The average bias for the SWE_{acc} coefficient estimate for the pre-wolf realizations was -0.001, with 0.025 and 0.975 quantiles of -0.040 and 0.035, respectively (see Figure 1C in Appendix C). The average bias for the post-wolf realizations was -0.005, with 0.025 and 0.975 quantiles of -0.082 and 0.062, respectively. The average bias for the RivDeep coefficient estimate for the post-wolf realization was -0.004, with 0.25 and 0.75 quantiles of -0.022 and 0.012, respectively (see Figure 3C in Appendix C). Some bias in the RivDeep coefficient estimate was the result of using non time-varying (fixed) RivDeep values for the simulation exercise.

I further investigated the effects of a lack of independence introduced by repeated measures on the same females by running top models post-hoc using Generalized Estimating Equations (GEEs) with an exchangeable correlation structure to assess the degree to which standard errors of the coefficients obtained from GLM may be misleadingly small as a result of such dependence.

RESULTS

Adult Female Mortality and Wolf Presence

A total of 108 instrumented female elk were monitored throughout the 18-year study, resulting in 595 and 662 (total of 1257) animal sample intervals for pre- and post-wolf periods respectively, with 55 total mortalities recorded. Twelve of the mortalities during the pre-wolf years were attributed to starvation, two to grizzly bears or cougars, and one to unknown causes. Two mortalities by wolf predation when wolves were beginning to colonize the area were removed (censored) from the dataset (only the observation for the time period during which the mortality took place was removed, resulting in all zeros for those individuals). Thirty mortalities during the post-wolf period were attributed to wolf predation, two to starvation, four to grizzly bears or cougars, and cause of death could not be determined for two individuals. A total of 47 observations were removed (censored) because the individual elk either died during the summer months (n = 19), permanently dispersed from the study area (n = 11) following wolf establishment (Gower et al. 2009), experienced premature collar drop or malfunction (n = 16), or did not have enough location data for constructing an approximate home range (n = 1). In addition, there were six individual collared elk still alive at the end of the study. Thus, 42% of the collared elk had all zeros (lived), even though many of these elk did in fact die during the study.

Ages of adult collared elk ranged from 1 to 17 years during the pre-wolf period, with a mean of 7.2 years (95% CI = 6.9, 7.5). The mean age of female elk killed by starvation during the pre-wolf period was 11.8 years (95% CI = 9.6, 14.0) and ranged

from 7 to 17 years (see Figures 2 and 3 below for distributions of these data). Average age of elk during the post-wolf period was 8.4 years (95% CI = 8.2, 8.7) and ranged from 1 to 17 years. The mean age of adult elk killed by wolves during the post-wolf period was 10.3 (95% CI = 8.7, 11.4) and ranged from 1 to 17 years (Figures 2 and 3).

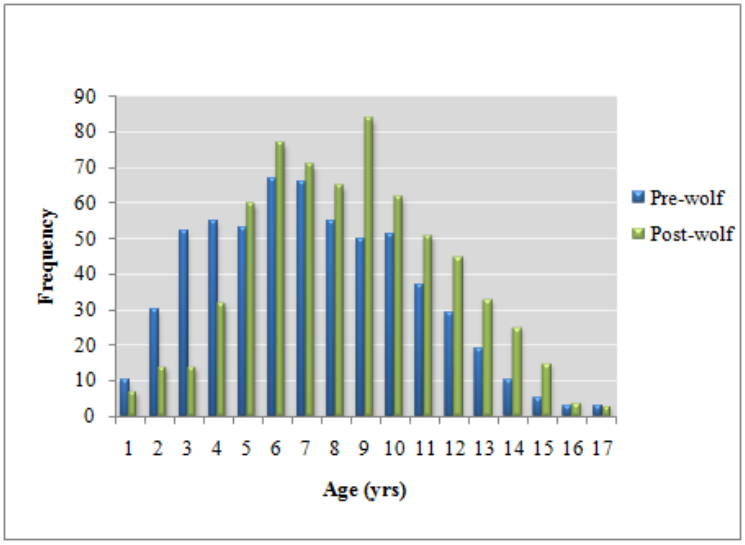


Figure 2: Distribution of elk ages for pre- and post-wolf periods.

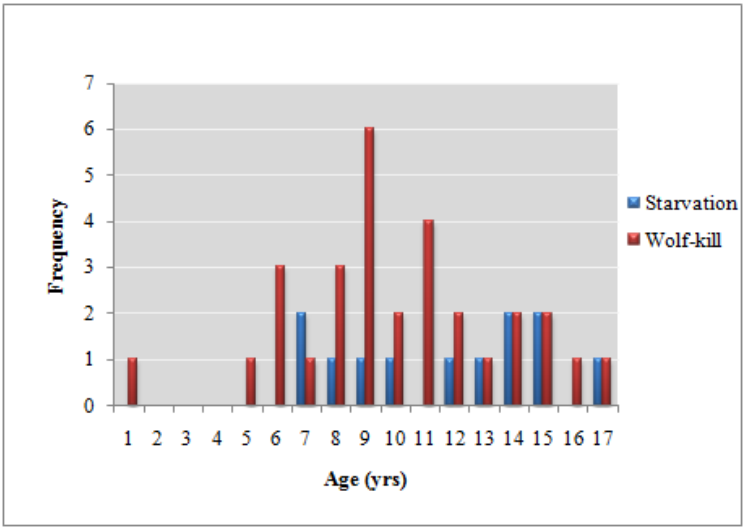


Figure 3: Age distribution for elk killed by starvation and wolf-killed elk for pre- and post-wolf periods respectively.

Over the course of the study, 1757 telemetry locations, 681visual locations, and 5343 km of backtracking were obtained to determine wolf presence and abundance in the Madison headwaters area. Wolf presence during the 167-day winter field season ranged from 55 wolf days (1996-97) to a peak of 3657 (2004-05) (Figure 4), while the total number of wolf days per winter period ($WOLF_{days}$) ranged from 196 to 1368 during 1999-00 to 2008-09, with a mean of 641 wolf days. Eight established wolf packs used the Madison headwaters area to varying degrees over the course of the study, and packs ranged in size from 4-25 wolves (mean = 11.1; 95% CI = 8.4, 13.8) (Table 2A, Appendix A).

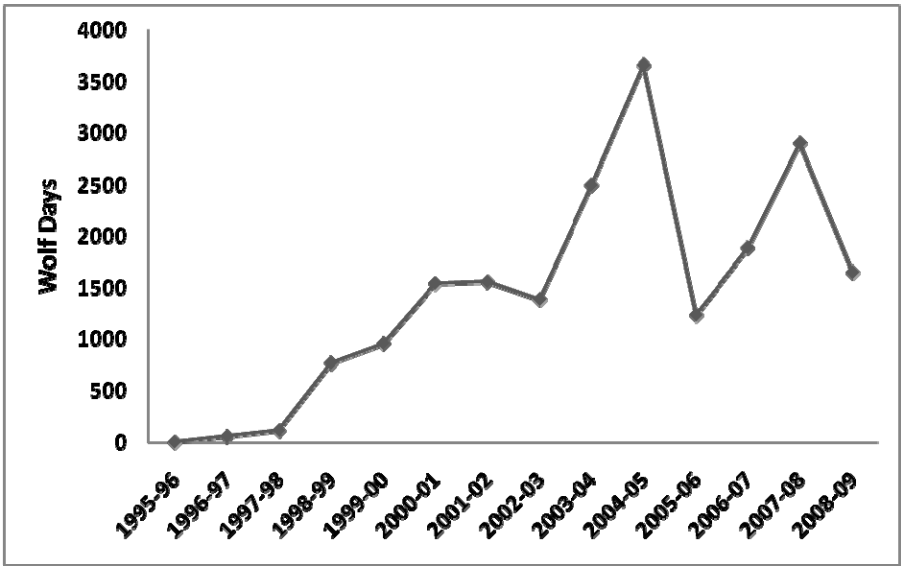


Figure 4: Plot showing total wolf days per winter.

Snow Pack

Snow pack accumulation typically began in late October (Watson et al. 2009b) and increased until late March with the onset of spring melt-off. During the study, mean

daily SWE per winter period (SWE_{mean}) ranged from 3.1 to 46.8 cm, with a mean of 15.3 cm (sd = 9.7 cm). Accumulated mean SWE (SWE_{acc}) ranged from 185 to 5955 cm per winter period, with a mean of 1479 cm (sd = 1195 cm). Annual variation in snow pack was substantial during the pre-wolf period, representing nearly the entire range of historical annual snow pack conditions. In general, mean SWE_{acc} was higher during the pre-wolf years (mean = 1962 cm, sd = 1426 cm), ranging from 223 to 5955 cm. Snow pack during the post-wolf years was below historical averages ranging from 185 to 2882 cm with a mean of 1152 cm (sd = 759 cm) (see Figure 5 below for a comparison).

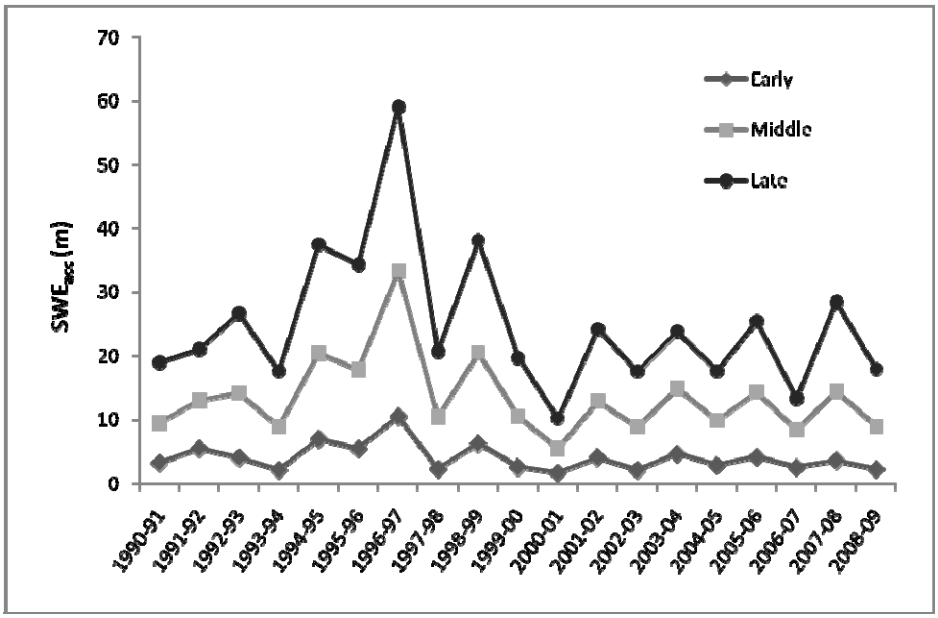


Figure 5: Mean SWE_{acc} for early, middle, and late winter periods across years.

Home Range Specific Attributes

In total, 12,649 randomly collected elk locations were obtained from repeated sampling of the 108 radio-collared adult female elk throughout the 18-year study. These data were used to generate 1257 home range circles to quantify landscape attributes

associated with areas occupied by each radio collared elk for each of the three winter periods across years. During the pre-wolf years, the size of home range circles ranged from 16.9 to 20.0 km^2 with a mean of 17.5 km^2 (sd = 1.1 km^2) and mean home range elevation ranged from 2137 to 2369 m with a mean of 2270 m (sd = 44.0 m). During the post-wolf years home range circles ranged from 20.8 to 31.7 km^2 with a mean of 24.4 km^2 (sd = 3.3 km^2), and mean home range elevation ranged from 2109 to 2387 m with a mean of 2274 m (sd = 42.6). On average, linear meters of deep river and edge per home range circle were higher in the post-wolf years compared to the pre-wolf years, while proportion of thermal area and meadow habitat per home range circle were slightly lower during the post-wolf years (Table 1).

Table 1: Descriptive statistics for landscape covariates pre-and post-wolf.

Covariate	Pre-wolf				Unit
	Mean	SD	Min.	Max.	
RivDeep	2448.9	2878.8	0.0	8409.2	Meters
THERM	0.03	0.03	0.00	0.13	Proportion
MEAD	0.11	0.05	0.03	0.40	Proportion
EDGE	481896.3	125657.1	226575.0	813119.3	Meters
BF	0.23	0.07	0.06	0.45	Proportion
UF	0.61	0.13	0.28	0.80	Proportion
SLOPE	9.92	3.99	1.99	17.23	Degrees
Covariate	Post-wolf				Unit
	Mean	SD	Min.	Max	
RivDeep	3463.7	3655.3	0.0	10038.6	Meters
THERM	0.02	0.03	0.00	0.12	Proportion
MEAD	0.09	0.05	0.02	0.37	Proportion
EDGE	656649.4	167519.5	281480.3	1208442.8	Meters
BF	0.25	0.06	0.05	0.48	Proportion
UF	0.62	0.11	0.32	0.82	Proportion
SLOPE	9.98	3.69	3.00	16.57	Degrees

Factors Related to Elk Mortality in the Absence of Wolves

I fit 65 models to the pre-wolf data to evaluate factors related to elk mortality in the absence of wolves. Model selection results supported four top models within two ΔAIC_c (totaling 38% of model weight) and 12 models within four ΔAIC_c (totaling 68% of model weight) of the top model, indicating some model selection uncertainty (Table 2). Nevertheless, the results indicate that the additive effects of elk age, accumulated snow pack, and to a lesser extent the interaction between proportion of thermal area and accumulated snow pack, were the most important factors related to elk mortality before wolves were in the system. All 12 top models contained the covariates AGE and SWE_{acc} and produced consistent coefficient estimates in the predicted direction with corresponding 95% confidence intervals not overlapping zero (Table 3). The top ranked model included the covariates THERM and THERM * SWE_{acc} in addition to AGE and SWE_{acc}, while the second ranked model contained only the AGE and SWE_{acc} covariates. All other top models contained one or more additional landscape covariates. However, these models were nested and gained support because they contained the important AGE and SWEacc covariates. Furthermore, these additional landscape parameters were considered uninformative given their inclusion resulted in ΔAIC_c scores close to the maximum penalty of adding the additional parameter(s) to the model and had 95% confidence intervals for the respective covariates that spanned zero (Arnold 2010).

As predicted, AGE was positively related to the odds of elk dying in the absence of wolves ($\beta_{AGE} = 0.55$, 95% CI = 0.34 to 0.82) (Figure 6). Based on the top model coefficient estimates, the odds of dying for adult elk was 1.73 times greater for every one

year increase in age with associated 95% CI for the odds from 1.41 to 2.27. As predicted, accumulated mean SWE was positively related to the odds of mortality for elk after accounting for age of elk. However, the effect of SWE_{acc} also depended on proportion of thermal area within a home range circle. The interaction between SWE_{acc} and THERM was negative ($\beta_{THERM * SWEacc}$ = -1.06, 95% CI = -2.16 to -0.06) such that as accumulated snow pack increased, the odds of dying increased, however the effect was greater in areas with less thermal influence compared to those with high thermal influence (Figure 7). For example, the odds of mortality at high levels of mean accumulated SWE (0.75^{th} quantile = 2692 cm) were 9.4 times the odds of mortality at low levels of mean accumulated SWE (0.25^{th} quantile = 751 cm) for elk with a low proportion of thermal area (0.25^{th} quantile = 0.00) within their home range (95% CI for the odds ratio = 3.2 to 27.4). In contrast, elk with a high proportion of thermal area within their home range (0.75^{th} quantile = 0.049) had only 3.5 times the odds of mortality at high versus low levels of mean accumulated SWE (95% CI for the odds ratio = 1.6 to 7.8).

An exploratory analysis replacing SWE_{acc} with SWE_{mean} for all pre-wolf models resulted in the top model containing only the AGE and SWE_{mean} covariates (Table 5A, Appendix A), further supporting our hypothesis that landscape attributes had little effect on elk mortality in the absence of wolves. However, replacing SWE_{acc} with SWE_{mean} did not improve model fit as the AIC_c score for the top model increased from 99.2 to 100.1. Though there was some model selection uncertainty (14 models within four ΔAIC_c from the top model), this was due to models being nested and gaining support because they contained the important AGE and SWE_{mean} covariates. Furthermore, AGE and SWE_{mean} were the only covariates producing coefficient estimates with corresponding 95% CIs not

spanning zero. Lastly, model selection results did not support adding the quadratic form for AGE to the top model in post-hoc exploratory analyses (Table 6A, Appendix A).

Table 2: Model selection results for the pre-wolf model suite. Table only includes those models within four ΔAIC_c from the top model (see Table 3A in Appendix A for selection results for all models in the suite).

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	AGE + SWE_{acc} + THERM + THERM * SWE_{acc}	5	99.21	0.00	0.16
2	AGE + SWE_{acc}	3	100.02	0.81	0.10
3	AGE + SWE_{acc} + MEAD	4	101.06	1.86	0.06
4	AGE + SWE_{acc} + RivDeep	4	101.19	1.99	0.06
5	AGE + SWE_{acc} + UF	4	101.33	2.12	0.05
6	AGE + SWE_{acc} + THERM	4	101.51	2.30	0.05
7	AGE + SWE_{acc} + EDGE	4	101.62	2.41	0.05
8	AGE + SWE_{acc} + BF	4	102.03	2.83	0.04
9	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + THERM + THERM * SWE_{acc}	7	102.27	3.07	0.03
10	AGE + SWE_{acc} + EDGE + EDGE * SWE_{acc}	5	102.34	3.14	0.03
11	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc}	5	102.64	3.43	0.03
12	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + THERM + THERM * SWE_{acc}	8	103.06	3.86	0.02

Table 3: Estimated coefficient values (β_i) and 95% confidence intervals (in parentheses) for covariates with confidence intervals not overlapping zero from those models within four ΔAIC_c from the top model for the pre-wolf model suite (for coefficient values (β_i) and 95% confidence intervals for all covariates in the most supported models (see Table 4A in Appendix A).

