Assessment of prey vulnerability through analysis of wolf movements and kill sites
by Eric James Bergman

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish
and Wildlife Management
Montana State University
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Abstract:

Predator-prey models have traditionally been built on the assumption that neither predators nor prey are capable of learning or adapting behavior based on past interactions. As such, these models typically account for predation by forcing prey to experience a fixed level of predation risk. In order to develop species specific and more realistic models, the enemy-victim interaction behaviors of both predators and prey need to be studied. We quantified selection patterns for 2 fine scale behaviors of a recovering wolf population in Yellowstone National Park, Wyoming. Wolf spatial data were collected between November and May from 1998-1999 until 2001 -2002. Over four winters; 244 aerial locations, 522 ground based telemetry locations, 1,287 km of movement data from snow-tracking and the locations of 279 wolf kill sites were recorded. There was evidence that elk (*Cervus elaphus*) and bison (*Bison bison*) densities had a weak effect on the sites where wolves traveled and made kills. Wolf movements showed a strong selection for geothermal areas, meadows and areas in close proximity to edge. Proximity to edge and habitat class also had a strong influence on the locations where elk were most vulnerable to predation. There was little evidence that wolf kill sites differed from the places where wolves traveled, indicating that wolves selected to travel in areas where they were most successful at killing elk. Our results indicate that prey are more vulnerable to predators under certain conditions, predators are capable of selecting for these conditions, and as such, the notion of a fixed predation risk is largely inadequate.

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A thesis submitted in partial fulfillment
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of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2003

N378
B4539

ii

APPROVAL

Of a thesis submitted by

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

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ACKNOWLEDGEMENTS

This research was funded by the National Science Foundation and logistical support was provided by the United States Department of Interior – National Park Service – Yellowstone National Park. I would like to gratefully acknowledge those who have contributed to this project: R. Jaffe provided the first two years of wolf spatial data used in this study. Yellowstone National Park biologists P.J. White, D.W. Smith and R. Wallen provided additional biological data and/or insight for this work. E.M. Joyce, T.D. Smucker, M.D. Johnston, C.N. Gower and M. Becker assisted with all aspects of field work and data collection. Dr. Fred Watson and the CSUMB field team provided field support as well as snow modeling, geothermal mapping and vegetation mapping for this project. C.A. Van De Polder, W. Wimbery and the Madison Junction maintenance workers provided mechanical assistance and logistical support. D. Young, K. Dimmick, L. Baker, R. Siebert, M. Keator and all other rangers from the Madison Junction, Old Faithful and West Entrance ranger stations also provided support during data collection. Critical review of this manuscript was provided by P. Hernandez, J. Warren, L. Steinbech and J. Salix. Much appreciated insight for this work came from dialogue with J.A. Gude and M.A. Messer. Special thanks go to my graduate committee; R.A. Garrott, S. Creel and J.J. Borkowski provided a wealth of expertise, support and constructive criticism on all aspects of this work. I would also like to acknowledge my family for the infinite support and encouragement they provided.

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ABSTRACT

Predator-prey models have traditionally been built on the assumption that neither predators nor prey are capable of learning or adapting behavior based on past interactions. As such, these models typically account for predation by forcing prey to experience a fixed level of predation risk. In order to develop species specific and more realistic models, the enemy-victim interaction behaviors of both predators and prey need to be studied. We quantified selection patterns for 2 fine scale behaviors of a recovering wolf population in Yellowstone National Park, Wyoming. Wolf spatial data were collected between November and May from 1998-1999 until 2001-2002. Over four winters; 244 aerial locations, 522 ground based telemetry locations, 1,287 km of movement data from snow-tracking and the locations of 279 wolf kill sites were recorded. There was evidence that elk (*Cervus elaphus*) and bison (*Bison bison*) densities had a weak effect on the sites where wolves traveled and made kills. Wolf movements showed a strong selection for geothermal areas, meadows and areas in close proximity to edge. Proximity to edge and habitat class also had a strong influence on the locations where elk were most vulnerable to predation. There was little evidence that wolf kill sites differed from the places where wolves traveled, indicating that wolves selected to travel in areas where they were most successful at killing elk. Our results indicate that prey are more vulnerable to predators under certain conditions, predators are capable of selecting for these conditions, and as such, the notion of a fixed predation risk is largely inadequate.

INTRODUCTION

Spatial distributions of animals are rarely uniform. Movements and distributions are a response to patchworks of resources, changing environmental conditions, as well as behavioral characteristics. Changes in forage quality, interspecific and intraspecific competition, dispersal, aggression and avoidance of predators are all cause for animal movement (Pyke 1983). Within the context of predator-prey interactions, there is interest in how systems remain stable given the potential heterogeneity caused by predator-prey races (Hastings 1977).

As opportunities arise for the study of space use patterns and behavior of predators, there is a parallel need to assimilate this knowledge into behavioral models of predator-prey interactions. Predator-prey models have traditionally been built on the assumption that prey experience a fixed level of predation risk and predators cannot respond to spatial changes in prey density (Lima 2002). By learning how predators respond to the anti-predator movements of prey, how prey respond to predators and how predators exert variable amounts of pressure on prey, risk to prey can be realistically incorporated into these models as more than a fixed value at any single location (Lima 2002). In order to develop species-specific and more realistic behavioral models, the behaviors of both predator and prey must be studied.