Covariate	Model ID					
	1	**2**	**3**	**4**	**5**	**6**
AGE	**0.55 (0.34, 0.82)**	**0.49 (0.30, 0.72)**	**0.52 (0.32, 0.75)**	**0.51 (0.31, 0.74)**	**0.52 (0.32, 0.77)**	**0.51 (0.31, 0.75)**
SWE_{acc}	**0.12 (0.06, 0.18)**	**0.07 (0.04, 0.12)**	**0.08 (0.04, 0.12)**	**0.08 (0.04, 0.12)**	**0.08 (0.04, 0.12)**	**0.08 (0.04, 0.12)**
THERM	**39.02 (4.18, 74.13)**	-	-	-	-	-
THERM * SWE_{acc}	**-1.06 (-2.16, -0.06)**	-	-	-	-	-
Covariate	Model ID					
	7	**8**	**9**	**10**	**11**	**12**
AGE	**0.51 (0.31, 0.74)**	**0.49 (0.30, 0.72)**	**0.59 (0.35, 0.89)**	**0.52 (0.32, 0.78)**	**0.52 (0.32, 0.77)**	**0.62 (0.37, 0.94)**
SWE_{acc}	**0.08 (0.04, 0.12)**	**0.08 (0.04, 0.12)**	-	**0.15 (0.02, 0.29)**	-	-
THERM	-	-	**38.36 (2.77, 73.98)**	-	-	**42.97 (4.87, 82.06)**
THERM * SWE_{acc}	-	-	-	-	-	**-1.2 (-2.46, -0.09)**

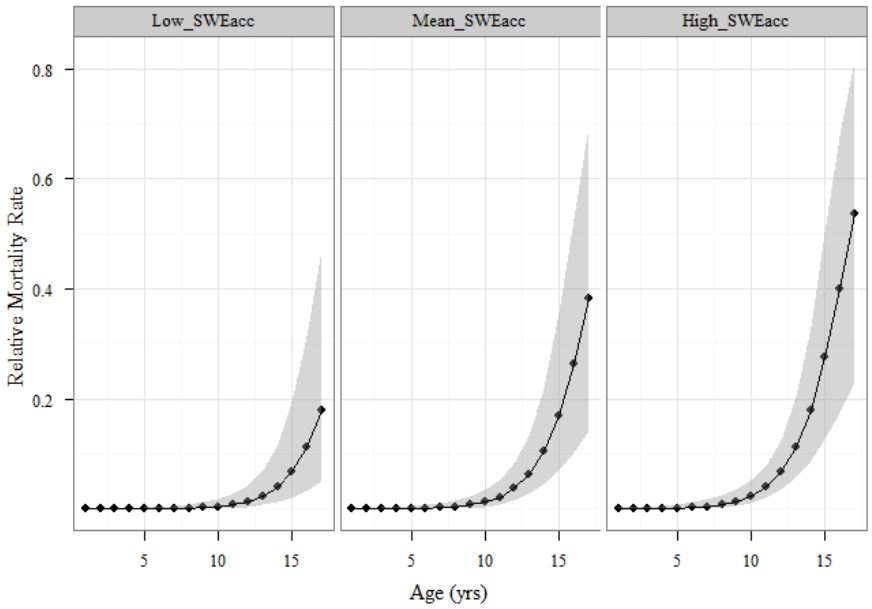


Figure 6: Predicted relative mortality rate with 95% confident intervals (grey shading) for increasing elk age at low (0.25th quantile), average, and high (0.75th quantile) levels of accumulated mean SWE.

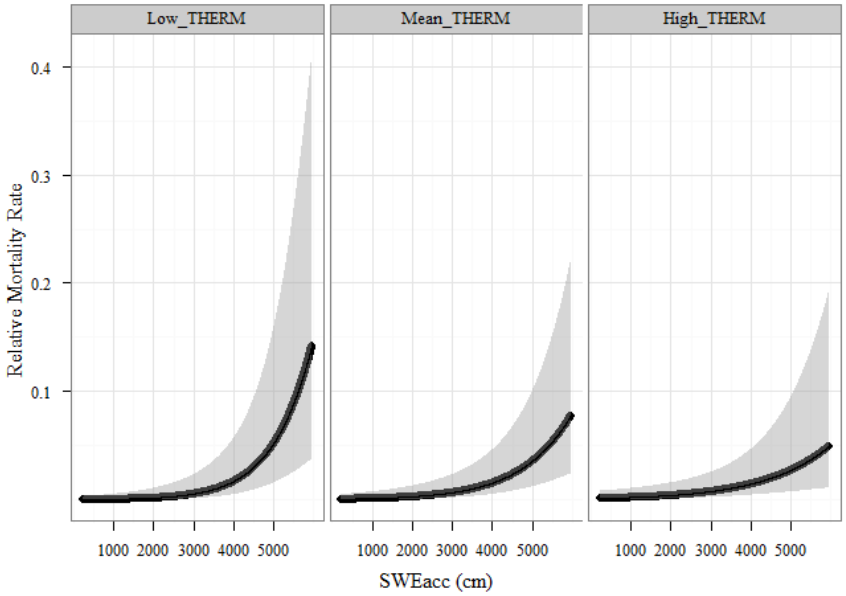


Figure 7: Predicted relative mortality rate with 95% confident intervals (grey shading) for increasing accumulated mean SWE at low (0.25th quantile), average, and high (0.75th quantile) proportion of thermal area for average aged elk.

Non-Landscape Factors Related to Elk Mortality in the Presence of Wolves

I fit 16 models from the *a priori* base model suite to the post-wolf data. The results indicate substantial model selection uncertainty, with five top models within 2 ΔAIC_c (carrying a total of 75% of model weight) and nine top models within 4 ΔAIC_c (totaling 94% of model weight) of the top ranked model (Table 4). The top two models were virtually identical in their ability to explain variation in the data with AIC_c scores of 278.19 and 278.27, and carrying 23% and 22% of model weight respectively. Both models contained the covariates AGE, SWE_{acc}, and AGE * SWE_{acc} and differed in structure only by the inclusion of $WOLF_{days}$ in the second top model. The covariate AGE was included in all nine top models and AGE * SWE_{acc} in the top three models. However, given the nested nature of these models, the additional covariates AGE * $WOLF_{days,}$ in the 3rd ($\Delta AIC_c = 1.52$), 7th ($\Delta AIC_c = 3.42$), and 9th ($\Delta AIC_c = 3.99$) ranked models, and $WOLF_{days,}$ * SWE_{acc} in the 5th ($\Delta AIC_c = 1.81$) and 7th ($\Delta AIC_c = 3.42$) ranked models, apparently had little importance.

In all models, the coefficient estimates for AGE * SWE_{acc} were positive, with corresponding 95% confidence intervals that did not span zero (Table 5). Likewise, wolf abundance, as estimated by the covariate $WOLF_{days,}$ was positively related to the odds of elk mortality, though confidence intervals for the coefficient estimate spanned zero for all models that included the covariate. However, given the top two models were virtually identical in explaining variation in the data (with ΔAIC_c scores of 0.00 and 0.08 respectively), we used the 2nd top model containing $WOLF_{days}$ in addition to AGE, SWE_{acc}, and AGE * SWE_{acc} as the base model for the post-wolf landscape model suite.

Table 4: Model selection results for post-wolf base model suite. Table only includes those models within four ΔAIC_c from the top model (see Table 7A in Appendix A for selection results for all models in the suite).

Model ID	Model	K	AICc	deltAICc	w_ic
1	$AGE + SWE_{acc} + AGE * SWE_{acc}$	4	278.19	0.00	0.23
2	$AGE + WOLF_{days} + SWE_{acc} + AGE * SWE_{acc}$	5	278.27	0.08	0.22
3	$AGE + WOLF_{days} + SWE_{acc} + AGE * SWE_{acc} + AGE * WOLF_{days}$	6	279.71	1.52	0.11
4	AGE	2	279.84	1.65	0.10
5	$AGE + WOLF_{days} + SWE_{acc} + AGE * SWE_{acc} + WOLF_{days} * SWE_{acc}$	6	280.00	1.81	0.09
6	$AGE + WOLF_{days}$	3	280.36	2.17	0.08
7	$AGE + WOLF_{days} + SWE_{acc} + AGE * SWE_{acc} + WOLF_{days} * SWE_{acc} + AGE * WOLF_{days}$	7	281.61	3.42	0.04
8	$AGE + SWE_{acc}$	3	281.85	3.66	0.04
9	$AGE + WOLF_{days} + AGE * WOLF_{days}$	4	282.18	3.99	0.03

Table 5: Estimated coefficient values (β_i) and 95% confidence intervals (in parentheses) for covariates from the top ranked models within 4 ΔAIC_c from the top model for the post-wolf base model suite. Values with confidence intervals not spanning zero are bolded.

Model ID	Covariate					
	AGE	SWE_{acc}	$WOLF_{days}$	AGE * SWE_{acc}	AGE * $WOLF_{days}$	SWE_{acc} * $WOLF_{days}$
1	0.02 (-0.16, 0.20)	**-0.17 (-0.34, -0.02)**	-	**0.016 (0.003, 0.031)**	-	-
2	0.01 (-0.18, 0.19)	**-0.19 (-0.36, -0.03)**	0.001 (-0.000, 0.002)	**0.017 (0.004, 0.032)**	-	-
3	0.09 (-0.19, 0.38)	**-0.20 (-0.37, -0.04)**	0.002 (-0.002, 0.005)	**0.018 (0.004, 0.033)**	-0.0001 (-0.0004, 0.0002)	-
4	**0.20 (0.10, 0.31)**	-	-	-	-	-

Table 5 Continued

5	0.00 (-0.18, 0.19)	-0.16 (-0.36, 0.03)	0.001 (-0.001, 0.003)	**0.017 (0.004, 0.032)**	-	0.0000 (-0.0002, 0.0001)
6	**0.20 (0.10, 0.30)**	-	0.001 (-0.000, 0.002)	-	-	-
7	0.08 (-0.22, 0.37)	-0.18 (-0.39, 0.02)	0.002 (-0.001, 0.006)	**0.018 (0.004, 0.032)**	-0.0001 (-0.0004, 0.0002)	0.0000 (-0.0002, 0.0001)
8	**0.20 (0.10, 0.31)**	0.00 (-0.04, 0.04)	-	-	-	-
9	0.25 (-0.01, 0.52)	-	0.001 (-0.002, 0.005)	-	-0.0001 (-0.0004, 0.0003)	-

Landscape Factors Related to Elk Mortality in the Presence of Wolves

I fit 69 models to the post-wolf data to evaluate factors related to elk mortality in the presence of wolves. Model selection results for the post-wolf landscape model suite supported three top models within four ΔAIC_c of the top model, with Akaike model weights of 0.44, 0.16, and 0.16, respectively (Table 6). The top three models included the covariates ELEV, ELEV * SWE_{acc}, RivDeep, RivDeep * $WOLF_{days}$, EDGE, and EDGE * $WOLF_{days}$ in addition to the base model covariates, and carried 76% of model weight combined. The structure of the three models differed only in the inclusion of the ELEV * $WOLF_{days}$ and EDGE * SWE_{acc} interactions in the second and third ranked models, respectively. However, these interactions may have had little importance given the corresponding 95% confidence intervals for the coefficient estimates both spanned zero (Table 7) and the models were approximately 2 ΔAIC_c from the top ranked model (Table 6) (Arnold 2010). The null model was the 65th ranked model ($\Delta AIC_c = 30.4$) and

carried 0% of model weight and each one of the landscape covariates was included within a model that was higher ranked than the null model.

Table 6: Model selection results for post-wolf landscape model suite. Table only includes those models within 6 ΔAIC_c from the top model (see Table 8A in Appendix A for selection results for all models in the suite). Note: BM = Base Model = AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc}.

Model ID	Model	K	AICc	deltAICc	w_ic
1	BM + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	11	247.89	0.00	0.44
2	BM + ELEV + ELEV * SWE_{acc} + **ELEV * $WOLF_{days}$** + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	12	249.86	1.97	0.16
3	BM + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + **EDGE * SWE_{acc}** + EDGE * $WOLF_{days}$	12	249.91	2.03	0.16
4	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$	13	251.91	4.02	0.06
5	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * $WOLF_{days}$	12	252.26	4.37	0.05
6	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	252.98	5.10	0.03

The odds of mortality for female elk in the presence of wolves were higher at older ages and at high levels of accumulated SWE (β_{AGE} = 0.01, 95% CI = -0.19 to 0.22; β_{SWEacc} = 4.02, 95% CI = 1.76 to 6.42; $\beta_{AGE*SWEacc}$ = 0.018, 95% CI = 0.003 to 0.034). The magnitude of change depended on home range elevation and age of elk, with older elk more likely to die than younger elk in higher snow pack conditions (Figure 8). For example, in high snow pack conditions (0.75th quantile of SWE_{acc} = 1774 cm) and average elevation (mean = 2277 m), the odds of dying for a 16 year old elk was 14.3 times that of an 8 year old elk (95% CI for the odds ratio = 3.70 to 55.26).

Table 7: Estimated coefficient values (β_i) and 95% confidence intervals (in parentheses) for covariates from the three top ranked models (within four ΔAIC_c from the top model) for the post-wolf landscape model suite. Values with confidence intervals not spanning zero are bolded.

Model ID	Covariate					
	AGE	$WOLF_{days}$	SWE_{acc}	ELEV	RivDeep	EDGE
1	0.01 (-0.19, 0.22)	**0.010 (0.003, 0.017)**	**4.02 (1.76, 6.42)**	**2.81 (1.25, 4.51)**	0.02 (-0.02, 0.06)	0.12 (-0.52,0.80)
2	0.01 (-0.18, 0.22)	0.025 (-0.070, 0.117)	**4.00 (1.73, 6.40)**	**3.27 (0.10, 6.68)**	0.02 (-0.03, 0.08)	0.14 (-0.51, 0.83)
3	0.01 (-0.19, 0.21)	**0.010 (0.003, 0.017)**	**4.00 (1.74, 6.42)**	**2.82 (1.26, 4.53)**	0.02 (-0.02, 0.07)	0.09 (-0.57, 0.81)
Model ID	**Covariate**					
	AGE * SWE_{acc}	SWE_{acc} * ELEV	$WOLF_{days}$ * RivDeep	$WOLF_{days}$ * EDGE	$WOLF_{days}$ * ELEV	SWE_{acc} * EDGE
1	**0.018 (0.003, 0.034)**	**-0.18 (-0.29, -0.09)**	**-0.00007 (-0.00013, -0.00001)**	-0.001 (-0.002, 0.000)	-	-
2	**0.018 (0.003, 0.034)**	**-0.18 (-0.29, -0.09)**	**-0.00007 (-0.00013, -0.00001)**	-0.001 (-0.002, 0.000)	-0.001 (-0.005, 0.003)	-
3	**0.018 (0.003, 0.035)**	**-0.19 (-0.29, -0.09)**	**-0.00007 (-0.00014, -0.00002)**	-0.001 (-0.002, 0.000)	-	0.00 (-0.03, 0.03)

Exploratory analyses replacing SWE_{acc} with SWE_{mean} for all post-wolf models resulted in the same top model, but model fit was not improved because the AIC_c score for the top model increased only slightly from 247.9 to 248.00.

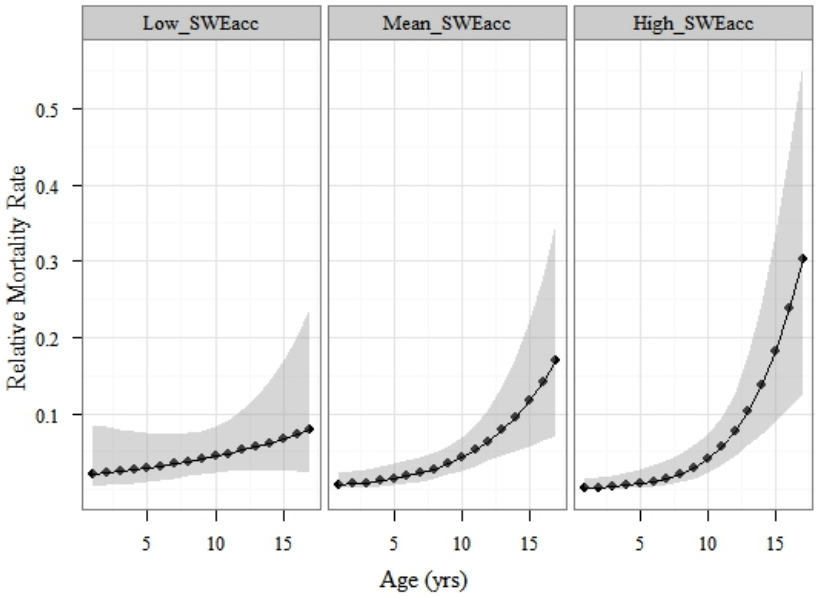


Figure 8: Predicted relative mortality rate with 95% confident intervals (grey shading) for low (25th quantile = 4.32 m), average (mean = 11.5 m), and high (75th quantile = 17.5 m) levels of SWE_{acc} as elk age increases.

$WOLF_{days}$ was positively related to the odds of mortality for elk ($\beta_{WOLFdays}$ = 0.01, 95% CI = 0.003 to 0.02), but the magnitude of the effect depended on the amount of deep river and possibly edge associated with elk home ranges, with the effect of wolf days substantially reduced in areas with deep river ($\beta_{RivDeep*WOLFdays}$ = -0.00007, 95% CI = -0.00013 to -0.00001) (Figure 9). For example, the odds of mortality for an elk living in a home range with no deep river was 16.4 times (95% CI = 3.9 to 69.9) the odds of mortality for an elk with high deep river (0.75 quantile = 7200.7 m) when wolf days were high (0.75 quantile = 826 wolf days).

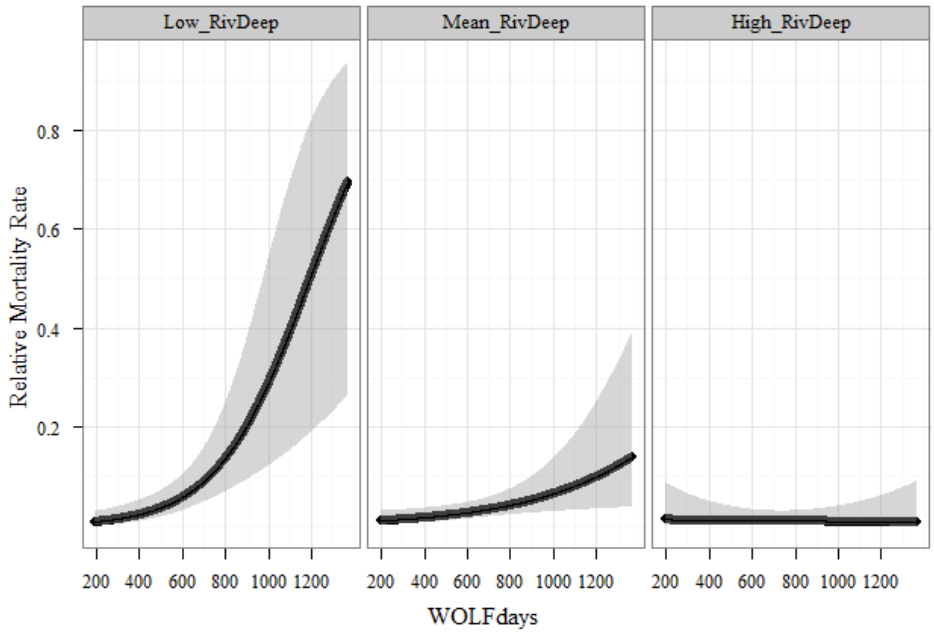


Figure 9: Predicted relative mortality rate (solid line) with 95% confident intervals (grey shading) for average aged elk for low, average, and high levels of deep river as wolf days increase (all other covariates held constant at their mean value).

As predicted, EDGE was positively related to the odds of elk mortality (β_{EDGE} = 0.12, 95% CI = -0.52 to 0.80), but contrary to my predictions the coefficient estimate for the EDGE * $WOLF_{days}$ interaction was negative ($\beta_{EDGE * WOLFdays}$ = -0.001, 95% CI = -0.002 to 0.000), as $WOLF_{days}$ increased, the edge effect became less important. However, the results for EDGE were somewhat equivocal because the 95% confidence intervals for the estimated coefficients both overlapped zero. The contradictory and unclear results for edge may have been due to collinearity between edge and the important covariates, elevation and deep river, in addition to an unexpected positive correlation (r = 0.41) with wolf presence (i.e., $WOLF_{days}$) (Figures 5A, 6A, and 7A, Appendix A).