An objective of this study was to expand the understanding of fine-scale predator selection patterns and movement behavior, in response to changing prey and landscape variables, such that it can be applied in further understanding of predator-prey interactions. Within the context of fine-scale selection, predators should utilize landscapes in manners that maximize hunting efficiency. For coursing predators,

efficiency is maximized as a result of occupying patches of high prey density, maintaining a high rate of prey detection, and subsequently increasing successful captures (Taylor 1984). However, for stalking predators, high prey density might increase the collective vigilance of prey, thereby increasing the distance at which predators are detected and decreasing capture success (Creel and Creel 2002). As such, the mechanisms driving hunting efficiency are not fixed; rather, it changes dynamically depending on the behavior employed by both the predator and prey. Another traditional assumption of efficient hunting strategies concerns prey management. For a predator to maximize hunting efficiency within a territory, recently exploited patches within a territory should receive reduced hunting pressure to allow prey dynamics to be restored in terms of density (Greenwood and Swingland 1983) and spatial distribution (Bell 1991). However, this theory of prey-management is not always empirically supported. Leopards (*Panthera pardus*) have been found to increase their distance traveled the day following a kill as opposed to the days prior (Bailey 1993), but Schaller (1972) found that lions (*Panthera leo*) did not vacate areas of recent predatory activity. African wild dogs (*Lycaon pictus*) have been found to show preferential selection for areas of lower preferred prey density (Mills and Gorman 1997, Creel and Creel 2002). However, for wild dogs this behavior was attributed not to prey management, but to avoidance of areas of high lion densities (an interspecific competitor as well as predator of wild dogs).

For many large predators, prey is detected primarily through visual mechanisms (Eaton 1974; Schaller 1972). Wolves (*Canis lupus*), however, have been found to rely on olfactory detection of prey (Mech 1970). After prey is detected, predator movements should maximize the potential for prey capture. In the case of culling less fit individuals,

movement should occur in a manner that separates a selected individual from a group. Under many circumstances, the surrounding habitat might facilitate predator movement or impede prey escape.

This study focused on the movements of wolves through a heterogeneous landscape containing both elk (*Cervus elaphus*) and bison (*Bison bison*) in Yellowstone National Park (YNP), Wyoming, USA. Prior to 1995, wolves were very rarely seen in the Greater Yellowstone Ecosystem (GYE) since deliberate extermination in the 1940's (Fritts et al. 1995). After wolf reintroductions to YNP in 1995 and 1996, there was a rapid recolonization throughout the GYE (Smith et al. 2003). Largely unexploited space and prey populations allowed for the study of wolf recolonization dynamics.

We studied the space use patterns of wolves at three scales. At the coarsest scale, we studied the patterns wolves exhibited when recolonizing our study area. These recolonization patterns are described primarily in terms of annual changes in the overlap between winter home ranges and core use areas and the study area. On an intermediate-scale, we analyzed wolf travel routes to isolate and quantify the effects that certain landscape variables had on movement. At the finest scale, we analyzed wolf kill sites to determine the conditions under which elk were most vulnerable to wolf predation.

For broad-scale patterns, we predicted that wolves would use areas of high prey density. For our movement analysis, we predicted that wolves selected one of three strategies when moving across the landscape. Wolves could have, 1) selected areas of high prey density, 2) focused movements in areas where elk were most vulnerable, or 3) moved randomly through the landscape. For kill site data, we expected that kills would be concentrated in areas of high prey density. A priori, we believed that the likelihood of

making a kill in a specific location was directly related to the number of individuals encountered. As such, we expected to see wolves concentrate movements in areas of high elk density.

METHODS

Study Area

The approximately 31,000 hectare study site was located in the west central portion of Yellowstone National Park (Fig. 1). Centered on the Gibbon, Firehole and upper-Madison River drainages, the site was defined by the wintering areas of both a non-migratory elk population and the migratory Central bison herd (Bjornlie and Garrott 2001, Ferrari and Garrott 2002).

Figure 1. The Madison-Firehole study area was located in the western-central portion of Yellowstone National Park, Wyoming. The study area, defined by the wintering ranges for both the non-migratory Madison-Firehole elk herd and the migratory Central bison herd, was typified by three major river corridors that were surrounded by intermittent meadow complexes before giving way to high elevation plateaus.

The climate of the study area was typical of northern mountainous regions. Peak snow-water equivalents (SWE) ranged from 58.4 - 113 cm during the winter months (December to May) (Natural Resource Conservation Service SNOTEL data). SWE is a measurement of the amount of water in a column of snow at a point. Snow typically started accumulating in October and began melting in early March. Elevations in the study area ranged from 2250-2800 meters. The Gibbon and Firehole Rivers experienced direct geothermal influence from geyser basins before flowing together to form the Madison River. Drainages were typified by intermittent meadows before giving rise to surrounding high-elevation plateaus. Topography within the study area had a large influence on snow accumulation and snow melt.

The primary vegetation type within the study area was a matrix of mature and regenerating lodgepole pine (*Pinus contorta*). Approximately 50% of the study area burned during the summer of 1988. Areas of regrowth were composed of young lodgepole pines, sedges (*Carex* spp.) and leafy aster (*Aster foliaceus*) (Despain 1990). Unburned forests were primarily composed of lodgepole pine as well as subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), and Douglas fir (*Pseudotsuga menziesii*) (Despain 1990). Non-forested habitat within the study area was composed of wet and dry meadow. Wet meadows were primarily composed of sedges and marsh reedgrass (*Calamagrostis* spp.) and dry meadows were primarily composed of tufted hairgrass (*Deschampsia caespitosa*), and grasses (*Festuca idahoensis*, *Poa* spp.) (Despain 1990).

The ungulate prey base in the study area fluctuated with winter conditions. The Madison-Firehole elk herd was composed of 500-800 animals (Singer 1991, Eberhardt et

al. 1998). In order to avoid the large energetic costs of traveling through deep snow, winter activities for elk were largely restricted to the valley bottoms and geothermal areas within the study area (Craighead et al. 1973). The study area was also the primary winter range for the Central bison herd, comprising 60% to 70% of the YNP bison population (Thorne et al. 1991, Meagher 1993). Estimates for the Central bison herd during the study ranged from 1,678 to 2,167 animals (Hess 2002). Bison density within the study area was also dependent on the severity of snow pack on the summer range (Bjornlie and Garrett 2001).

As part of the YNP wolf reintroduction program, wolves were released from an acclimation pen within the Madison-Firehole study area in April of 1996, in April and June of 1997 and again in June of 1998. The initial release was made up of 6 animals. All 6 left the Madison-Firehole study area and wandered widely over the GYE (Phillips and Smith 1997). Of the 16 animals released in April and June of 1997 (8 in each release), none established territories within the study area until late 1997 (Smith 1998). In the spring of 1998, 2 wolves bred in close proximity to the release site while 4 adults produced a litter within the pen. After the final release in June of 1998, these 2 groups joined. Early in the winter of 1998 this pack of 7 animals established the first winter territory since reintroduction efforts began within the Madison-Firehole study area (Smith 1998).

Wolf spatial data

Wolves were captured and fitted with radio-collars by darting or net-gunning from helicopters during January and February of each winter (Smith 1998). New wolf packs were discovered by monitoring known packs for dispersal and by monitoring for

tracks and sightings of animals unassociated with known packs. Four types of spatial data were collected. Aerial telemetry flights were conducted year-round by YNP biologists and provided temporally coarse data. These data allowed us: 1) to map pack home ranges that overlapped with the study area and, 2) to help describe the recolonization patterns of wolves as they established and expanded their use of the study area. Two intermediate scales of data were collected, we estimated wolf locations throughout the December- April period 1-3 times daily by radio-telemetry triangulation from the ground (White and Garrott 1990). These locations were used to determine core winter home ranges and identify the portions of the study area that were preferred for newly forming wolf territories. On the finer of the intermediate scales, we used snow tracking to record movement vectors taken by wolves as they traveled through the study area (Snyder and Bissonette 1987, Kunkel and Pletscher 2001). Snow tracking allowed us to determine what landscape attributes had the greatest influence on wolves as they moved across the study area. The finest scale of data we collected consisted of the locations of all known wolf-killed ungulates. These data provided an opportunity to determine what landscape attributes influenced the vulnerability of prey at short time scales, i.e. once a hunt began.

Aerial locations were collected year round. For 2 30-day periods of each year (15 November-14 December and 1 March-30 March) wolves were located on a daily basis, weather permitting, via aerial telemetry. However, due to inclement weather, the number of locations actually collected typically ranged between 10 and 15. During all other times, wolves were aerially located approximately 4 times per month. Further details on YNP wolf research are provided in Phillips and Smith (1997), Smith (1998)

and Smith et al. (1999, 2000). Aerial telemetry locations were entered into a Geographic Information System (GIS) as points. All aerial and ground locations collected for each pack between 1 November and 30 April of each year were used to generate winter home ranges. All home ranges were generated as minimum convex polygons (Hooge and Eichenlaub 1997). Minimum convex polygons were used in order to characterize wolf home range overlap with the study area, thus reflecting how much of the study area was potentially exposed to wolf presence.

Every day that wolves were detected in the study area, we attempted to acquire ground-based telemetry locations within the first 2 hours of daylight. Triangulations using 3-5 bearings were made from park roads and were plotted in the field on 7.5-minute USGS topographical quadrangle maps. While conducting fieldwork during the day, locations were also collected as needed to prevent working too close to the wolves. We also attempted to estimate locations within 2 hours of nightfall. Additionally, as part of a parallel study during the final winter, nocturnal locations were periodically collected 1-3 hours after sunset and 1-2 hours before sunrise. All opportunistic visual locations were noted and included with the telemetry datasets.

For each wolf pack, ground telemetry locations were entered into the GIS as points and used to generate 65% adaptive kernel core-use isopleths (Hooge and Eichenlaub 1997). To estimate ground radio-telemetry triangulation accuracy, we measured the distance between triangulation locations and known locations from snow tracks (Withey et al. 2001). Only a subset of our sample could be used for this analysis as certain, snow-free, conditions precluded the detection of tracks or too much time passed between the time when a triangulation was estimated and the triangulation was

investigated. We felt that these conditions were independent of where the wolves were located and thus did not introduce any bias in our assessment of telemetry accuracy. Based on these measured distances ($n=70$), our average telemetry error was estimated to be 325 meters ($SD = 239$ m).

When possible, wolves were snow tracked on a daily basis following procedures described by Jaffe (2001). We searched for tracks by bisecting expected travel routes between consecutive telemetry locations. Typically, consecutive telemetry locations consisted of a location from the morning on which tracking was to occur and a location from the previous day. If trails split while snow tracking, we followed the trail that appeared to have the greatest amount of wolf use. Secondary trails were followed later, as time allowed. Wolf tracks encountered opportunistically on the road were followed immediately to determine the points of arrival and departure. In the field, all wolf tracks were recorded as continuous vectors onto 7.5minute USGS topographical quadrangle maps.

Wolf travel routes were transcribed from field maps into the GIS as lines and systematically sampled by creating points at known distances/intervals (Lead 2002). Initial sampling was done at a 120 m interval. This initial distance was selected based on several criteria. Primarily, throughout the course of data collection, many snow tracking vectors were opportunistically collected after wolves crossed roads. However, it was not uncommon for these tracks to be lost after a short distance when the wolves either: 1) returned to the road but tracks had already been destroyed by over-snow vehicles, 2) crossed a river and tracks were not found on the opposite side, or, 3) a brief segment of tracks were recorded but other fieldwork obligations prevented us from following them

immediately and the tracks had disappeared by the time we returned. We decided that each wolf tracking vector had to have at least 2 points sampled from it to be included in analysis. This decision was intended to help reduce potential bias resulting from over sampling wolf tracks along road corridors. Additionally, we wanted to sample all movement data at a scale that was easily divisible by the broadest grid from other GIS layers (30 m). Finally, while autocorrelation between points was expected, sampling at short intervals eliminated the potential loss of valuable information from under sampling.