Elevation was positively related to the odds of mortality in the presence of wolves (β_{ELEV} = 2.81, 95% CI = 1.25 to 4.51). Contrary to our predictions, however, the coefficient estimate for the interaction between elevation and SWE_{acc} was negative ($\beta_{ELEV * SWEacc}$ = -0.18, 95% CI = -0.29 to -0.09), such that the odds of elk dying was higher in high elevation areas when accumulated snow pack was low (Figure 10). Though I expected the elevation effect to be an artifact of increasing snow pack at higher elevations, this result was likely due to collinearity and lack of data/samples across all gradients of covariate conditions. For example, during the winter (2007-08) with the highest snow pack after wolf restoration, few (if any) elk still remained in high elevation areas such as in the Gibbon River drainage. As a result, there were no mortalities in these areas. However, a few elk were still being killed in the average and lower elevation areas that winter (Figure 8A, Appendix A).

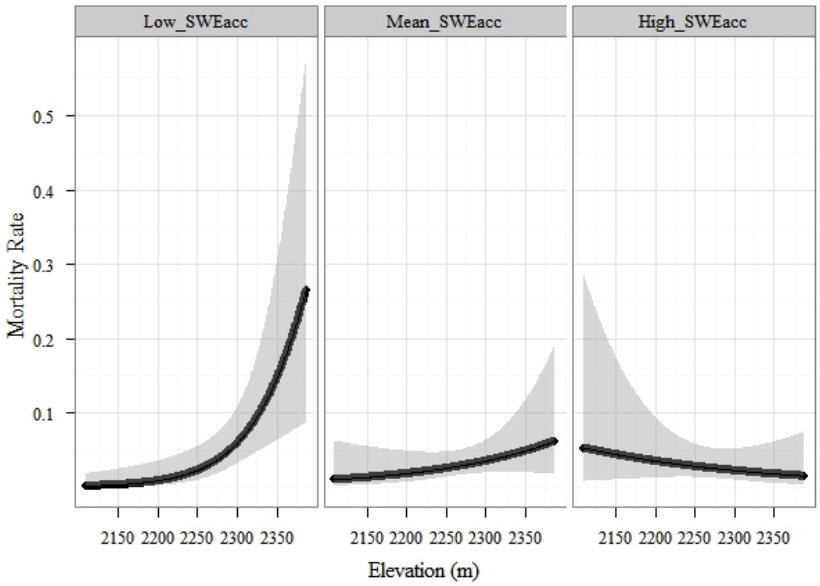


Figure 10: Predicted relative mortality rate with 95% confident intervals (grey shading) for low (25th quantile = 4.32 m), average (mean = 11.5 m), and high (75th quantile = 17.5 m) levels of SWE_{acc} as elevation increases for average aged elk (all other covariates held constant at their mean value).

Evaluating the Importance of Individual Landscape Attributes

The elevation, deep river, thermal, meadow, and slope models all received more support than the null model (AGE + $WOLF_{days}$ + SWE_{acc} + AGE * SWE_{acc}), while all models containing EDGE, BF, and UF were outcompeted by the null model though they still received some support (Table 12; Tables 13-20, Appendix D). Aside from the ELEV * SWE_{acc} interaction, coefficient estimates were in the predicted direction (especially when interacting with $WOLF_{days}$) and though some estimates had 95% confidence intervals spanning zero, the model selection results indicated they still may have had some importance based on respective ΔAIC_c scores and model weights. Coefficient estimates for the post-wolf base model covariates were consistent with the *a priori* post-wolf results.

Results for the elevation model suite supported two top models within 2 ΔAIC_c, carrying 66% and 33% of model weight, respectively, for the first and second ranked models (Table 8). Both top models contained the covariates ELEV and ELEV * SWE_{acc} in addition to the base model covariates, and differed only by the inclusion of the ELEV * $WOLF_{days}$ interaction in the second ranked model. All other models were >8 AIC_c units from the top model, and the null model was the lowest ranked model (ΔAIC_c = 19.29) and carried no model weight. Elevation was positively related to the odds of elk mortality (β_{ELEV} = 3.31, 95% CI = 1.94 to 4.94), but again depended on SWE_{acc} ($\beta_{ELEV * SWEacc}$ = -0.16, 95% CI = - 0.26 to -0.06), such that elevation had less of an effect at high levels of SWE_{acc} (or more of an effect at low levels of SWE_{acc}). As predicted, the coefficient estimate for the interaction between $WOLF_{days}$ and ELEV was positive, but the

corresponding 95% confidence interval spanned zero ($\beta_{ELEV * WOLFdays}$ = 0.001, 95% CI = -0.002 to 0.005).

Consistent with the *a priori* landscape model results, selection results for the deep river suite supported both deep river models, while the null model received no support (ΔAIC_c =15.13, AIC_c weight = 0.00) (Table 8). The second ranked model included the additional RivDeep * $WOLF_{days}$ covariate and a ΔAIC_c score of 1.06. As predicted, deep river was negatively related to the odds of elk mortality ($\beta_{RivDeep}$ -0.02 =, 95% CI = - 0.03 to - 0.01) and the coefficient estimate for the RivDeep * $WOLF_{days}$ interaction in the second ranked model was also negative as predicted, though the corresponding 95% confidence interval barely spanned zero ($\beta_{RivDeep * WOLFdays}$ = -0.00001, 95% CI = -0.00006 to 0.00001). However, given the model containing RivDeep * $WOLF_{days}$ had a ΔAIC_c of only 1.06, the interaction likely had some importance.

Three top models fell within 2 AIC_c units of the top model in the thermal suite, while all five models fell within 4ΔAIC_c, indicating some model selection uncertainty (Table 8 below, Table 3D in Appendix D). The top ranked model contained the covariates THERM and THERM * $WOLF_{days}$ (with a AIC_c model weight = 0.38), while the second ranked model, containing only the main effect THERM, had a ΔAIC_c = 1.00 and model weight = 0.23. The model containing the THERM * SWE_{acc} interaction in addition to THERM and THERM * $WOLF_{days}$ was ranked 3rd, but the ΔAIC_c was just under 2 and the 95% confidence intervals for the THERM * SWE_{acc} coefficient estimate spanned zero ($\beta_{THERM * SWEacc}$ = 0.42, 95% CI = -1.35 to 2.16) (Arnold 2010). Both coefficient estimates for THERM * $WOLF_{days}$ and THERM in the top and second ranked models, respectively, were positive as predicted, though the corresponding 95%

confidence intervals for both estimates barely spanned zero ($\beta_{THERM * WOLFdays} = 0.04$, 95% CI = 0.00 to 0.08; $\beta_{THERM} = 11.09$, 95% CI = - 1.05 to 22.58), providing some evidence that the positive effect of $WOLF_{days}$ on the odds of elk dying became stronger in areas with more thermal influence (Figure 11).

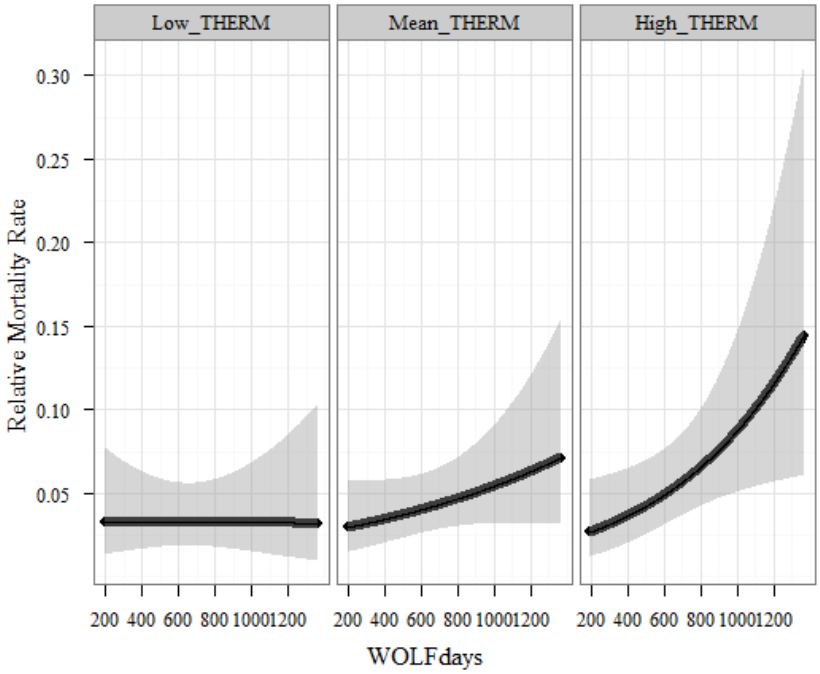


Figure 11: Predicted relative mortality rate with 95% confident intervals (grey shading) for low, average, and high levels of THERM as wolf days increase for average aged elk.

The single landscape model suite for edge excluded the $WOLF_{days}$ covariate given the collinearity between $WOLF_{days}$ and EDGE. The top model was the post-wolf base model (minus $WOLF_{days}$), though the model containing EDGE gained some support (AIC_c weight = 0.37) and was only 0.63 AIC_c units from the top model (Table 8). Furthermore, the coefficient estimate for EDGE was positive as predicted, but the corresponding 95% confidence interval spanned zero ($\beta_{EDGE} = 0.12$, 95% CI = -0.08,

0.30). Thus, edge may have had some minor importance post-wolf and as predicted, was positively related to the odds of elk dying.

The null model was the best supported model in both the burned and unburned forest model suites (Table 8). However, burned forest may have had some importance, given the second ranked model in the suite containing the BF covariate was only 0.25 ΔAIC_c from the top model and carried 32% (versus 36% by the top model) of model weight. Furthermore, the third ranked model in the suite was just under 2 ΔAIC_c with the addition of two parameters, BF and BF * $WOLF_{days}$, also indicating some support in the data for BF. The interaction between BF and $WOLF_{days}$ in the third ranked model was positive as predicted though the 95% CIs for the corresponding coefficient estimate spanned zero ($\beta_{BF * WOLFdays} = 0.01$, 95% CI = -0.02, 0.03). Likewise unburned forest was considered to have some biological importance given the low ΔAIC_c score (1.11) of the second ranked model containing the two additional covariates UF and UF * $WOLF_{days}$ (AIC_c model weight = 0.21). As predicted, the coefficient estimate for the UF * $WOLF_{days}$ interaction was negative, indicating that the effect of increasing $WOLF_{days}$ on the odds of elk dying may have been slightly less in areas with high amounts of unburned forest, though the confidence interval for the interaction coefficient barely spanned zero ($\beta_{UF * WOLFdays=}$ -0.008, 95% CI = -0.019, 0.001).

The best supported model in the meadow habitat suite contained the covariates MEAD and MEAD * SWE_{acc} (AIC_c model weight = 0.29). Thus, the relationship between meadow and the odds of elk mortality may have depended on accumulated snow pack. The coefficient estimate for the interaction provides some support of a positive relationship, but results were somewhat equivocal because the 95% confidence intervals

for the estimated coefficient just overlapped zero ($\beta_{MEAD * SWEacc} = 0.79$, 95% CI = -0.04, 1.69). The third ranked model had a ΔAIC_c score of 0.74 and contained the additional covariate MEAD * $WOLF_{days}$. Likewise, the coefficient estimate for MEAD * $WOLF_{days}$ was positive, but the corresponding 95% CI spanned zero ($\beta_{MEAD * WOLFdays} = 0.02$, 95% CI = -0.01, 0.04).

Slope was related to all landscape covariates except elevation (Figure 4A, Appendix A) and, therefore, was only considered in post-hoc exploratory analysis. Model selection results indicate slope was important in the presence of wolves (Table 8). The top model in the suite contained the covariates SLOPE and SLOPE * $WOLF_{days}$, and all four models containing SLOPE fell within 4 ΔAIC_c of the top model (Table 8D, Appendix D). The null model was the lowest ranked model ($\Delta AIC_c > 4$) and carried only 4% of model weight. As predicted, the interaction between SLOPE * $WOLF_{days}$ was negative, though the 95% confidence intervals spanned zero ($\beta_{SLOPE * WOLFdays} = -0.0002$, 95% CI = -0.0006, 0.00005). However, the coefficient estimate for SLOPE from the second ranked model ($\Delta AIC_c = 0.59$) without the SLOPE * $WOLF_{days}$ interaction was negative and the corresponding 95% confidence interval did not span zero ($\beta_{SLOPE =} -0.12$, 95% CI = -0.22, -0.02).

Table 8: Model selection results for the post-wolf single landscape model suites. Only top landscape models within 2 ΔAIC_c of the top model and the base (null) model were included in the table below (see Appendix D for complete model selection results including all models considered). Note: BM = Base Model = AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc}.

			Within Suite	
Model Structure	***K***	**AIC_c**	**ΔAIC_c**	w_{ic}
Elevation Suite				
BM+ ELEV + ELEV * SWE_{acc}	7	258.99	0.00	0.66
BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$	8	260.36	1.38	0.33
BM	5	278.27	19.29	0.00
Deep River Suite				
BM + RivDeep	6	263.15	0.00	0.63
BM + RivDeep + RivDeep * $WOLF_{days}$	7	264.20	1.06	0.37
BM	5	278.27	15.13	0.00
EdgeSuite				
BM	4	278.19	0.00	0.50
BM + EDGE	5	278.82	0.63	0.37
Thermal Suite				
BM + THERM + THERM * $WOLF_{days}$	7	276.09	0.00	0.38
BM + THERM	6	277.08	1.00	0.23
BM + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	8	277.91	1.82	0.15
BM	5	278.27	2.19	0.13
Meadow Suite				
BM + MEAD + MEAD * SWE_{acc}	7	277.73	0.00	0.29
BM	5	278.27	0.55	0.22
BM + MEAD + MEAD * SWE_{acc} + MEAD * $WOLF_{days}$	8	278.46	0.74	0.20
BM + MEAD + MEAD * $WOLF_{days}$	7	278.90	1.17	0.16
BM + MEAD	6	279.16	1.44	0.14
Burned Forest Suite				
BM	5	278.27	0.00	0.36
BM + BF	6	278.52	0.25	0.32
BM + BF + BF * $WOLF_{days}$	7	280.26	1.99	0.13
Unburned Forest Suite				
BM	5	278.27	0.00	0.36
BM + UF + UF * $WOLF_{days}$	7	279.39	1.11	0.21
BM + UF + SWE_{acc} * UF	7	280.05	1.77	0.15
BM + UF + UF * SWE_{acc} + UF * $WOLF_{days}$	8	280.08	1.81	0.15
BM + UF	6	280.13	1.85	0.14
Slope Suite				
BM + SLOPE + SLOPE * $WOLF_{days}$	7	273.54	0.00	0.39
BM + SLOPE	6	274.13	0.59	0.29
BM + SLOPE + SLOPE * SWE_{acc} + SLOPE * $WOLF_{days}$	8	275.21	1.67	0.17
BM	5	278.27	4.74	0.04

Post-Hoc Exploratory Results

Removing AGE and AGE * SWE_{acc} from the top post-wolf landscape model did not improve model fit, with the original top model containing AGE and AGE * SWE_{acc} carrying 86% of model weight (Table 1E, Appendix E). However, comparing the strength of the coefficient estimates for AGE between pre- and post-wolf models suggests age was less important in the presence of wolves. For example, during the pre-wolf years the odds of dying for a 16-year-old elk was 84 times that of an 8-year-old elk for any level of SWE_{acc} (95% CI for the odds ratio = 12.4 to 564.4). However, in the presence of wolves, the odds of dying for a 16-year-old elk was only 14 times that of an 8-year-old elk at high levels of SWE_{acc} (95% CI for the odds ratio = 3.7 to 55.3). Furthermore, the distributions of elk age show a clear discrepancy between the pre-wolf age distribution and age of elk killed by starvation. Only older age classes were killed by starvation, (Figures 2 and 3) whereas the age distribution of elk killed by wolves more closely matched the distribution of the available age classes of elk. The age distribution for wolf-killed elk was directly proportional to the age distribution of living elk, suggesting that wolves were not selecting for older age classes—rather, they were taking what was proportionally available to them (Figures 2 and 3). See Appendix E for post-hoc exploratory results and discussion for removing non-wolf predations and adding dispersal events.

Landscape Vulnerability Maps

Landscape vulnerability maps representing areas of relative vulnerability or "risk" across the study area illustrate the contrast in landscape dependent mortality risk between pre- and post-wolf years and between low and high levels of wolf presence based on results from the analysis (Figure 12). Mortality risk for an average/prime age elk in low snow pack conditions during the pre-wolf years was extremely low and uniform across the study tract (upper left). However, older aged individuals in high snowpack conditions experienced a modest increase in mortality risk across the study tract during the pre-wolf years (upper right), with slightly elevated risk in some geothermally influenced areas where elk often congregated. Though not apparent here, in extreme snowpack conditions mortality risk was actually greater in those areas with less thermal influence according to the results. Likewise, mortality risk for prime age elk was relatively low and homogenous across the study tract in mean snow pack conditions and at low levels of wolf presence in the post-wolf years (lower left). However, at high levels of wolf presence, elk experienced highly spatially heterogeneous mortality risk across the study tract, with distinct areas that were much more (i.e. Gibbon and Firehole) or much less (i.e. Madison and northern portion of the Firehole) risky (lower right).