Movement data were analyzed as a correlated random walk (CRW). CRW was used because most animals exhibit some degree of correlation in their direction of travel while moving. Oftentimes this correlation is due to directional inertia (Turchin 1998). For valid inference to be drawn from analysis of movements, this idiosyncrasy of persistence in direction traveled must be understood on a species-specific basis. After sampling all vectors at 120 m intervals, a test for autocorrelation among points, within a single vector, was developed. For CRW analysis, serial correlations are most easily quantified by autocorrelation of turning angles for successive line segments (Turchin 1998). To address this, an autocorrelation function (ACF) was built using the cosine of the turning angles (Turchin 1998). However, a problem with using average cosine of the difference between turning angles is that the appropriate distribution for these types of data is largely unknown (Cain 1989, Turchin 1998). To address this problem, data were systematically resampled at increasing intervals by leaving out points, lag, from the initial 120 m sampling. For instance, lag 0 had no data excluded, lag 1 had every other point included and lag 2 had every third point included. Data were resampled up to lag 10 (points extracted every 1200 m). For each resampling, the deviation in turning angle

between consecutive points was calculated and restricted such that it fell between -180° and 180° . An ACF of the average cosine of these deviations was then created using 10,000 bootstrap replicates. Bootstrap means and confidence intervals were used to determine the lag at which the autocorrelation had reached maximum decay. We defined maximum decay as the point where the average cosine between turning angles stopped decreasing. For final analysis, all movement data were resampled at the scale determined by this analysis.

To test if wolf snow tracking vectors were non-random, we created random movement data by taking an original vector and assigning both a random orientation and a random relocation of the vector within the study area. When generating the random movement data sets, each vector was restricted to fall entirely within the study area. That is, if any part of the random vector fell outside of the study area, it was discarded and another was created. Random movement data were also sampled according to the ACF output. Points drawn from movement data were assigned coded binary response variables and subsequently analyzed as use versus availability data using logistic regression. The use of random vectors for comparison in our analysis was deemed beneficial for 2 primary reasons. First, we assumed there were inherent behavioral patterns in wolf movements that we did not understand or took place at too fine of a scale for us to detect. By requiring each random vector to have the same movement pattern as an actual vector (albeit in a different location with a different orientation) these behavioral patterns were not ignored. Secondly, by accommodating for the behaviors we could not detect, we felt that our results would be more applicable for utilization in rule-based modeling of wolf movements.

Most wolf kill sites were found while snow tracking wolves. However, kill sites were also found during aerial telemetry flights and during other research activities. Large groups of ravens (*Corvus corax*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*) and coyotes (*Canis latrans*) were excellent indicators of carcass presence. All carcasses encountered were necropsied to determine sex, species, cause of death, approximate date of death and percent consumed (Thurber et al. 1994, Mech et al. 1995, Jaffe 2001). Carcasses with no sign of pre-mortem damage were considered to be natural starvation, the most common source of mortality prior to re-establishment of wolves in the study area (Garrott et al. 2003). Carcasses with wounds and subcutaneous hemorrhaging, but surrounded only by coyote tracks and in areas of no recent wolf presence were considered to be coyote kills. Due to hibernation, grizzly bear (*Ursus arctos*) kills were not a large source of potential error until the final few weeks of each field season. Additionally, grizzly bear damage to carcasses at kill sites was largely distinguishable from that of wolves (Hornbeck and Horejsi 1986). We assumed that the final location of each carcass was the site of death unless there was evidence it had been dragged. For carcasses that were moved, the start of the drag mark was recorded as the site of death.

Wolf kill sites were entered in the GIS as points. To capture the availability of resources and landscape features across the study area, we generated a GIS layer of systematic data points that provided complete coverage of the study area. A total of 2,448 points were proportionately allocated, based on area, throughout 18 strata that encompassed the study area. A systematic approach, as opposed to use of random points, was chosen to assure that complete coverage of the study area occurred (Wolter 1984).

To estimate bison density, elk density and SWE values (all temporally dynamic variables) for data in this systematic sample, points were attributed with a random date from the field season. All kill sites and systematic points were assigned coded binary response variables and analyzed using logistic regression. One additional analysis was done to determine if there were differences between attributes that characterized places where wolves traveled and places where elk were killed. For this analysis, kill sites and points drawn from movement data were assigned coded binary response variables and were analyzed using logistic regression.

Landscape and prey density data

For both movement and kill site data, locations were attributed with: elevation, slope, distance to rivers, distance to roads and vegetative class. Additionally, SWE values, bison densities and elk densities were estimated for both types of data (see below). Elevation and slope data were extracted from 10 m grid digital elevation model layers composed by the United States Geological Survey. Proximity to roads was measured in the GIS based on a road map layer built by YNP scientists. Vegetation and geothermal classifications were extracted from 30 m grid layers (F. Watson, unpublished data). Proximity to the nearest edge was measured in a 10 m grid edge layer (F. Watson, unpublished data). An edge was defined as any point where the vegetation class changed or any point along a river bank.

SWE values were estimated for movement data and kill site locations using a mechanistic-based snow model (F. Watson, unpublished data). Daily SWE estimates for any point in the study area were generated from daily SWE measurements from 2 SNOTEL sites as well as dynamic temperature data. SNOTEL sites were located just

west and northeast of the study area. Spatially explicit slope, elevation, habitat, aspect, and ground heat flux data were used to capture snow accumulation and spring melt dynamics (F. Watson, unpublished data).