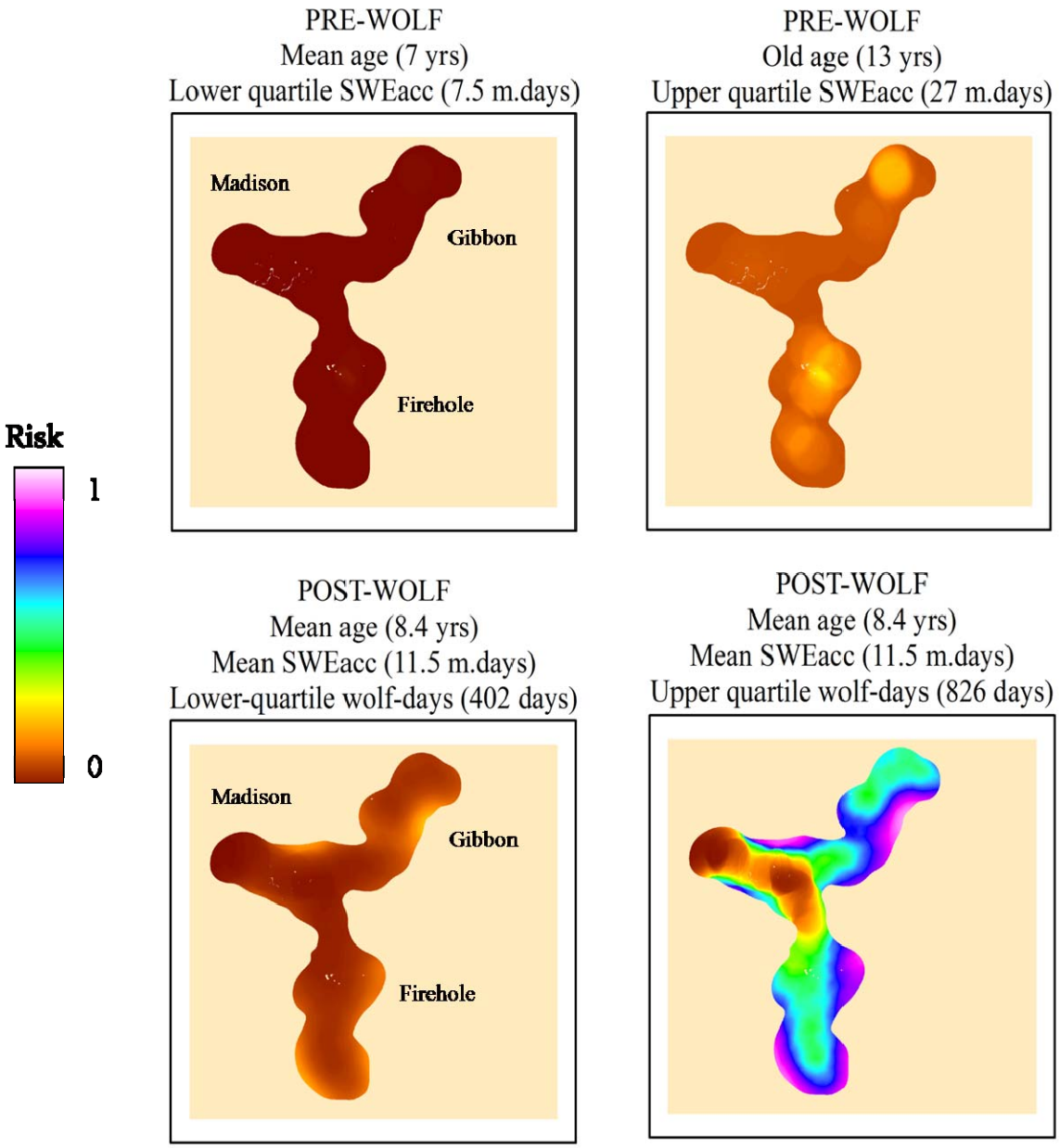


Figure 12: Landscape vulnerability maps representing areas of relative vulnerability or "risk" across the study area for pre and post-wolf periods based on coefficient estimates from the top pre and post-wolf models. The pre-wolf maps illustrate risk across the landscape for two age classes (prime age individuals (i.e., mean age = 7 years) and older individuals (13 years) at two levels of snow pack (low = 7.5 m (0.25^{th} quantile) and high = 27 m (0.75^{th} quantile) SWE_{acc}). The post-wolf maps illustrate landscape risk at two levels of wolf presence, low (wolf days = 402 (25^{th} quantile)) and high (wolf days = 826 (75^{th} quantile)), for average aged individuals (mean age = 8.4 years) and at mean snow pack levels (mean SWE_{acc} = 11.5). The maps are plotted on a probability scale though actual predictions cannot directly be interpreted as probabilities as discussed in the Investigation of Potential Assumption Violations section.

Assessing Lack of Independence: Results from the Analysis Using Generalized Estimating Equations

According to the results obtained from using Generalized Estimating Equations (GEEs) there was little evidence of cluster effects due to repeated measures on individual elk or within a year. The standard errors for the fixed effects were essentially the same for a model allowing for dependence among observations from the same individual (Table 9) and for one allowing for dependence among observations from the same year (Table 10). Thus, I concluded that any lack of independence did not result in misleading confidence intervals and was therefore confident in using the standard errors from the GLM analysis for interpretation.

Table 9: Coefficient estimates and corresponding standard errors for the top post-wolf landscape model using Generalized Estimating Equations (GEEs) with a random effect for Elk ID, compared to the results obtained from using GLM.

Coefficient	GEE		GLM	
	Estimate	Std.error	Estimate	Std.error
(Intercept)	-68.5900	20.3100	-69.9500	20.0100
AGE	0.0227	0.1043	0.0110	0.1020
$WOLF_{days}$	0.0095	0.0030	0.0095	0.0037
SWE_{acc}	3.9340	1.0770	4.0170	1.1770
ELEV	2.7460	0.8621	2.8060	0.8262
RivDeep	0.0180	0.0156	0.0189	0.0223
EDGE	0.1105	0.2838	0.1169	0.3347
AGE:SWE_{acc}	0.0179	0.0076	0.0181	0.0078
SWE_{acc}:ELEV	-0.1809	0.0463	-0.1846	0.0509
$WOLF_{days}$:RivDeep	-0.0001	0.0000	-0.0001	0.0000
$WOLF_{days}$:EDGE	-0.0007	0.0004	-0.0007	0.0004

Table 10: Coefficient estimates and corresponding standard errors for the top post-wolf landscape model using Generalized Estimating Equations (GEEs) with a random effect for YEAR, compared to the results obtained from using GLM.

Coefficient	GEE		GLM	
	Estimate	Std.error	Estimate	Std.error
(Intercept)	-78.7900	26.2400	-69.9500	20.0100
AGE	-0.0155	0.1269	0.0110	0.1020
$WOLF_{days}$	0.0119	0.0016	0.0095	0.0037
SWE_{acc}	4.3240	0.8134	4.0170	1.1770
ELEV	3.1470	1.0950	2.8060	0.8262
RivDeep	0.0253	0.0152	0.0189	0.0223
EDGE	0.2679	0.1323	0.1169	0.3347
AGE:SWE_{acc}	0.0195	0.0088	0.0181	0.0078
SWE_{acc}:ELEV	-0.1985	0.0327	-0.1846	0.0509
$WOLF_{days}$:RivDeep	-0.0001	0.0000	-0.0001	0.0000
$WOLF_{days}$:EDGE	-0.0010	0.0002	-0.0007	0.0004

DISCUSSION

This is the first study to use survival data for radio-collared elk before and after wolf restoration to account for the influence of age and condition (i.e., physical vulnerability), in addition to landscape and climatic variables associated with individual elk home ranges. I demonstrated the importance of environmental vulnerability in a large mammal system through analysis of 18 years of elk survival data across varying temporal and spatial scales of wolf predation risk. In the absence of wolf predation, mortality risk for elk was primarily related to physical attributes of elk due to age and condition, the latter indexed by accumulated snow pack. Following wolf reintroduction, mortality risk was related to these elk physical characteristics in addition to landscape attributes and climatic variables within an animal's home range. While the complexity of significant spatial correlation and configuration of landscape attributes within the study area made evaluating the relative effects of individual attributes difficult, my results clearly demonstrate the importance of landscape and environmental vulnerability in relation to wolf predation risk.

In the absence of wolves, prime age animals were less likely to die from starvation compared to senescent individuals and elk of all ages were more likely to die as snow pack increased. Evidence of this climate-age interaction as the primary driver in large ungulate survival or mortality risk supports general findings in many large ungulate systems lacking effective predators (Gaillard et al. 2000). This finding is also consistent with conclusions drawn from previous studies in the Madison headwaters system before wolf reintroduction, demonstrating survival senescence in older animals, with the

magnitude of snow pack effects differing depending on age of animal (Garrott et al. 2003, Garrott et al. 2009b). As predicted, the magnitude of the effect of snow pack in our system depended to some extent on the amount of geothermal area associated with elk home ranges, with starvation mortality risk reduced for elk occupying areas with higher proportions of geothermal area in severe snow pack conditions - likely due to geothermal heat allowing access to forage in otherwise deep snow conditions (Garrott et al. 2003, White et al. 2009b).

In contrast to pre-wolf years, landscape attributes were strongly associated with the odds of elk mortality following wolf establishment. Age was positively related to the odds of mortality at high levels of snow pack, but both age and snow pack assumed less importance than other landscape variables and compared to pre-wolf years. As expected, wolf presence was important and positively related to the odds of elk mortality, but depended on landscape attributes associated with elk home ranges. Some attributes such as higher elevation, and to a lesser extent increasing thermal area, meadow, and edge, were related to an increased wolf effect, while others such as deep river and slope were related to a decreased wolf effect. Thus, more wolves did not necessarily equate to more risk without considering the interactive effects of certain landscape attributes that rendered elk more or less vulnerable to predation depending on where they were on the landscape.

The two most important landscape attributes related to predation risk were elevation and deep river. The positive effect of wolf presence on the odds of elk dying was substantially reduced in areas with access to deep river habitat. The use of rivers and lakes as escape terrain by ungulates when being attacked by wolves has been well

documented (Carbyn 1974, Nelson and Mech 1981) and this was shown to be an important response/strategy in our system with areas containing sufficiently deep river serving as a partial refuge from wolf predation (White et al. 2009a). Conversely, elk were more likely to be killed by wolves in higher elevation areas, though given the spatial correlation of landscape attributes, the functional effect of elevation may also be due to attributes of the landscape that are associated with high versus low elevation areas (i.e., elevation serving as a surrogate for other landscape attributes) in addition to snow pack effects.

Though the results for other landscape attributes were less clear or in some cases confounded, the results indicate they still may have had some biological importance. For example, elk may have also experienced increased vulnerability in areas with high amounts of habitat edge, a finding consistent with previous work by Bergman et al. (2006) demonstrating that wolf kills often occurred along habitat edges that impeded effective escape by fleeing elk. In addition, predation risk may have been positively related to the proportion of meadow habitat associated with elk home ranges when levels of snow pack and wolf presence were high, a finding consistent with other studies demonstrating that ungulates avoided open grassland habitats presumably to reduce predation risk (Kunkle and Pletscher 2000, Creel and Winnie 2005, Fortin et al. 2005). Likewise, geothermal patches surrounded by deep snow may have served as environmental traps, representing areas of increased risk in the presence of wolves (Bergman et al. 2006, White et al. 2009a), while steep slopes were associated with a significant decrease in the odds of dying, perhaps due to increased detection of incoming predators below, allowing elk time to escape by moving to higher ground or fleeing into

deep water if available in the vicinity (Lingle and Pellis 2002, Kunkel et al. 2004). The results for both forest habitat attributes appeared to have very minor importance, though the coefficient estimates were in the predicted directions.

Landscape is inherently a multivariate concept, defined more by the configuration and interaction between various habitat and landscape attributes and less by its individual parts. Furthermore, in temperate high latitudes it is the collective characteristics of the landscape interacting with climatic conditions (i.e. snow pack) that defines a risky versus safe place on the landscape, and therefore do not suggest that these specific attributes will be similarly related to predation risk in other systems. Rather I emphasize that in the context of this study, despite the challenges of collinearity and complex model structure, I still detected a clear relationship between predation risk and deep river and elevation, and that in aggregate, combinations of the various attributes considered, clearly resulted in areas that were much more or much less dangerous to elk in the presence of wolves.

Overall, my results suggest that elk occupying areas with attributes that impede fleeing from attacking wolves (e.g., deep snow, geothermal terrain traps, habitat edges) were more vulnerable to predation. Conversely, elk occupying areas with shallow snow pack at lower elevations and with deep, swift river channels were less vulnerable to predation. This landscape level gradient in predation risk is further demonstrated by the dramatic contrast in landscape-dependent mortality risk between pre- and post-wolf years and between low and high levels of wolf presence illustrated by the vulnerability or risk maps presented in the results (Figure 12). These maps illustrate the contrast between landscape level mortality risk in the absence of wolves, where risk was spatially homogenous across the study area and essentially dependent on age of elk and snow

pack, compared to the highly spatially heterogeneous risk associated with high levels of wolf presence, with distinct areas that are much more (i.e., Gibbon and Firehole drainages) or much less (i.e., Madison drainage) risky.

Though various packs frequently hunted within the Madison drainage, they appeared to have a difficult time making kills there (Becker et al. 2009b). Based on my results, a large portion of this apparent refuge effect is due to the deep, wide, ice-free river channel amid a meadow complex bordering steep and extensive south facing slopes which have reduced snow pack (White et al. 2009a). Furthermore, the Madison drainage is the lowest in elevation, has the least amount of edge and the most unburned forest of the three drainages in the headwaters area, and has little geothermal influence potentially creating terrain traps in high snow pack conditions. In contrast, the Gibbon drainage is characterized by landscape attributes that are positively related to predation risk, resulting in an area of particularly high vulnerability. The Gibbon River is shallow and narrow in its entirety, and the drainage has the highest elevation (deepest snow pack) of the three drainages, with a substantial amount of geothermal influence creating extensive geothermal terrain traps where many wolf kills have been found (Bergmann et al. 2006). The Firehole drainage represents an area of moderately high vulnerability. Though it contains the highest amount of edge and has the most geothermal habitat of the three drainages, it also contains a few small segments of river both deep and wide enough to serve as potential escape terrain. Also, the Firehole drainage has several large interconnected thermally influenced basins with reduced snow pack potentially allowing for effective escape from wolf attacks by fleeing elk.

If these models are indeed indicative of elk vulnerability to predation then we would predict/expect substantial changes in elk distribution as the system transitioned from a landscape devoid of wolves (when elk were formally equally distributed among the three drainages in the study area) to a well-established wolf-ungulate system, and based on long-term mark-resight studies conducted in the Madison headwaters area this prediction was indeed realized (Figure 13). This landscape-level heterogeneity in wolf predation risk resulted in a dramatic change in distribution and abundance of elk in the Madison headwaters area. By the end of our study > 92% of the remaining elk population used the Madison drainage, with no elk detected wintering in the Gibbon drainage and a few elk residing in the Firehole drainage (Figure 13; White et al. 2009a). This change in distribution resulting in the virtual disappearance of elk wintering in the Gibbon and Firehole drainages was primarily due to wolf predation removing animals and a modest level of dispersal by elk from their winter home ranges to areas outside the Madison headwaters - presumably in an attempt to reduce predation risk following wolf re-establishment (Gower et al. 2009).

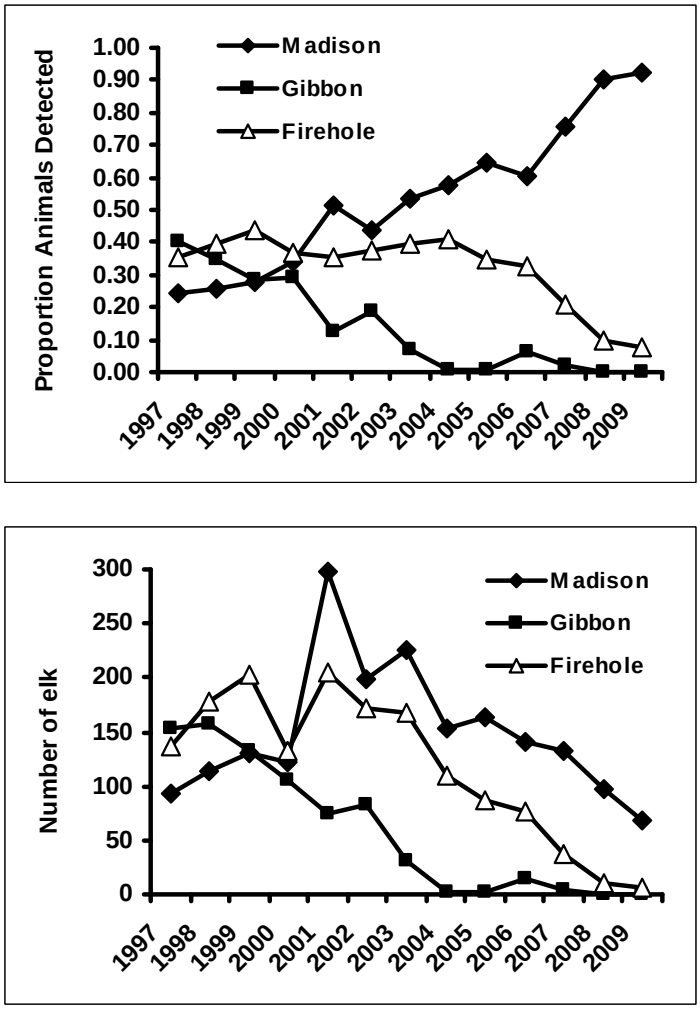


Figure 13: Estimated changes in the proportion of the elk population and the total number of the elk occupying the Madison, Gibbon, and Firehole River drainages from 1997 through 2009. Estimates were based on replicate (n= 10-33) mark-resight surveys conducted during spring green-up in April when elk were concentrated in meadows adjacent to the road system (Garrott et al. 2009c).

Wolves have the propensity to seek out and kill the sick, weak, young or old individuals in a population (see Mech and Peterson 2003), sometimes referred to as the "doomed surplus" (Errington 1946, 1967), given the formidable challenge associated with killing larger often dangerous prey (Mech and Peterson 2003, Smith et al. 2003, MacNulty et al. 2007, Garrott et. al 2007). In some cases wolf predation may be

primarily compensatory as a result, with predation simply replacing other mortality sources (Errington 1946, 1967). However, in the Madison headwaters system interactions between physical, and behavioral vulnerability and characteristics of the environment resulted in mortality that was substantially additive due to characteristics of the landscape creating traps for what could otherwise be considered healthy animals - the good animals in bad places concept (Garrott et al. 2009a,b,c). Following wolf reestablishment, elk continued to use high risk habitats such as meadows and geothermal areas in places within close proximity to refuge habitat (White et al. 2009a). Elk also became more predictable in space and time, congregating in the open meadow complexes along river ways in the Madison drainage and along deep portions of the Firehole River. Though wolves frequently hunted in the Madison drainage (Becker et al. 2009a,b), resulting in a high probability of wolf encounter, elk also realized a high probability of escape due to the collective characteristics of the landscape promoting a predation refuge (Lima 1992, Abrams and Walters 1996, Berryman and Hawkins 2006, White et al. 2009a). This preference for apparently dangerous habitat (i.e., in open and highly predictable areas) is consistent with Lima's (1992) hypothesis that prey can tolerate a high risk of encounter by predators in a particular area provided there is also a high probability of escape due to the existence of refuge habitat (Lima 1992).

In general, my findings suggest environmental vulnerability can result in additive mortality for otherwise healthy animals, which could have broad ecological implications for predator-prey dynamics. Also, the dramatic change from a broadly distributed prey in the absence of effective predators, to a dramatically reduced distribution consisting of landscape refuges following predator restoration, emphasizes the importance of refuges

and their consequences on predator-prey dynamics in general (Lima 1992, Abrams and Walters 1996, Berryman and Hawkins 2006). Ultimately, the extent of refuge habitat may in part dictate the carrying capacity of predator and prey populations by serving as a limiting resource within a system, where prey compete for occupancy and predators compete to exploit the high density prey area (Berryman and Hawkins 2006; White et al. 2009a). As a result the stability and persistence of predator-prey systems may depend largely on variation in predation rates and prey vulnerability caused by landscape heterogeneity (Kareiva and Wennegren, 1995, Ellner et al. 2001) and the presence of prey refugia (Ruxton 1995, Berryman and Hawkins 2006).