Prey distribution data were congruently collected as part of a parallel study for all years of this study (R.A. Garrott, unpublished data). Radio-collared elk were sampled using a stratified random sample without replacement technique and tracked until visually located, and subsequent group composition and behaviors recorded (Garrott et al. 1996). Bison abundance and distribution in the study area was monitored each year of the study using a bimonthly census technique (Ferrari and Garrott 2002). Elk densities were projected based on elk location data that were collected for all 4 years of this study (R. Garrott, unpublished data). We used projected bimonthly SWE distribution maps to capture the changing dynamic of snow across the landscape (F. Watson, unpublished data). SWE values were also estimated for the sites of all elk locations. Using: 1) dynamic bimonthly maps that extrapolated the SWE values for all points in the study area, 2) elk spatial data that reflected how elk were distributed across different SWE regimes, and 3) annual elk population estimates (R. Garrott, unpublished data), we were able to project elk densities for all wolf movement and kill site locations.

To estimate bison densities, we performed bimonthly census counts through the entire study area (Jaffe 2001, Ferrari and Garrott 2002). Censuses were conducted over a 2-day period, during which all known bison habitat within the study area was visited by at least one person. We recorded location, group size and subsequent sex and age class of all individuals that were encountered. To minimize double counting of bison groups during the 2-day surveys, survey blocks were designed such that movements of bison

from counted into uncounted blocks were unlikely to occur and easily detected if they did occur. Density was determined by summing all bison counted within one of ten possible continuous blocks. At the start of the third field season, the bison census area was expanded. To complete the datasets for the first two years for this newly expanded area, YNP biologists provided data collected through aerial surveys. As part of YNP bison research, these flights had been conducted approximately every two weeks. All bison groups located in the expanded area during these flights were treated in the same manner as observations made during the ground based censuses.

Analytical Techniques

Regression models were built and fitted to identify the most influential drivers for: 1) wolf movement data compared to random tracks, 2) wolf kill sites compared to the systematic sample of the study area, and 3) wolf kill sites compared to snow tracking data. Prior to analyses, all continuous covariates were centered and scaled to fall between -1 and 1 according to the formula

$$X_1 = (Y_1 - \text{midpoint}) / \text{midrange}$$

in which the midpoint was found by adding the minimum and maximum values and dividing by 2 and the midrange was found by subtracting the minimum value from the maximum value and dividing by 2. Covariates were centered and scaled in order to make the magnitude of differences in coefficient estimates indicative of the relative influence each covariate had in the model.

We formulated and evaluated sets of competing a priori models for all three types of data. While the list of potential and biologically interesting models that could be built was extensive, we restricted our models: 1) to those justified and explained by hypotheses

we developed through field observations, 2) to those justified and supported by published results of previous studies, and 3) to those that could be evaluated given the amount of data available (Burnham and Anderson 1998, Garrott et al. 2003). Due to these criteria, we did not include potential interactions in a priori models. Because we didn't know exactly how wolves responded to our different predictor variables, we allowed a priori models to take either linear or pseudothreshold (linear with an asymptote) forms. For linear and pseudothreshold models, all continuous covariates were prepared according to methods described by Franklin et al. (2000). Linear models could be written as

$$\theta = \beta_0 + \beta_1(x_1) + \dots + \beta_n(x_n)$$

and pseudothreshold models could be written as

$$\theta = \beta_0 + \beta_1 \log_e(x_1 + .05) + \dots + \beta_n \log_e(x_n + .05).$$

Exploratory analyses followed a non-automated, yet systematic, backward elimination approach. Covariates were removed from the saturated model until the best model, based on AIC_c values, was isolated. This approach reduced efficiency but forced all models to have reasonable biological explanations. This informal approach also allowed variables on different scales to be included in a single model, i.e. elk density could be entered on the arithmetic scale while distance to edge could be entered in the logarithmic scale. Due to the loss of inferential power when relying on exploratory analyses, we did not interpret or discuss exploratory model results, rather, they are presented in order to provide insight for future studies.

Prior to any modeling, we tested for collinearity between main effects as well as between all first order interactions and main effects. To be considered as predictors, the correlation between covariates was limited to fall between -0.30 and 0.30. We were

primarily concerned with the collinearity between SWE data and projected elk densities. The correlation between these two predictors (-0.34 for snow tracking data and -0.32 for kill site data) was deemed to be too high. Due to this result and to our belief that elk density was biologically more meaningful in terms of wolf movement, we did not include SWE as a predictor variable in any a priori models. Correlations between all other covariates were between -0.30 and 0.30 and determined to be acceptable.

To determine 1) the types of edges that wolves selected for while traveling, and 2) the type of edge that was typically nearest kill sites, we performed a chi-square analysis on wolf movement data and wolf kill site data (Neu et al. 1974). For this analysis, edge was defined as any point where a shift between vegetation classes occurred or where land gave way to a river. Vegetation classes included in this analysis were burned forest, unburned forest and meadows. We tested the hypotheses that when wolves were traveling, they utilized each type of edge in exact proportion to its occurrence within the study area and that for wolf kill sites, no single type of edge occurred nearer to kills more or less frequently than the proportion of that type of edge across the study area.

All models were fitted using PROC LOGISTIC (SAS Institute Inc. 2000). Models were compared using Akaike's Information Criterion (AIC), as described by Burnham and Anderson (1998). AIC values that had been corrected for small sample sizes, AIC_c , were used for all model comparisons (Burnham and Anderson 1998). Delta AIC_c (ΔAIC_c) scores were calculated according to Burnham and Anderson (1998) and AIC_c weights were calculated according to Franklin et al. (2000). We tested for overdispersion ($\hat{c}$) and goodness-of-fit in each of our global models by dividing the Pearson χ^2 by the degrees of freedom (Burnham and Anderson 1998). However, no

evidence of lack-of-fit or overdispersion was found for movement data ($\chi^2 = 15,604$, $df = 8,461$, $\hat{c} = 1.84$) or kill site data ($\chi^2 = 3,510$, $df = 2,713$, $\hat{c} = 1.29$).