Many large mammal predator-prey studies assume predator distribution is a surrogate for prey vulnerability to predation (Creel et al. 2005, Fortin et al. 2005) and that prey habitat is representative of prey availability for predators (see Keim et al. 2011). In real landscapes with large highly mobile predator and prey populations, however, predation risk is not necessarily highest in areas where predators are most abundant or where prey are most likely to come in to contact with predators (Wirsing et al. 2010). As I have demonstrated, predation risk also depends on landscape and environmental factors as well as prey escape modes (e.g., anti-predation tactics) (Heithaus et al. 2009, Wirsing et al. 2010) and predator hunting strategies (Atwood et al. 2009). Indeed, wolves in our system successfully exploited those elk made vulnerable by their surrounding landscape, rather than targeting areas with the highest prey densities (Bergmann et al. 2006). Furthermore, the elk distributional changes following wolf re-establishment did not result in a decoupling of wolves and elk (i.e., wolves remained closely associated with elk). Thus, variation in predation risk across the study area was not due to differences in

detection or encounter probabilities, but differences in vulnerability of elk once attacked (Bergman et al. 2006, Garrott et al. 2009a).

Furthermore, the vast majority of our knowledge regarding the effects of spatial heterogeneity on predator-prey dynamics comes from systems of smaller taxa, or sessile organisms (Gorini et al. 2011), where encounter rates are of primary importance and environmental factors primarily influence probability of detection (e.g. Stoner 2009). In these systems, prey are typically smaller than their predator and thus their primary means of reducing predation risk is through hiding or avoiding detection (often by use of cover in complex habitats) (Beukers and Jones 1997, Lewis and Eby 2002), and thus the outcome of the predation attempt largely depends on whether the predator can find/encounter its prey (e.g. low encounter rates, but high likelihood of capture/kill once encountered) (e.g. Stoner 2009). These insights however, may be less applicable to some systems of larger taxa, where encounter rates (as they relate to predation risk) may assume less importance for large conspicuous prey such as elk for example, that typically congregate in large/open predictable places such as meadow complexes to gain access to forage in the winter months, and whose primary escape mode or means of reducing predation risk, is through fleeing (MacNulty et al. 2007). Thus, intelligent, coursing predators such a wolves are less limited in their ability to locate elk (e.g., encounter rates high) than by the challenging, often dangerous, act of capturing and killing prey once they are encountered (Mech and Peterson 2003, Smith et al. 2003, Garrott et al. 2007, MacNulty et al. 2007).

Furthermore, because the primary escape mode for elk is through fleeing (MacNulty et al. 2007), they naturally interact with the landscape because physical

structures can impede their ability to effectively escape and avoid predation. In contrast, other large ungulates may use grouping and aggression to reduce predation risk (Carbyn et al. 1993, MacNulty et al. 2007), tactics that are much less affected by physical surroundings. Landscape may also assume more importance for prey with cursorial predators that are unpredictable and continuously moving (Lima and Bednekoff 1999) because prey cannot simply avoid areas with high predator presence, compared to sit-and-wait/ambush predators that provide more information about local predation risk (Thaker et al. 2011, Gorini et al. 2011). Furthermore, the pursuit is likely the most important stage of the predation process for cursorial predators (Kunkel et al. 1999), with the outcome depending heavily on the type of terrain through which the pursuit takes place (Gorini et al. 2011). Overall, the importance of landscape and environmental vulnerability clearly depends on the system, landscape, and type of predator and prey involved. Consequently, continued studies looking at the effects of landscape and environmental vulnerability on predator-prey dynamics in large mammal systems have the potential to yield significant insights (Hobbs 1996, Garrott et al. 2007).

Elk and Wolf Dynamics: Implications for Management

The dramatic wolf impact seen in the Madison headwaters area demonstrates the importance and potential consequences of environmental vulnerability and a highly risky landscape. Overall, the study area is a high elevation deep snow pack environment that has a significant amount of habitat complexity creating terrain traps and hard edges between habitats affecting prey mobility, and the ability of fleeing elk to effectively escape predation. In this type of system, we can expect a biologically significant

proportion of predation to be additive, resulting in substantial declines in elk numbers and changes in distribution to the extent that remaining elk primarily occupy landscape refuges as I have demonstrated here. Throughout the greater Yellowstone ecosystem, we can expect broad landscape-level shifts in elk distribution, to lower elevation low snow pack environments such as the large continuous wind-swept grassland meadows found outside of Yellowstone National Park (i.e. Madison Valley, Paradise Valley), and indeed these distributional shifts are already being documented. Elk are coursing animals and have evolved to outrun predators in open habitats (Geist 2002), and as a result have a relatively high probability of escape when attacked by wolves in open environments (Mech et al. 2001). Thus, these lower elevation areas likely represent areas of decreased vulnerability to wolf predation, resulting in predation that is more compensatory, where wolves primarily target and successfully kill young, old, sick, and weak individuals (Mech and Peterson 2003). Historically, elk and wolves may have coexisted in large numbers because elk took advantage of altitudinal migration to lower elevation habitats such as these to reduce predation risk (Fryxell et al. 1988). Thus, these broad landscape level shifts may eventually result in a distribution that more closely reflects the historical ranges of elk before wolves were extirpated. The restoration of top predators such as wolves emphasizes the need for management at the landscape scale by ensuring suitable habitat is available for predator and prey to effectively maintain long-term predator-prey assemblages. Of utmost importance is the protection of low elevation, extensive grassland winter ranges and predation refuges, allowing elk to successfully employ behaviors that reduce predation risk (i.e., fleeing and seasonal migration).

Conclusion

I demonstrated the importance of landscape in relation to vulnerability to predation and the potential for environmental vulnerability in driving dynamics of large mammal predator-prey systems. Following wolf re-establishment, elk mortality risk was strongly related to characteristics of the landscape and climate within an animal's home range in addition to age and body condition. As a result of this landscape level heterogeneity in predation risk, a dramatic change in elk distribution in the Madison headwaters area was realized following wolf re-establishment, from a broadly distributed prey to a dramatically reduced one occupying a landscape refuge, perhaps representing the historical distribution (and abundance) of elk during the winter in the Madison Headwaters area before wolves were extirpated. This change in distribution to areas with a high probability of encounter, but also a high probability of escape, further emphasizes the importance of refuges in an otherwise risky landscape (Lima 1992). The study also highlights the importance of variation in predation rates and prey vulnerability caused by landscape heterogeneity (Kareiva and Wennegren, 1995; Ellner et al., 2001) and the presence of prey refugia (Ruxton 1995, Berryman and Hawkins 2006) in driving predator-prey dynamics and promoting stability and persistence of predator–prey systems. Overall, the demonstrated relationship between environmental /landscape attributes and prey vulnerability to predation has broad applications to other wolf-elk systems and large mammal predator prey dynamics in general. My findings suggest that snow pack severity and the spatial distribution and abundance of landscape attributes that serve as refuges that decrease predation risk, or traps that increase predation risk, will

determine elk distribution (White et al. 2009a), abundance, and ultimately persistence within a system (Garrott et al. 2009a).

Empirical evidence demonstrating the importance of landscape and habitat heterogeneity on predation risk, while accounting for physical attributes such as age and condition, is lacking for non sessile organisms in real life settings. Gorini et al. (2011) suggested that quantifying the number and availability of vulnerable prey as a function of spatial features in addition to physical state (i.e. age) would be a promising extension of field studies. This study represents an initial contribution towards understanding the relationship between habitat, landscape, and climatic variables and large mammal prey vulnerability while independently accounting for physical vulnerability of prey. I recognize that this investigation represents an initial case study and that additional field studies will be required to strengthen our ability to infer direct impacts and applicability across systems. In the face of landscape transformation and global efforts to restore top predators to ecosystems, that the impacts of environmental vulnerability are highly variable, and context and predator and prey-dependent, further emphasizes the need for additional long-term field studies of large mammal predator-prey dynamics. Specifically, evaluating the contribution of physical, behavioral, and environmental vulnerability and the interactions between them in natural systems could vastly improve our understanding of large mammal predator-prey dynamics.

LITERATURE CITED

Abrams, P. A., G. G. Mittlebach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371-395 in G. A. Polis and K. O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, London, UK.

Abrams, P. A., and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. Ecology 77:1125-1133.

Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89:2273–2280.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. Journal of Wildlife Management 73:876-884.

Becker, M. S., R. A. Garrott, P. J. White, C. N. Gower, E. J. Bergman, and R. Jaffe. 2009a. Wolf prey selection in an elk-bison system: choice or circumstance?, Pages 305-337 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Becker, M. S., R. A. Garrott, P. J. White, R. Jaffe, J. J. Borkowski, C. N. Gower, and E. J. Bergman. 2009b. Wolf kill rates: predictably variable? Pages 339-369 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Bergerud, A. T., H. E. Butler, and D.R. Miller. 1984. Antipredator tactics of calving caribou: Dispersion in mountains. Canadian Journal of Zoology 62:1566-75.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological applications 16:273-284.

Berryman, A. A., and B. A. Hawkins. 2006. The refuge as an integrating concept in ecology and evolution. Oikos 115:192-196.

Beukers, J. S., and G. P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114:50-59.

Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K, Maier. 1999. Birth-site selection by Alaskan moose: Maternal strategies for copying with a risky environment. Journal of Mammalogy 80:1070-83.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, second edition. Springer, New York, New York.

Caro, T. 2005. Antipredator Defenses in Birds and Mammals. University of Chicago Press, Chicago, Illinois.

Carbyn, L. N. 1974. Wolf Predation and Behavioral Interactions with Elk and Other Ungulates in an Area of High Prey Diversity. Canadian Wildlife Service, Edmonton, Alberta, Canada.

Carbyn, L. N., S. M. Oosenbrug, and D. W. Anions. 1993. Wolves, Bison and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute, Alberta, Canada.

Christian, K. A., and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia 49:218-223.

Clark, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). Behavioral Ecology and Sociobiology 13:205-209.

Creel, S., J. A. Winnie Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Cooch, E. G., and G. C. White [ONLINE]. 2009. Program MARK: A Gentle Introduction. www.phidot.org/software/mark/docs/book/ (16 October 2009).

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997-1012

Eberhardt, L. L., P. J. White, R. A. Garrott, and D. B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. Journal of Wildlife Management 71:594-602.

Ellner, S. P., E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, and W. W. Murdoch. 2001. Habitat structure and population persistence in an experimental community. Nature 412:538-542.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology 21:145-177, 221-245.

Errington, P. L. 1967. Of Predation and Life. Iowa State University Press, Ames, Iowa.

FitzGibbon, C. D., and J. Lazarus. 1995. Anti-predator behavior of Serengeti ungulates: individual differences and population consequences. Pages 274-296 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fryxell, J.M., J. Greever, A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131, 781-798.

Gaillard, J. -M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components of population dynamics in large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Garrott, R. A., P. J. White, D. B. Vagoni, and D. M. Heisey. 1996. Purine derivatives in snow-urine as a dietary index for free ranging elk. Journal of Wildlife Management 60:735-743.

Garrott, R. A., L. L. Eberhardt, P. J. White, J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81: 33-45.

Garrott, R. A., J. E. Bruggeman, M. S. Becker, S. T. Kalinowski, and P. J. White. 2007. Evaluating prey switching in wolf-ungulate systems. Ecological Applications 17:1588-1597.

Garrott, R. A., P. J. White, M. S. Becker, and C. N. Gower. 2009a. Apparent competition and regulation in a wolf-ungulate system: interactions of life history characteristics, climate, and landscape attributes Pages 519-577 inR. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Garrott, R. A., P. J. White, and J. R. Rotella. 2009b. The Madison headwaters elk herd: Stability in an inherently variable environment. Pages 191-216 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen years of Integrated Field Studies. Elsevier, San Diego, California.

Garrott, R. A.,P. J. White, and J. Rotella. 2009c. The Madison headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. Pages 489-517 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Geist, V. 2002. Adaptive behavioral strategies. Pages 389-433 in D. E. Toweill, and J. W. Thomas, editors. North American Elk: Ecology and Management. Smithsonian Institute Press, Washington, D.C..

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. B. Nilsen. 2011. Habitat heterogeneity and mammalian predator-prey interactions. Mammal Review. doi: 10.1111/j.1365-2907.2011.00189.x

Gower, C. N., R. A. Garrott, P. J. White, F. G. R. Watson, S. S. Cornish, and M. S. and Becker. 2009. Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. Pages 373-399 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Grabowski, J. H., and S. P. Powers. 2004. Habitat complexity mitigates trophic transfer on oyster reefs. Marine Ecology Progress Series 277:291-295.

Gregory, R.S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions American Fisheries Society 127:275-285.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441-449.

Hamlin, K. L., R. A. Garrott, P. J. White, and J. A. Cunningham. 2009. Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. Pages 541-577 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier Academic Press, San Diego, California.

Heithaus M. R., A. J. Wirsing, D. Burkholder, J. Thomson, and L. M. Dill. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. Journal of Animal Ecology 78:556-562.

Hebblewhite, M., E. H. Merrill and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: An example in a wolf elk predator-prey system. Oikos 111:101-111.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of European pine sawfly. Canadian Entomology 91:293-320.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559-566.

Jaffe, R. 2001. Winter Wolf Predation in an Elk-Bison System in Yellowstone National Park, Wyoming. Thesis, Montana State University, Bozeman, Montana.

Jedrzejewski,W., B. Jedrzejewska, H. Okarma, and A.L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialoweiza National Park, Poland. Oecologia 90:27-36.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302.

Kauffman, M. J., N. Varley, D. W. Smith, D.R. Stahler, D.R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecological Letters 10:690-700.

Keim, J. L., P. D. DeWitt, and S. R. Lele. 2011. Predators choose prey over prey habitats: evidence from a lynx-hare system. Ecological Applications 21:1011-1016.

Kerfoot, W. C., and A. Sih, editors. 1987. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover, New Hampshire.

Knapp, C. R, S. Alvarez-Clare, and C. Perez-Heydrich. 2010. The influence of landscape heterogeneity and dispersal on survival of neonate insular iguanas. *Copeia* 62-70.

Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78:150-157.

Laundré, J. W., and L. Hernández. 2003. Winter hunting habitat of pumas (*Puma concolor)* in northwestern Utah and southern Idaho, USA. Wildlife Biology 9:123-129.

Lewis, D. B., and L. A. Eby. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos 96:119-129.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S. L. 1992. Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. Oikos 64:597-600.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649–659.

Loison, A., M. Festa-Bianchet, J.- M. Gaillard, J. T. Jorgenson, and J.- M. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539-2554.

MacNulty, D. R., L. D. Mech, and D. W. Smith. 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. Journal of Mammalogy 88:595-605.

Mech, L. D., T. J. Meir, J. W. Burch, and L. G. Adams. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. Pages 231-243 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.

Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65:998-1003.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131-160 in L.D. Mech and L. Boitani, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois.

Messer, M. A., R. A. Garrott, S. Cherry, P. J. White, F. G. R. Watson, and E. Meredith. 2009. Elk winter resource selection in a severe snow pack environment. Pages 138-156 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1-131.

Nelson, M. E., and D. L. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 77: 3-53.

Nelson, M. E., and D. L. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-74.

Newman, W. B., and F. G. R. Watson. 2009. The central Yellowstone landscape: terrain, geology, climate, vegetation. Pages 18-35 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: SixteenYears of Integrated Field Studies. Elsevier, San Diego, California.

Panzacchi, M., J. Linnell, M. Odden, J. Odden, and R. Andersen. 2009. Habitat and roe deer fawn vulnerability to red fox predation. Journal of Animal Ecology 78:1124-1133.

Peckarsky, B. L. 1984. Predator-prey interactions among aquatic insects. Pages 196-254 in V. H. Resh and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York.

Preisser, E. L., D. I. Bolnick, and M. F. Bernard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

Quinn, J. L., and W. Cresswell. 2004. Predator hunting behavior and prey vulnerability. Journal of Animal Ecology 73:143-154.

Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth: A course in methods of data analysis. Duxbury Press. Pacific Grove, CA.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ruxton, G. D. 1995 Short term refuge use and stability of predator-prey models. Theoretical Population Biology 47:1-17.

Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. Trends in Ecology and Evolution 12:143-149.

Schauber, E. M., M. J. Connors, B. J. Goodwin, C. G. Jones, and R. S. Ostfeld. 2009. Quantifying a dynamic risk landscape: heterogeneous predator activity and implications for prey persistence. Ecology 90:240-251

Schmitz O. J., 1998. Direct and indirect effects of predation and predation in old-field interaction webs. American Naturalist 151:327-342.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 in W. C. Kerfoot and A. Sih, editors. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover, New Hampshire.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288-290.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. BioScience 53:330-340.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management 68:153-166.

Smith D. W., D. R. Stahler, and M. S. Becker. 2009. Wolf recolonization of the Madison headwaters area in Yellowstone. Pages 283-303 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Stephens, P. W., and R. O. Peterson. 1984. Wolf-avoidance strategies of moose. Holarctic Ecology 7:239-244.

Stephens D. W., and J. R. Krebs.1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

Stoner A. W. 2009. Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. Journal of Experimental Marine Biology and Ecology 382:54-60.

Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from their prey populations? Ecology 68:669-674.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology. 92: 398-407.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491-9.

Venables, W. N. and Ripley, B. D. 2002 Modern Applied Statistics with S. Fourth edition. Springer.

Watson, F.G.R., W.B. Newman, T.N Anderson, R. E. Lockwood, and R.A. Garrott. 2009a. Effects of Yellowstone's unique geothermal landscape on snow pack. Pages 53-66 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Watson, F. G. R., T. N Anderson, W. B. Newman, S. S. Cornish, and T. R. Thein. 2009b. Modeling spatial snow pack dynamics. Pages 85-112 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

Weisberg, S. 2005. Applied Linear Regression, Third Edition. Wiley, Hoboken, New Jersey.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA.

White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. Wildlife Society Bulletin 33:942-955.

White, P. J., R. A. Garrott, S. Cherry, F. G. R. Watson,, C. N. Gower,, M. S. Becker, and E. Meredith. 2009a. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. Pages 451-476 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California.

White, P. J., R. A. Garrott, J. J. Borkowski, K. L. Hamlin, and J. G. Berardinelli. 2009b. Elk nutrition after wolf recolonization of central Yellowstone. Pages 477-488 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier, San Diego, California, pp.477-488.

Wirsing, A. J., K. E. Cameron, and M. R. Heithaus. 2010. Spatial responses to predators vary with prey escape mode. Animal Behaviour 79:531-537.