RESULTS

Wolf presence and spatial data

For all winters of the study, the primary pack that utilized the study area was the Nez Perce pack (Fig. 2). During the four consecutive field seasons the pack numbered 7, 13, 21, and 15 animals, with the number of animals carrying radio collars gradually increasing from 4 to 7 over the study period. Additional packs and individual wolves were detected in the study area 10-11 times during each of the first three winters. The Chief Joseph pack made several forays into our study area during each of these winters. This pack consisted of 8, 13, and 11 animals during each consecutive winter and the number of radio collared animals ranged from 3-6 annually. Also during the third winter, the Cougar pack (4 animals / 1 collar) established a home range along the western boundary of the study area. During the final winter of data collection, non-Nez Perce wolves were detected on 28 occasions. Chief Joseph animals were never detected in the study area; however, the Cougar pack, having increased to 6 animals with 3 radio collars, continued to use the western boundary of the study area. In addition, a new pack of 5 animals without any radio collars (Gibbon) established a territory in the northern portion of the study area.

In summary, 15, 26, 36 and 26 wolves used the study area during the 4 respective winters. Wolf presence in the study area was not constant within winters. Wolves were detected in the study area on 117, 102, 107 and 133 days during each of the 4 170-day field seasons, resulting in an estimated 787, 1051, 1812, and 1622 wolf days of use for the 4 consecutive winters. Over the 4 winters, the Nez Perce wolf pack accounted for 94%, 99%, 97% and 94% of these wolf days.

Figure 2. Minimum convex polygons are used to depict winter home ranges for all wolf packs that used the Madison-Firehole study area. All polygons were generated from aerial and ground based telemetry locations collected between 1 November and 30 April.

During the 4 winters of field effort, 244 aerial locations and 522 ground-based triangulations of wolf packs in the study area were collected. For each pack in the study area that had at least one radio-collar, all aerial and ground locations were combined to define winter home ranges (Fig. 2). For the uncollared Gibbon pack, present during the fourth winter, a home range was defined by creating a polygon around all visual locations and kill sites found for this pack. Wolf occupancy of the study area increased for the first three winters, at which point there was complete coverage, before slightly declining during the fourth winter (38%, 80%, 100% and 84% coverage for the four respective winters).

All ground-based telemetry locations, regardless of pack, were used to define wolf winter core-use areas within the study area. Total coverage of the study area by core-use areas, defined by 65% adaptive kernel isopleths, was fairly constant for all 4 winters (9%, 15%, 15% and 16% coverage). Core-use areas were concentrated in the Firehole River drainage, however, an increasing presence was also detected in the Gibbon River drainage during the fourth winter (Fig. 3).

During the four winters, 327 snow tracking vectors were recorded, representing 1,287 km of movement data (229, 314, 338 and 406 km for each respective winter) (Fig. 4). The mean length for vectors was 4.05 km (SD 4.15 km), with a maximum vector length of 29.3 km. Peak periods for snow tracking were contingent upon wolf presence and snow pack. For all years of the study, wolves were most consistently present between mid-February and early May. Adequate snow coverage was typically present between late November and early April. Thus, most snow tracking data were recorded between mid-February and early April. As was the case with telemetry data, in excess

Figure 3. Wolf core use areas in the Madison-Firehole study area were defined by 65% adaptive kernel isopleths generated from all telemetry locations. The area encompassed was 30 km², 48 km², 49 km² and 53 km² for each of the four winters respectively.

Figure 4. Annual changes in geographic distribution of snow tracking data collected between mid-November and April in Yellowstone National Park, Wyoming.

Table 1. Wolf-killed ungulates found during four winters of data collection in the Madison-Firehole study area in Yellowstone National Park, Wyoming.

Year	Elk				Total	Bison			Total	Kills
	Bulls	Cows	Calves	Unk.		Adults	Calves	Unk.		
1998-99*	8	11	31	1	51	0	12	0	12	63
1999-00*	2	19	28	0	49	1	1	1	3	52
2000-01	1	30	39	1	71	0	2	0	2	73
2001-02	10	32	33	0	75	7	9	0	16	91
Totals	21	92	131	2	246	8	24	1	33	279

* from Jaffe (2002).

of 95% of the movement data was from the Nez Perce pack. For the finest scale of data, snow tracking, investigation of telemetry locations and aerial observations resulted in the location of 279 wolf kill sites (Table 1).

Through the analysis of the ACF, it was determined that at lag 7 (i.e. resampling data at 840 meter intervals) autocorrelation between points had reached maximum decay (Fig. 5). While the overall change in cosine between points 1 and 8 was still high (0.68), indicating a high level of correlation, it was concluded that this was the biological minimum to be expected for wolves. Subsampling our wolf tracking data according to the results of our ACF resulted in a reduction from 10,356 points to 1,556 points in our analysis.

Prey density and landscape data

A total of 1,768 elk locations were collected over four years. Estimated SWE values for these locations were used to project bimonthly elk density estimates for all wolf locations. As SWE values increased across the study area, elk densities tended to decrease in the higher elevations and increase in the lower elevations of the study area. During early winter (November through January) periods, peak projections ranged

Figure 5. Autocorrelation between consecutive points from wolf tracking vectors, with ninety-five percent confidence intervals, was used to determine the appropriate distance at which data needed to be sampled. Estimates were based on 10,000 bootstrap replicates for the average cosine of turning angles of wolf movement data that were sampled at various lag intervals. Maximum decay of autocorrelation was observed at lag 6. For final analysis, all vectors were sampled at a lag 7 interval (840 m).

between 1.5 and 3.1 elk/km² (mean = 2.3 elk/km²), while late season projections ranged between 2.9 and 14.8 elk/km² (mean = 10.8 elk/km²).

Forty-nine bimonthly bison census surveys were conducted over 4 winters.

During all four years of the study, the total number of bison in the study area tended to increase throughout the winter. Bison abundance in the study area was driven primarily by the amount of snow in higher elevation meadow complexes to the east of our study area (Bjornlie and Garrott 2001). Early winter counts of bison ranged between 151 and 368 bison in the study area, while late season counts ranged between 756 and 1061. As

the total number of bison in the study area increased, the average occupancy of the total winter range increased from 39% to 83% and densities increased from 4.7 bison/km² to 15.4 bison/km².

Results of the chi-square analysis showed strong preference or avoidance for almost all types of edge for both wolf movement data and wolf kill site data. While traveling, regardless of present habitat type, wolves showed selection for both burned and unburned forest edges as well as river edges (Table 2). They showed avoidance for meadow edges. For kill sites, regardless of habitat type at the kill site, preference was shown for both burned forest edges and river edges while there was avoidance of unburned forest edges (Table 3). Based on 95% confidence intervals, we were unable to detect any difference in utilization of meadow edges for kill sites.

Model comparison

Comparisons of competing a priori models for both movement and kill data resulted in a clear distinction between linear models and pseudothreshold models. For both response variables, linear models were better approximating models. Therefore, pseudothreshold models were not considered any further (Table 4). For both types of data, the best approximating model had strong habitat effects and moderate prey density effects.

Given our data, the strongest a priori model for our movement response variable was composed of vegetation type, distance from edge, elk density and bison density. As expected, both types of prey density were positive effects, while distance from edge was a negative effect (Fig. 6). In terms of vegetation classes, wolves showed avoidance of both burned and unburned forest, favoring to travel in meadow and geothermal

Table 2. Occurrence of wolf locations extracted from snow tracking data near different edge classes. Data were collected between mid-November and early May from 1998-1999 through 2001-2002 in the Madison-Firehole region of Yellowstone National Park, WY.

Edge	Proportion of total edge	Proportion of locations in each edge type (p_i)	95% confidence intervals of proportion of occurrence (p_i)
Burned	.12	.47	$.44 \leq p_i \leq .50$
Unburned	.68	.19	$.16 \leq p_i \leq .22$
Meadow	.19	.23	$.20 \leq p_i \leq .26$
River	.01	.11	$.09 \leq p_i \leq .13$

Table 3. Occurrence of wolf kill sites near different edge classes. Data were collected between mid-November and early May from 1998-1999 through 2001-2002 in the Madison-Firehole region of Yellowstone National Park, WY.

Edge	Proportion of total edge	Proportion of locations in each edge type (p_i)	95% confidence intervals of proportion of occurrence (p_i)
Burned	.12	.38	$.31 \leq p_i \leq .45$
Unburned	.68	.22	$.16 \leq p_i \leq .28$
Meadow	.19	.23	$.17 \leq p_i \leq .29$
River	.01	.17	$.11 \leq p_i \leq .23$

environments. Within these selection patterns, selection for meadow complexes was twice that for geothermal areas.

Exploratory analysis of our movement response variable resulted in several competing models (Table 5). Given the data, vegetation class, distance from edge, distance from road, distance from river, elevation, elk density, slope, and SWE were influential main effects. For the best model, as well as the second and third best models, bison density was not included. The only difference between the top two models was the form in which distance to edge was entered. The model that did not include elk density was less than 4 AIC_c units from the overall best approximating model, but its model weight was considerably lower. When combined, models that included elk density

Table 4. Ranking of a priori hypothesized models concerning the effects of prey density and habitat features on the location of wolf movements in the Madison-Firehole study area in Yellowstone National Park, Wyoming.

Model ^{†‡}	k*	AICc	ΔAICc	Coefficient (SE)	
Prey Suite					
ELK	2	8290	537	ELK = 1.78 (0.15)	
BD	2	8255	502	BD = 1.39 (0.11)	
ELK + BD	3	8168	415	ELK = 1.52 (0.16)	BD = 1.25 (0.11)
Habitat Suite					
EDG	2	8326	124	EDG = -1.92 (0.24)	
VEG	4	7877	550	Burn = -1.38 (0.07)	Unburned = -0.90 (0.08)
				Meadow = 0.41 (0.09)	Thermal = 0.76 (0.10)
Combined Suite					
ELK + VEG	5	7859	106	Burn = 0.57 (0.19)	Unburned = -0.90 (0.08)
				Meadow = 0.41 (0.09)	Thermal = 0.47 (0.12)
				ELK = 0.89 (0.20)	
ELK + EDG	3	8209	456	ELK = 1.74 (0.15)	EDG = -1.86 (0.24)
VEG + ELK + BD + EDG	7	7753	0	Burn = -1.87 (0.32)	Unburned = -0.82 (0.08)
				Meadow = 0.40 (0.09)	Thermal = 0.38 (0.12)
				ELK = 0.84 (0.20)	BD = 0.70 (0.12)
				EDG = -2.06 (0.26)	

† ELK = elk density, BD = bison density, EDG = distance from edge, VEG = vegetation class

‡ Model weights were not calculated for a priori models due to the magnitude of difference (ΔAIC_c values) between the best approximating models and all other models. As such, the model weight for each best approximating model is 1, while model weights for all other models are zero.

* number of estimated parameters

received 86% of the weight. Also of note, no first order interaction effects were included in any of our top models.