APPENDICES

APPENDIX A

COVARIATE DEVELOPMENT PLOTS AND TABLES, DATA SUMMARY AND PAIRWISE PLOTS, AND FULL MODEL SELECTION RESULTS FOR PRE- AND POST-WOLF ANALYSES

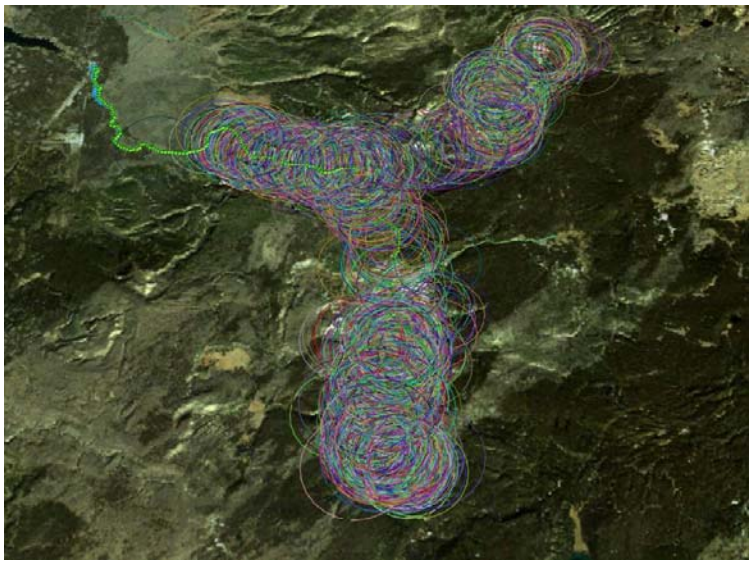


Figure 1A: Variable-radius circles representing each elk's home range for a given winter period constructed using GIS techniques.

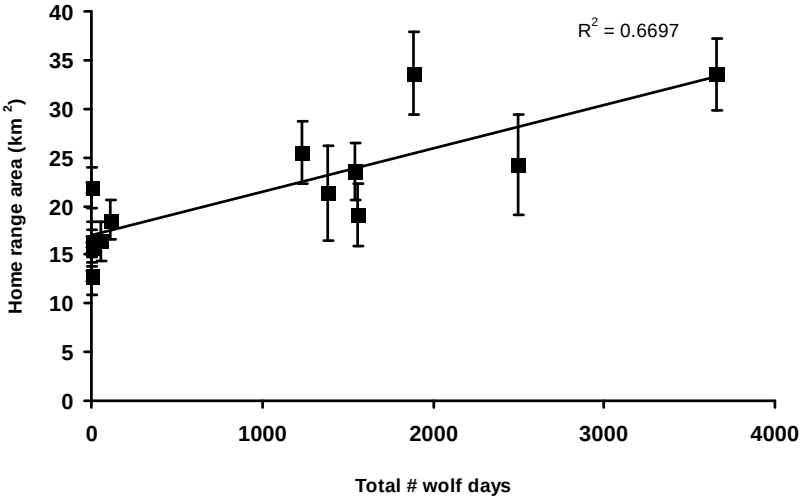


Figure 2A: Relationship between mean annual 95% fixed kernel elk home range areas vs. total number of wolf days (from Gower *et al.* 2009a).



Suitable escape habitat

Not suitable escape habitat

Figure 3A: Map used to delineate deep vs. shallow areas based on watershed area.

Table 1A: Covariate descriptions and predicted relationship with the odds of dying pre- and post-wolf.

Covariate Name	Description	Metric	Pre-wolf Prediction	Post-wolf Prediction	Comments
$WOLF_{days}$	Total # of wolf days study area-wide per winter period.		NA	+	
AGE	AGE of elk	years	+	+	Stronger relationship pre-wolf.
SWE_{mean}	Mean daily SWE, study area wide per winter period.	cm	+	+	Stronger relationship pre-wolf.
SWE_{acc}	Accumulated mean daily SWE.	m	+	+	Stronger relationship pre-wolf.
BF	Proportion of elk home range.	Originally km^2	0	+	
UF	Proportion of elk home range.	Originally km^2	0	-	
MEAD	Proportion of elk home range.	Originally km^2	0	-	
THERM	Proportion of elk home range.	Originally km^2	-	+	
EDGE	Total linear meters of edge within home range.	Rescaled: 100km	0	+	
RivDeep	Total number of linear meters within home range.	Rescaled: 10^2m	0	-	
ELEV	Average elevation per home range.	Rescaled: 10^2m	0	+	
SLOPE	Average % slope per home range.	%	- or 0	-	Weak or no relationship pre-wolf.
AGE * $WOLF_{days}$	-	-	NA	+ or 0	Weak or no relationship post-wolf.
$WOLF_{days}$ * SWE_{acc}	-	-	NA	+	
BF * $WOLF_{days}$	-	-	NA	+	

Table 1A Continued

UF * $WOLF_{days}$	-	-	NA	-	
MEAD * $WOLF_{days}$	-	-	NA	-	+ at high snowpack levels
THERM * $WOLF_{days}$	-	-	NA	+	
EDGE * $WOLF_{days}$	-	-	NA	+	
RivDeep * $WOLF_{days}$	-	-	NA	-	
ELEV * $WOLF_{days}$	-	-	NA	+	
SLOPE * $WOLF_{days}$	-	-	NA	-	
AGE * SWE_{acc}	-	-	+	+	
BF * SWE_{acc}	-	-	0	+	
THERM * SWE_{acc}	-	-	-	+	
EDGE * SWE_{acc}	-	-	0	+	
ELEV * SWE_{acc}	-	-	+ or 0	+	Weak or no relationship pre-wolf.



Figure 4A: Pairwise plots and distributions of all home range specific landscape covariates (pre and post-wolf data combined).

Table 2A: Total wolf days and numbers of wolves and packs per year in the Madison Headwaters area of Yellowstone National Park during 1995-2008. Criteria for total wolf days: total from Nov. 15th-April 30th, EXCLUDING wolves located in Cougar Meadows and therefore the Cougar pack is NOT included here.

Pack	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07	'08
Biscuit Basin										11				
Canyon														4
Gibbon Meadows									5	8	9	12	19	25
Hayden													4	
Madison													7	8
Mollie's*													8	12
Nez Perce		6	5	7	13	22	18	20	15	14	4			
Totals		6	5	7	13	22	18	20	20	33	13	12	38	49
No. of packs	0	1	1	1	1	1	2	2	3	4	3	2	4	5
Total wolf days per year	0	55	112	767	955	1543	1559	1386	2495	3657	1234	1883	2898	1648

* = Mollie's pack was never in the study area in their entirety.

Table 3A: Full model selection results for the Pre-wolf Model Suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	AGE + SWE_{acc} + THERM + THERM * SWE_{acc}	5	99.21	0.00	0.16
2	AGE + SWE_{acc}	3	100.02	0.81	0.10
3	AGE + SWE_{acc} + MEAD	4	101.06	1.86	0.06
4	AGE + SWE_{acc} + RivDeep	4	101.19	1.99	0.06
5	AGE + SWE_{acc} + UF	4	101.33	2.12	0.05
6	AGE + SWE_{acc} + THERM	4	101.51	2.30	0.05
7	AGE + SWE_{acc} + EDGE	4	101.62	2.41	0.05
8	AGE + SWE_{acc} + BF	4	102.03	2.83	0.04
9	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + THERM + THERM * SWE_{acc}	7	102.27	3.07	0.03
10	AGE + SWE_{acc} + EDGE + EDGE * SWE_{acc}	5	102.34	3.14	0.03
11	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc}	5	102.64	3.43	0.03
12	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + THERM + THERM * SWE_{acc}	8	103.06	3.86	0.02
13	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + THERM + THERM * SWE_{acc}	8	103.43	4.22	0.02
14	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep	6	103.55	4.34	0.02
15	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + MEAD	6	103.62	4.42	0.02
16	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + MEAD + THERM + THERM * SWE_{acc}	8	103.69	4.48	0.02
17	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF	6	103.74	4.54	0.02
18	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + THERM + THERM * SWE_{acc}	8	103.86	4.65	0.02
19	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + THERM	6	103.94	4.74	0.01
20	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE	6	103.97	4.76	0.01
21	AGE + SWE_{acc} + BF + BF * SWE_{acc}	5	104.05	4.85	0.01

Table 3A Continued

22	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF	6	104.64	5.43	0.01
23	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + MEAD + THERM + THERM * SWE_{acc}	9	104.90	5.69	0.01
24	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + EDGE * SWE_{acc} + THERM + THERM * SWE_{acc}	9	105.12	5.91	0.01
25	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + MEAD	7	105.32	6.11	0.01
26	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + MEAD + THERM + THERM * SWE_{acc}	9	105.38	6.17	0.01
27	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + MEAD + THERM + THERM * SWE_{acc}	9	105.46	6.26	0.01
28	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF	7	105.49	6.28	0.01
29	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + THERM + THERM * SWE_{acc}	9	105.49	6.28	0.01
30	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + EDGE	7	105.53	6.33	0.01
31	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + BF	7	105.56	6.35	0.01
32	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + THERM	7	105.56	6.36	0.01
33	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + MEAD + THERM	7	105.61	6.40	0.01
34	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + EDGE * SWE_{acc}	7	105.63	6.42	0.01
35	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + BF * SWE_{acc} + THERM + THERM * SWE_{acc}	9	105.64	6.43	0.01
36	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + THERM	7	105.74	6.53	0.01
37	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + THERM	7	105.95	6.74	0.01
38	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + BF * SWE_{acc}	7	106.47	7.26	0.00
39	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + EDGE + EDGE * SWE_{acc}	8	106.92	7.71	0.00

Table 3A Continued

40	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + EDGE * SWE_{acc} + MEAD + THERM + THERM * SWE_{acc}	10	106.96	7.75	0.00
41	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + EDGE * SWE_{acc} + THERM	8	107.05	7.85	0.00
42	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + BF * SWE_{acc} + MEAD + THERM + THERM * SWE_{acc}	10	107.19	7.98	0.00
43	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + BF * SWE_{acc} + THERM + THERM * SWE_{acc}	10	107.31	8.10	0.00
44	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + MEAD + THERM + THERM * SWE_{acc}	10	107.31	8.10	0.00
45	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + EDGE + MEAD	8	107.33	8.12	0.00
46	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF + MEAD	8	107.36	8.15	0.00
47	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + BF + MEAD	8	107.36	8.15	0.00
48	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF + BF	8	107.42	8.22	0.00
49	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + MEAD + THERM	8	107.43	8.23	0.00
50	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + BF + BF * SWE_{acc}	8	107.52	8.31	0.00
51	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + BF + BF * SWE_{acc}	8	107.52	8.31	0.00
52	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + MEAD + THERM	8	107.64	8.43	0.00
53	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + MEAD + THERM	8	107.65	8.45	0.00
54	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + THERM	8	107.73	8.52	0.00
55	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + BF * SWE_{acc} + THERM	8	107.87	8.67	0.00
56	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + EDGE + EDGE * SWE_{acc} + MEAD	9	108.73	9.53	0.00
57	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + EDGE + EDGE * SWE_{acc} + MEAD + THERM	9	108.93	9.73	0.00

Table 3A Continued

58	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + BF * SWE_{acc} + MEAD + THERM + THERM * SWE_{acc}	11	109.07	9.87	0.00
59	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF + BF + BF * SWE_{acc}	9	109.37	10.16	0.00
60	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF + BF + MEAD	9	109.42	10.21	0.00
61	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + BF + BF * SWE_{acc} + MEAD + THERM	9	109.50	10.30	0.00
62	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + MEAD + THERM	9	109.55	10.34	0.00
63	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + BF * SWE_{acc} + THERM	9	109.60	10.39	0.00
64	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + UF + BF + BF * SWE_{acc} + MEAD	10	111.33	12.13	0.00
65	AGE + SWE_{acc} + ELEV + ELEV * SWE_{acc} + UF + BF + BF * SWE_{acc} + MEAD + THERM	10	111.42	12.21	0.00

Table 4A: Coefficient values (β_i) and 95% confidence intervals (in parentheses) for all covariates from those models within four ΔAIC_c from the top model for the pre-wolf model suite.

Model ID	Covariate											
	AGE	SWE_{acc}	THERM	THERM * SWE_{acc}	MEAD	RivDeep	UF	EDGE	BF	ELEV	ELEV * SWE_{acc}	EDGE * SWE_{acc}
1	**0.55 (0.34, 0.82)**	**0.12 (0.06, 0.18)**	**39.02 (4.18, 74.13)**	**-1.06 (-2.16, -0.06)**	-	-	-	-	-	-	**-**	-
2	**0.49 (0.30, 0.72)**	**0.07 (0.04, 0.12)**	**-**	**-**	-	-	-	-	-	-	-	-
3	**0.52 (0.32, 0.75)**	**0.08 (0.04, 0.12)**	-	-	4.38 (-4.7, 12.02)	-	-	-	-	-	-	-
4	**0.51 (0.31, 0.74)**	**0.08 (0.04, 0.12)**	-	-	-	-0.01 (-0.04, 0.01)	-	-	**-**	**-**	**-**	-
5	**0.52 (0.32, 0.77)**	**0.08 (0.04, 0.12)**	-	-	-	-	-1.85 (-6.25, 2.44)	-	-	-	-	-
6	**0.51 (0.31, 0.75)**	**0.08 (0.04, 0.12)**	6.13 (-10.95, 21.85)	-	-	-	-	-	-	-	-	-
7	**0.51 (0.31, 0.74)**	**0.08 (0.04, 0.12)**	-	-	-	-	-	0.14 (-0.28, 0.55)	**-**	**-**	-	-
8	**0.49 (0.30, 0.72)**	**0.08 (0.04, 0.12)**	-	-	-	-	-	-	0.51 (-8.76, 9.35)	**-**	-	-
9	**0.59 (0.35, 0.89)**	1.26 (-0.92, 3.55)	**38.36 (2.77, 73.98)**	-1.00 (-2.13, 0.02)	-	-	-	-	-	1.69 (-1.84, 5.39)	-0.05 (-0.15, 0.05)	-
10	**0.52 (0.32, 0.78)**	**0.15 (0.02, 0.29)**	-	-	-	-	-	0.62 (-0.31, 1.49)	-	-	-	-0.02 (-0.04, 0.01)
11	**0.52 (0.32, 0.77)**	1.36 (-0.72, 3.43)	-	-	-	-	-	-	-	1.82 (-1.50, 5.17)	-0.06 (-0.15, 0.04)	-
12	**0.62 (0.37, 0.94)**	1.19 (-0.98, 3.50)	**42.97 (4.87, 82.06)**	**-1.2 (-2.46, -0.09)**	-	-	-	0.3 (-0.22, 0.87)	-	1.01 (-2.58, 4.90)	-0.05 (-0.15, 0.05)	-

Table 5A: Model selection results for the exploratory analysis replacing SWE_{acc} with SWE_{mean} in the pre-wolf model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	AGE + SWE_{mean}	3	100.09	0.00	0.14
2	AGE + SWE_{mean} + MEAD	4	100.93	0.83	0.09
3	AGE + SWE_{mean} + UF	4	101.41	1.32	0.07
4	AGE + SWE_{mean} + RivDeep	4	101.49	1.39	0.07
5	AGE + SWE_{mean} + THERM	4	101.69	1.59	0.06
6	AGE + SWE_{mean} + EDGE	4	101.71	1.62	0.06
7	AGE + SWE_{mean} + THERM + THERM * SWE_{mean}	5	101.73	1.64	0.06
8	AGE + SWE_{mean} + BF	4	102.12	2.03	0.05
9	AGE + SWE_{mean} + ELEV + ELEV * SWE_{mean}	5	102.62	2.53	0.04
10	AGE + SWE_{mean} + EDGE + EDGE * SWE_{mean}	5	102.87	2.78	0.03
11	AGE + SWE_{mean} + ELEV + ELEV * SWE_{mean} + MEAD	6	103.37	3.28	0.03
12	AGE + SWE_{mean} + ELEV + ELEV * SWE_{mean} + UF	6	103.83	3.73	0.02
13	AGE + SWE_{mean} + ELEV + ELEV * SWE_{mean} + RivDeep	6	104.00	3.91	0.02
14	AGE + SWE_{mean} + ELEV + ELEV * SWE_{mean} + THERM	6	104.05	3.95	0.02

Table 6A: Model selection results for adding the quadratic form for AGE to the top model in post-hoc exploratory analysis.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	AGE + SWE_{acc} + THERM + THERM * SWE_{acc}	5	99.21	0.00	0.72
2	AGE + **AGE.quad** + SWE_{acc} + THERM + THERM * SWE_{acc}	6	101.06	1.85	0.28

Table 7A: Full model selection results for the post-wolf base model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	Age + SWE_{acc} + Age * SWE_{acc}	4	278.19	0.00	0.23
2	Age + $WOLF_{days}$ + SWE_{acc} + Age * SWE_{acc}	5	278.27	0.08	0.22
3	Age + $WOLF_{days}$ + SWE_{acc} + Age * SWE_{acc} + Age * $WOLF_{days}$	6	279.71	1.52	0.11
4	Age	2	279.84	1.65	0.10
5	Age + $WOLF_{days}$ + SWE_{acc} + Age * SWE_{acc} + $WOLF_{days}$ * SWE_{acc}	6	280.00	1.81	0.09
6	Age + $WOLF_{days}$	3	280.36	2.17	0.08
7	Age + $WOLF_{days}$ + SWE_{acc} + Age * SWE_{acc} + $WOLF_{days}$ * SWE_{acc} + Age * $WOLF_{days}$	7	281.61	3.42	0.04
8	Age + SWE_{acc}	3	281.85	3.66	0.04
9	Age + $WOLF_{days}$ + Age * $WOLF_{days}$	4	282.18	3.99	0.03
10	Age + $WOLF_{days}$ + SWE_{acc}	4	282.35	4.16	0.03
11	Age + $WOLF_{days}$ + SWE_{acc} + Age * $WOLF_{days}$	5	284.17	5.98	0.01
12	Age + $WOLF_{days}$ + SWE_{acc} + $WOLF_{days}$ * SWE_{acc}	5	284.24	6.06	0.01
13	Age + $WOLF_{days}$ + SWE_{acc} + $WOLF_{days}$ * SWE_{acc} + Age * $WOLF_{days}$	6	286.07	7.88	0.00
14	$WOLF_{days}$	2	293.01	14.82	0.00
15	$WOLF_{days}$ + SWE_{acc}	3	294.95	16.76	0.00
16	SWE_{acc}	2	294.98	16.79	0.00

Table 8A: Model selection results for all models in the post-wolf landscape model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	BM + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	11	247.89	0.00	0.44
2	BM + ELEV + ELEV * SWE_{acc} + **ELEV * $WOLF_{days}$** + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	12	249.86	1.97	0.16
3	BM + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + **EDGE * SWE_{acc}** + EDGE * $WOLF_{days}$	12	249.91	2.03	0.16
4	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$	13	251.91	4.02	0.06
5	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * $WOLF_{days}$	12	252.26	4.37	0.05
6	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	252.98	5.10	0.03
7	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$	13	254.34	6.45	0.02
8	BM + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$	9	255.05	7.16	0.01
9	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	15	255.07	7.18	0.01
10	BM+ ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$	14	256.08	8.19	0.01
11	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	256.13	8.25	0.01
12	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	256.64	8.76	0.01
13	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$	10	256.78	8.89	0.01
14	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$	12	258.01	10.12	0.00
15	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$	15	258.17	10.28	0.00

Table 8A Continued

16	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	15	258.22	10.33	0.00
17	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	12	258.77	10.88	0.00
18	BM + ELEV + ELEV * SWE_{acc}	7	258.99	11.10	0.00
19	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	12	259.41	11.52	0.00
20	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	13	259.52	11.64	0.00
21	BM+ ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	16	260.05	12.16	0.00
22	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$	8	260.36	12.48	0.00
23	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	13	260.45	12.56	0.00
24	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	13	260.64	12.76	0.00
25	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	12	260.73	12.84	0.00
26	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	10	260.95	13.06	0.00
27	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	10	261.46	13.57	0.00
28	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	13	261.49	13.60	0.00
29	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	14	261.58	13.70	0.00
30	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	14	261.97	14.08	0.00
31	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * $WOLF_{days}$	10	262.11	14.22	0.00

Table 8A Continued

32	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	17	262.14	14.25	0.00
33	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	11	262.33	14.44	0.00
34	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	14	262.52	14.63	0.00
35	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	14	262.52	14.63	0.00
36	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	14	262.62	14.74	0.00
37	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	15	262.79	14.90	0.00
38	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	14	262.93	15.05	0.00
39	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	12	263.27	15.39	0.00
40	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	15	263.56	15.67	0.00
41	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	15	263.67	15.78	0.00
42	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	10	263.70	15.82	0.00
43	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	15	263.92	16.03	0.00
44	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	15	263.92	16.04	0.00
45	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$	10	263.93	16.05	0.00

Table 8A Continued

46	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	13	264.12	16.24	0.00
47	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$	11	264.17	16.28	0.00
48	BM + RivDeep + RivDeep * $WOLF_{days}$	7	264.20	16.32	0.00
49	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	15	264.60	16.71	0.00
50	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	15	264.70	16.81	0.00
51	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	16	264.83	16.94	0.00
52	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	12	264.85	16.97	0.00
53	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$	11	265.43	17.54	0.00
54	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	16	265.61	17.73	0.00
55	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	16	265.71	17.83	0.00
56	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	13	265.79	17.91	0.00
57	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	16	266.49	18.60	0.00
58	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	17	267.50	19.62	0.00
59	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$	17	268.58	20.69	0.00

Table 8A Continued

60	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * SWE_{acc} + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$ + THERM + THERM * $WOLF_{days}$ + THERM * SWE_{acc}	18	269.54	21.66	0.00
61	BM + THERM + THERM * $WOLF_{days}$	7	276.09	28.20	0.00
62	BM + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	8	277.91	30.02	0.00
63	**BM (Null)**	5	278.27	30.39	0.00
64	BM + MEAD + MEAD * $WOLF_{days}$	7	278.90	31.02	0.00
65	BM + UF + UF * $WOLF_{days}$	7	279.39	31.50	0.00
66	BM + BF + BF * $WOLF_{days}$	7	280.26	32.38	0.00
67	BM + EDGE + EDGE * $WOLF_{days}$	7	281.95	34.06	0.00
68	BM + BF + BF * SWE_{acc} + BF * $WOLF_{days}$	8	282.15	34.26	0.00
69	BM + EDGE + EDGE * SWE_{acc} + EDGE * $WOLF_{days}$	8	284.00	36.11	0.00

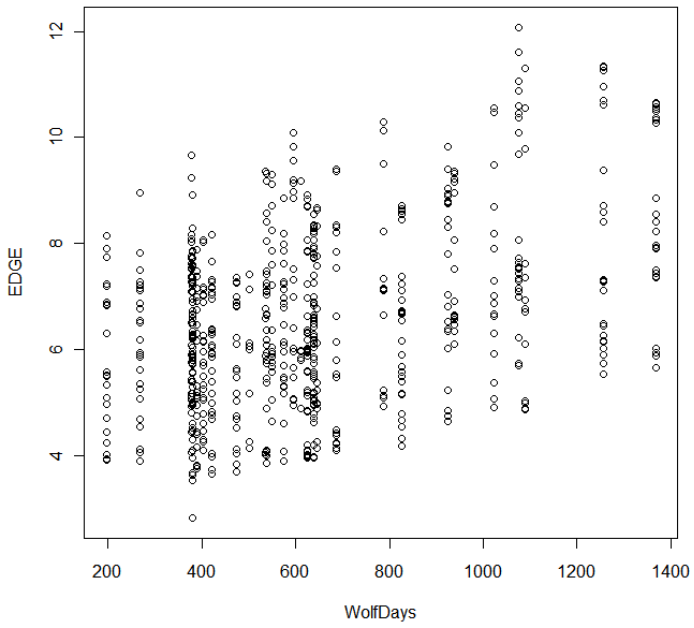
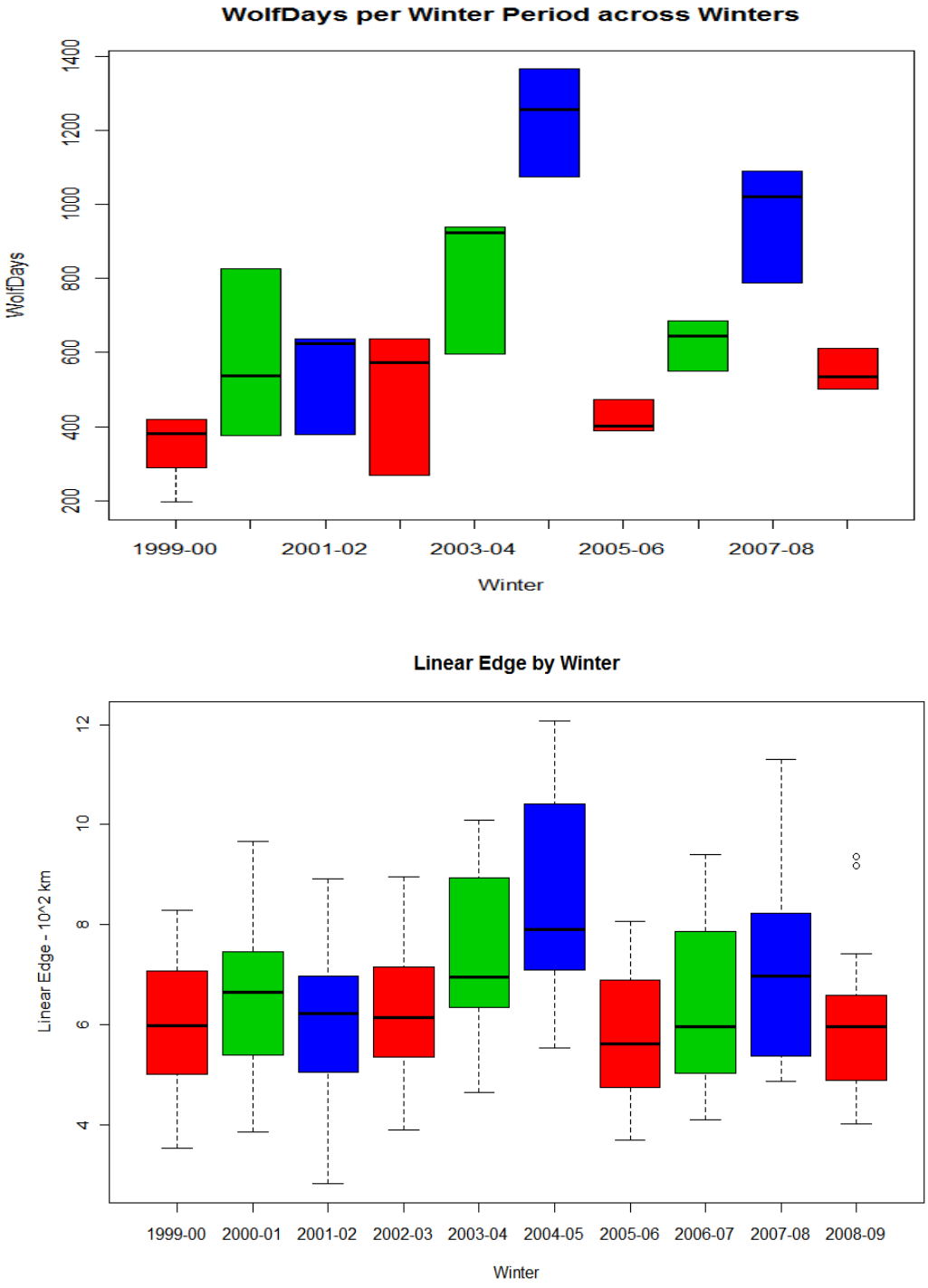


Figure 5A: Pairwise plot showing the positive correlation between EDGE and $WOLF_{days}$.



Figures 6A and 7A: Comparison of plots showing total $WOLF_{days}$ per winter period across years (top) and total EDGE per home range circle per winter period across years (bottom) demonstrating the strong correlation between the two.

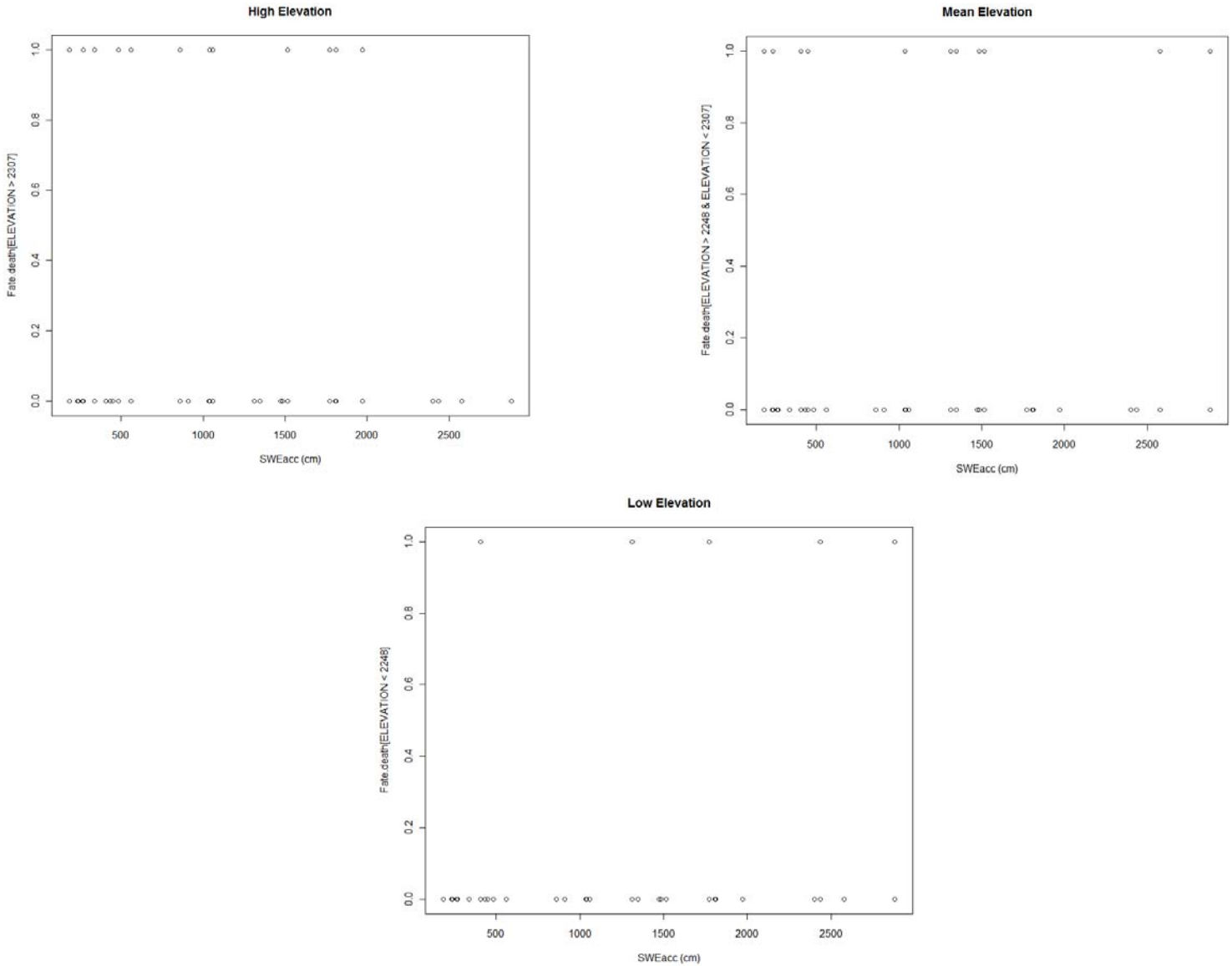


Figure 8A: Plots showing fates (alive = "0" and dead = "1") across the range of SWE_{acc} values for high (upper left), average (upper right), and low (lower center) elevations for the post-wolf data.

APPENDIX B

BOXPLOTS OF LANDSCAPE COVARIATES BY DRAINAGE

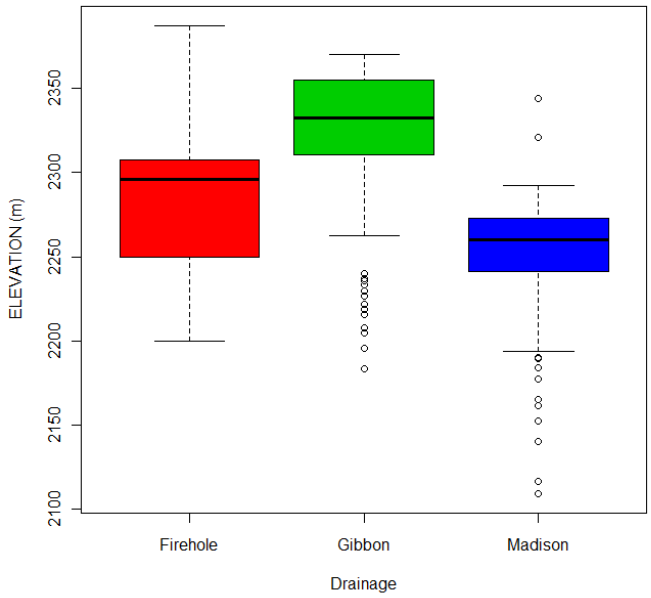


Figure 1B: Average elevation per home range by drainage.

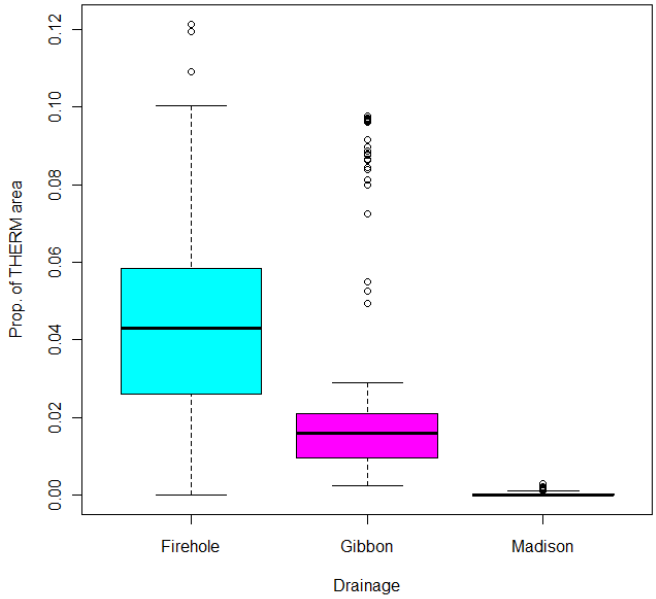


Figure 2B: Proportion of thermal area per home range by drainage.

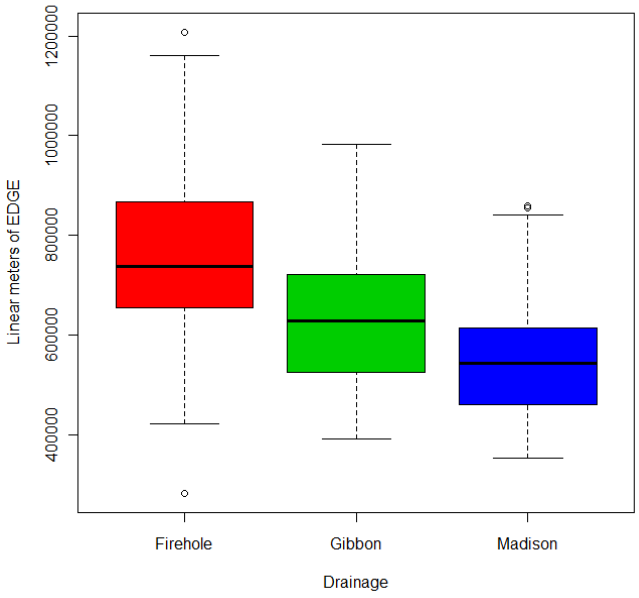


Figure 3B: Linear meters of edge per home range by drainage.

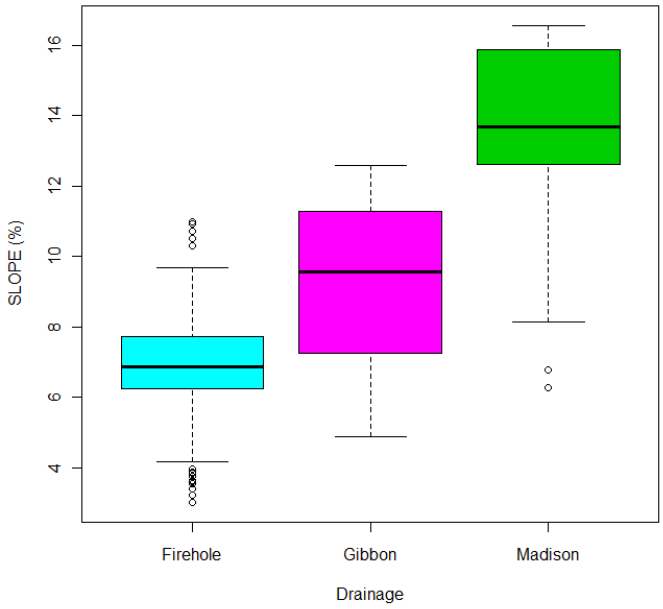


Figure 4B: Average percent slope per home range by drainage.

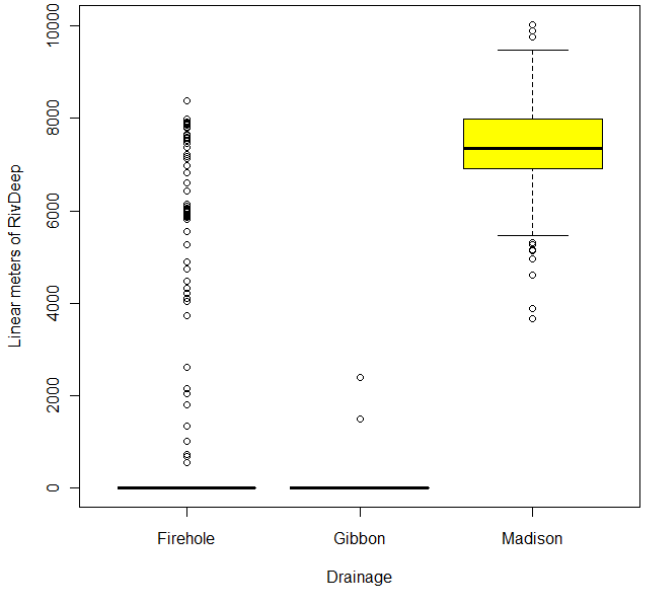


Figure 5B: Linear meters of deep river per home range by drainage.

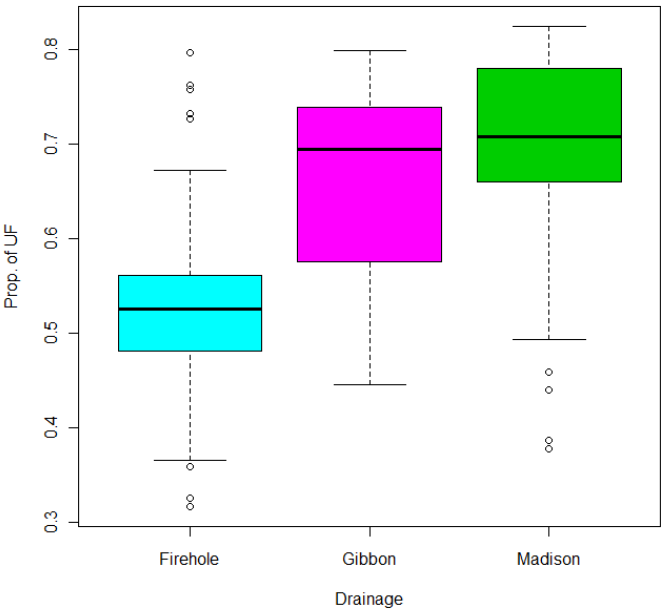


Figure 6B: Proportion of unburned forest per home range by drainage.

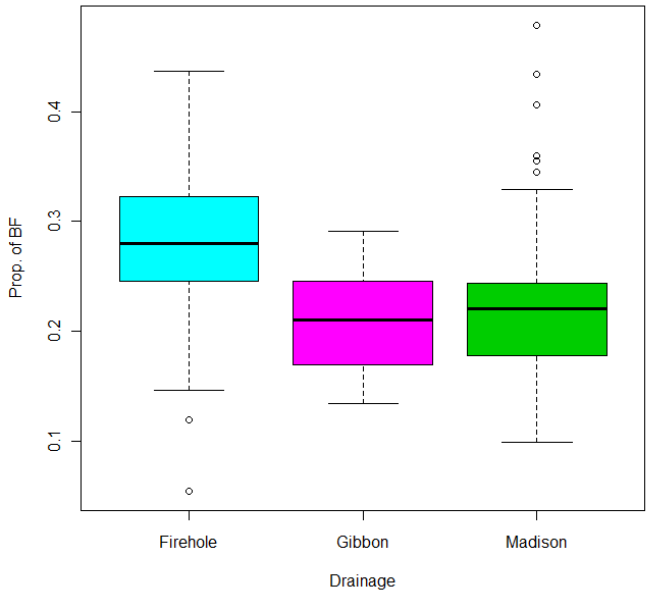


Figure 7B: Proportion of burned forest per home range by drainage.

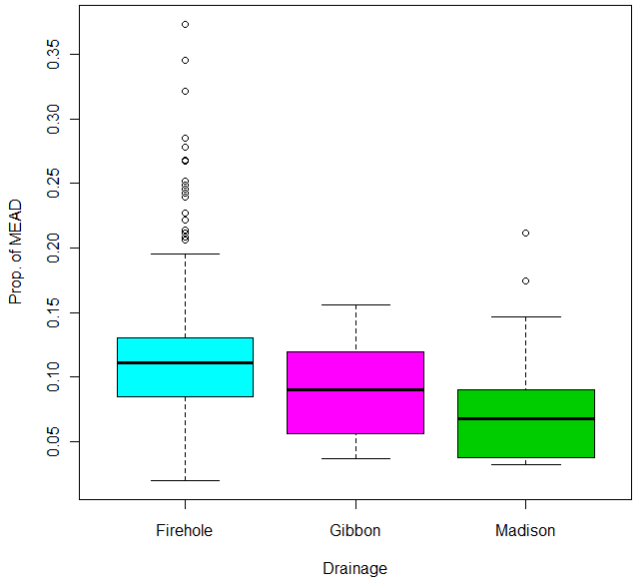


Figure 8B: Proportion of meadow habitat per home range by drainage.

APPENDIX C

SIMULATION PLOTS

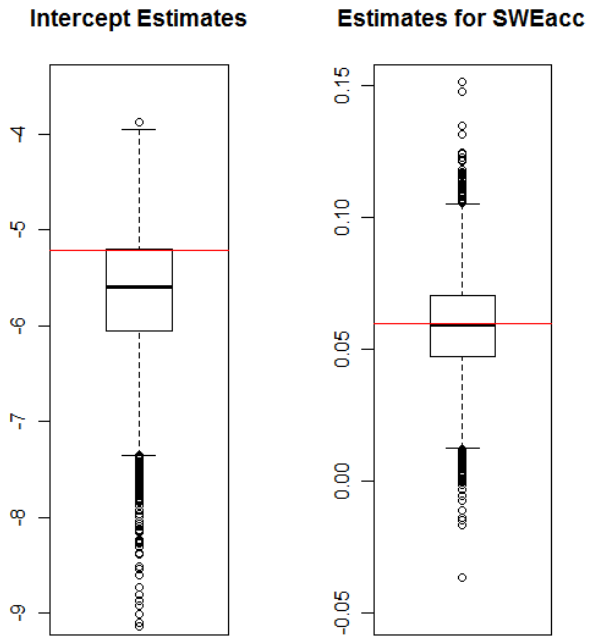


Figure 1C: Simulation results showing coefficient estimates for 5000 simulated data sets. The pre-wolf model contained only one covariate, SWEacc. Red lines represent the data-generating (true) coefficients which were chosen based on estimates obtained from fitting the same model to the real data.

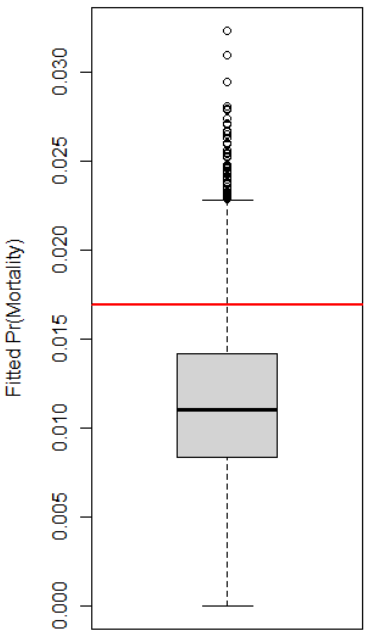


Figure 2C: Plot showing the fitted probabilities (p(mortality)) across all 5000 simulated data sets at an average level of SWE_{acc} for the pre-wolf data. Red line represents the true probability for that level of SWE_{acc} used to simulate the data sets.

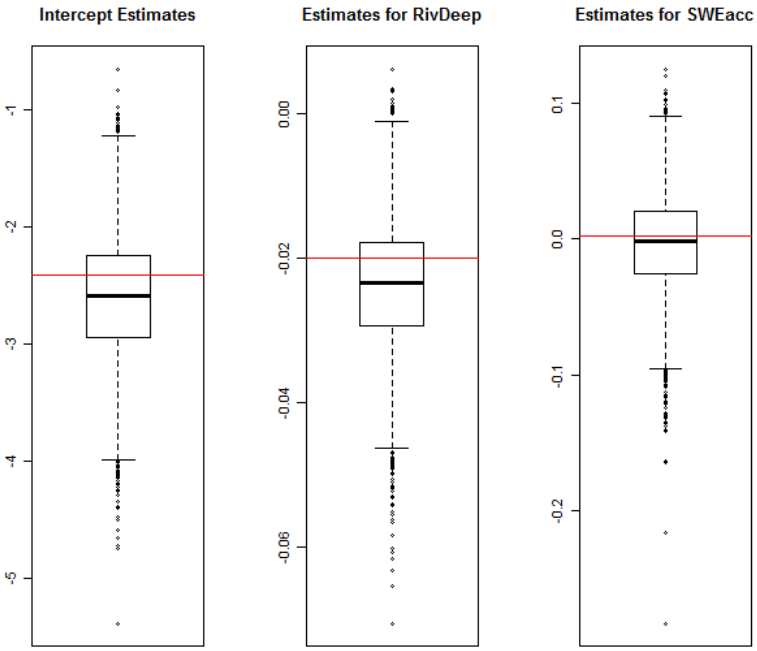


Figure 3C: Simulation results showing simulated coefficient estimates for 5000 simulated data sets. The post-wolf model contained the covariates, SWE_{acc} and RivDeep. Red lines represent the data-generating (true) coefficients which were chosen based on estimates obtained from fitting the same model to the real data.

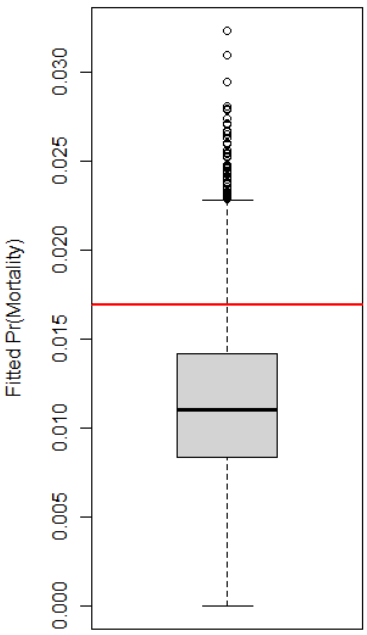


Figure 4C: Plot showing the fitted probabilities (p(mortality)) across all 5000 simulated data sets at average levels of SWE_{acc} and RivDeep for the post-wolf data. Red line represents the true probability for those levels of SWE_{acc} and RivDeep used to simulate the data sets.

APPENDIX D

MODEL SELECTION RESULTS FOR POST-WOLF SINGLE LANDSCAPE COVARIATE MODELS

Table 1D: Model selection results for the post-wolf elevation model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + ELEV + ELEV * SWE_{acc}$	7	258.99	0.00	0.66
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + ELEV + ELEV * SWE_{acc} + ELEV * WOLF_{days}$	8	260.36	1.38	0.33
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + ELEV$	6	267.61	8.62	0.01
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + ELEV + ELEV * WOLF_{days}$	7	269.61	10.62	0.00
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	19.29	0.00

Table 2D: Model selection results for the post-wolf deep river model suite.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + RivDeep$	6	263.15	0.00	0.63
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + RivDeep + RivDeep * WOLF_{days}$	7	264.20	1.06	0.37
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	15.13	0.00

Table 3D: Model selection results for the post-wolf thermal model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + THERM + THERM * WOLF_{days}$	7	276.09	0.00	0.38
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + THERM$	6	277.08	1.00	0.23
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + THERM + THERM * SWE_{acc} + THERM * WOLF_{days}$	8	277.91	1.82	0.15
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	2.19	0.13
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + THERM + THERM * SWE_{acc}$	7	278.67	2.59	0.10

Table 4D: Model selection results for the post-wolf single landscape model suite for EDGE.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	$AGE + SWE_{acc} + AGE * SWE_{acc}$	4	278.19	0.00	0.50
2	$AGE + SWE_{acc} + AGE * SWE_{acc} + EDGE$	5	278.82	0.63	0.37
3	$AGE + SWE_{acc} + AGE * SWE_{acc} + EDGE + EDGE * SWE_{acc}$	6	280.85	2.66	0.13

Table 5D: Model selection results for the post-wolf single landscape model suite for burned forest (BF).

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	0.00	0.36
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF$	6	278.52	0.25	0.32
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + BF * WOLF_{days}$	7	280.26	1.99	0.13
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + MEAD * BF$	7	280.31	2.03	0.13
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + BF * SWE_{acc} + BF * WOLF_{days}$	8	282.15	3.88	0.05

Table 6D: Model selection results for the post-wolf single landscape model suite for unburned forest (UF).

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	0.00	0.36
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + UF * WOLF_{days}$	7	279.39	1.11	0.21
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + SWE_{acc} * UF$	7	280.05	1.77	0.15
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + UF * SWE_{acc} + UF * WOLF_{days}$	8	280.08	1.81	0.15
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF$	6	280.13	1.85	0.14

Table 7D: Model selection results for the post-wolf single landscape model suite for meadow habitat (MEAD).

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * SWE_{acc}$	7	277.73	0.00	0.29
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	0.55	0.22
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * SWE_{acc} + MEAD * WOLF_{days}$	8	278.46	0.74	0.20
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * WOLF_{days}$	7	278.90	1.17	0.16
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD$	6	279.16	1.44	0.14

Table 8D: Model selection results for the post-wolf single landscape model suite for SLOPE.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + SLOPE + SLOPE * WOLF_{days}$	7	273.54	0.00	0.39
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + SLOPE$	6	274.13	0.59	0.29
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + SLOPE + SLOPE * SWE_{acc} + SLOPE * WOLF_{days}$	8	275.21	1.67	0.17
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + SLOPE + SWE_{acc} * SLOPE$	7	276.07	2.53	0.11
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	278.27	4.74	0.04

APPENDIX E

POST-HOC EXPLORATORY RESULTS

Table 1E: Post-hoc model selection results for top post-wolf landscape model with AGE and AGE * SWE_{acc} removed.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	AGE + $WOLF_{days}$ + SWE_{acc} + AGE * SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	11	247.89	0.00	0.86
2	AGE + $WOLF_{days}$ + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	10	251.59	3.71	0.14
3	$WOLF_{days}$ + SWE_{acc} + ELEV + ELEV * SWE_{acc} + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$	9	263.11	15.22	0.00

Adding Dispersers

In total, fifteen radio-collared cow elk permanently dispersed or became migratory and wintered outside of the Madison Headwaters study area following wolf establishment, five of which were censored for this analysis due to insufficient data. Model selection results supported four models within four ΔAIC_c of the top model, with Akaike model weights of 0.48, 0.11, 0.09, and 0.07, respectively (Table 2E below). Similar to the original results, the top four models included the covariates ELEV, ELEV * SWE_{acc}, RivDeep, and RivDeep * $WOLF_{days}$ in addition to the base model covariates. However, the top model did not include the EDGE and EDGE * $WOLF_{days}$ covariates, and instead included the covariates UF, UF * $WOLF_{days}$, MEAD, MEAD * $WOLF_{days}$, and ELEV * $WOLF_{days}$.

Table 2E: Model selection results for the post-hoc exploratory analysis adding dispersers in as mortalities for post-wolf landscape model suite.

Model ID	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
1	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	304.60	0.00	0.48
2	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	307.60	2.99	0.11
3	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + EDGE + EDGE * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	14	308.06	3.45	0.09
4	BM + ELEV + ELEV * SWE_{acc} + ELEV * $WOLF_{days}$ + RivDeep + RivDeep * $WOLF_{days}$ + UF + UF * $WOLF_{days}$ + BF + BF * $WOLF_{days}$ + MEAD + MEAD * $WOLF_{days}$	16	308.40	3.80	0.07

Due to significant multicollinearity, evaluation and interpretation of the effects for the individual covariates was done using results from single landscape covariate suites. After considering dispersers as mortalities, single landscape models for all landscape covariates except EDGE out-competed the null (base) model. The effect of RivDeep and Elevation did not change significantly, however the effects of THERM, MEAD, BF, and UF became significantly stronger, while AGE, and SWE_{acc} appeared to become less important with coefficient estimates from all models in all suites containing corresponding 95% confidence intervals spanning zero.

The coefficient estimate for the covariate THERM from the top ranked model in the thermal suite (Table 3E) was significantly positive as predicted ($\beta_{THERM} = 14.61$, 95% CI = 4.46 to 24.53). The top ranked model from the meadow suite (Table 4E) contained the interaction MEAD * $WOLF_{days}$ with a significantly positive coefficient estimate

($\beta_{MEAD * WOLFdays}$ = 0.019, 95% CI = 0.002 to 0.039). As predicted, the coefficient estimate for UF * $WOLF_{days}$ from the top ranked model (Table 5E) was significantly negative ($\beta_{UF * WOLFdays}$ = -0.009, 95% CI = -0.019 to -0.0003), however contrary to our predictions, the coefficient estimate for BF from the top ranked model (Table 6E) was also significantly negative (β_{BF} = -6.16, 95% CI = -11.76 to -0.94).

Table 3E: Model selection results for the post-hoc exploratory analysis adding dispersers in as mortalities for the single landscape model suite for THERM.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
2	AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc} + THERM	6	338.40	0.00	0.41
5	AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc} + THERM + THERM * $WOLF_{days}$	7	339.10	0.70	0.29
3	AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc} + THERM + THERM * SWE_{acc}	7	340.28	1.88	0.16
4	AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc} + THERM + THERM * SWE_{acc} + THERM * $WOLF_{days}$	8	340.77	2.37	0.12
1	AGE + SWE_{acc} + $WOLF_{days}$ + AGE * SWE_{acc}	5	344.15	5.75	0.02

Table 4E: Model selection results for the post-hoc exploratory analysis adding dispersers in as mortalities for the single landscape model suite for MEAD.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * WOLF_{days}$	7	332.98	0.00	0.58
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * SWE_{acc} + MEAD * WOLF_{days}$	8	334.83	1.86	0.23
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD$	6	335.88	2.91	0.14
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + MEAD + MEAD * SWE_{acc}$	7	337.81	4.83	0.05
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	344.15	11.18	0.00

Table 5E: Model selection results for the post-hoc exploratory analysis adding dispersers in as mortalities for the single landscape model suite for UF.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + UF * WOLF_{days}$	7	341.68	0.00	0.46
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + UF * SWE_{acc} + UF * WOLF_{days}$	8	343.56	1.88	0.18
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF$	6	343.76	2.08	0.16
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	344.15	2.47	0.13
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + UF + SWE_{acc} * UF$	7	345.78	4.10	0.06

Table 6E: Model selection results for the post-hoc exploratory analysis adding dispersers in as mortalities for the single landscape model suite for BF.

Model #	Model	*K*	AIC_c	ΔAIC_c	w_{ic}
2	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF$	6	340.79	0.00	0.48
3	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + SWE_{acc} * BF$	7	342.66	1.88	0.19
5	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + BF * WOLF_{days}$	7	342.80	2.01	0.18
1	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc}$	5	344.15	3.36	0.09
4	$AGE + SWE_{acc} + WOLF_{days} + AGE * SWE_{acc} + BF + BF * SWE_{acc} + BF * WOLF_{days}$	8	344.64	3.85	0.07

Removing Non-Wolf Predations

Removing four non-wolf predation mortalities (one grizzly kill, three mt. lion kills) from the post-wolf dataset during exploratory analysis did not significantly change the results. Model selection results supported the same top three models as the a priori post-wolf landscape model results (Table 6) and contrary to our predictions, coefficient estimates did not change significantly.