A priori modeling of our kill site response variable resulted in a best approximating model that included elk density, bison density, vegetation type and distance from edge (Table 6). As was the case with our movement models, both types of prey density were positive effects while distance from edge was negative (Fig. 7). However, the 95% confidence interval for the coefficient estimate of elk density included 0. Due to this, we post hoc tested for multicollinearity between predictors in this model. Multicollinearity was determined to not be influencing this result (the maximum variation inflation factor was 2.14), indicating that we couldn't detect the true nature of the

Figure 6. Predicted probabilities of wolf movement, relative to prey densities and distance from edge in the best approximating a priori model. The relationship between wolf movement and individual covariates are depicted under conditions where all other covariates are 0. Movement data were collected in the Madison-Firehole region of Yellowstone National Park, Wyoming.

Table 5. Ranking of models for exploratory analyses of wolf locations extracted from snow tracking data. Data were collected between mid-November and early May from 1998-1999 through 2001-2002 in the Madison-Firehole region of Yellowstone National Park, WY.

Model [†]	k*	AIC _c	ΔAIC _c	ω _i
VEG + EDG ² + LRD + RIV + RIV ² + ELV + ELV ² + LELK + SLP + SLP ² + SNOW + SNOW ² *	15	6958.8	0	0.547
VEG + EDG + EDG ² + LRD + RIV + RIV ² + ELV + ELV ² + LELK + SLP + SLP ² + SNOW + SNOW ²	16	6960.6	1.8	0.222
VEG + EDG + EDG ² + LRD + RIV + RIV ² + ELV + ELV ² + SLP + SLP ² + SNOW + SNOW ²	15	6962.2	3.4	0.010
VEG + EDG + EDG ² + LRD + RIV + RIV ² + ELV + ELV ² + LELK + LBD + SLP + SLP ² + SNOW + SNOW ²	17	6962.4	3.6	0.090
VEG + EDG + EDG ² + LRD + RIV + RIV ² + ELV + ELV ² + LBD + SLP + SLP ² + SNOW + SNOW ²	16	6964.0	5.2	0.041

[†] VEG = vegetation class, EDG = distance from edge, LRD = log of distance from road, RIV = distance from river, ELV = elevation, LELK = log of elk density, SLP = slope

* number of estimated parameters

Table 6. Ranking of a priori hypothesized models concerning the effects of prey density and habitat features on the location of wolf kills in the Madison-Firehole study area in Yellowstone National Park, Wyoming.

Model ^{††}	k*	AIC _c	ΔAIC _c	Coefficient (SE)
Prey Suite				
ELK	2	1791	235	ELK = 1.17 (0.23)
ELK + BD	3	1704	148	ELK = 1.11 (0.24) BD = 2.11 (0.21)
Habitat Suite				
EDG	2	1766	210	EDG = -3.83 (0.74)
VEG	4	1624	68	Burn = -1.97 (0.16) Unburned = -0.92 (0.19) Meadow = .33 (0.21) Thermal = 1.71 (0.22)
Combined Suite				
ELK + EDG	2	1749	193	ELK = 1.08 (0.23) EDG = -3.69 (0.74)
ELK + VEG	5	1626	70	Burn = -1.97 (0.30) Unburned = -0.92 (0.19) Meadow = 0.32 (0.21) Thermal = 1.71 (0.22) ELK = 0.01 (0.30)
VEG + ELK + BD	6	1597	41	Burn = -0.71 (0.37) Unburned = -0.81 (0.20) Meadow = 0.21 (0.21) Thermal = 1.46 (0.25) ELK = 0.12 (0.30) BD = 1.34 (0.23)
VEG + ELK + BD + EDG	7	1556	0	Burn = -4.48 (0.83) Unburned = -0.74 (0.20) Meadow = 0.35 (0.21) Thermal = 1.50 (0.25) ELK = 0.07 (0.30) BD = 1.42 (0.23) EDG = -4.16 (0.82)

[†] ELK = elk density, BD = bison density, EDG = distance from edge, VEG = vegetation class

^{††} Model weights were not calculated for a priori models due to the magnitude of difference (ΔAIC_c values) between the best approximating models and all other models. As such, the model weight for each best approximating model is 1, while model weights for all other models are zero.

* number of estimated parameters

Figure 7. Predicted probabilities of encountering wolf kill sites, relative to covariates deemed important in the best approximating a priori wolf kill model. The relationship between wolf kill sites and individual covariates are depicted under conditions where all other covariates are held at 0. Data were collected in the Madison-Firehole region of Yellowstone National Park, Wyoming.

Table 7. Ranking of models for exploratory analyses of wolf kill sites. Data were collected between mid-November and early May from 1998-1999 through 2001-2002 in the Madison-Firehole region of Yellowstone National Park, Wyoming.

Model†	k*	AICc	$\Delta AICc$	ω_i
VEG + EDG + RD + RD + LRIV + ELV + ELV ² + ELK + ELK ² + BD + SNOW + SNOW ²	15	1385.2	0	0.524
VEG + EDG + EDG ² + RD + RD ² + LRIV + ELV + ELV ² + ELK + ELK ² + BD + BD ² + SNOW + SNOW ²	17	1386.7	1.5	0.247
VEG + EDG + EDG ² + RD + RD ² + LRIV + ELV + ELV ² + ELK + ELK ² + BD + BD ² + LSLP + SNOW + SNOW ²	19	1387.8	2.6	0.143
VEG + EDG + EDG ² + RD + RD ² + LRIV + ELV + ELV ² + BD + BD ² + LSLP + SNOW + SNOW ²	16	1389.9	4.7	0.050
VEG + EDG + EDG ² + RD + RD ² + LRIV + ELV + ELV ² + ELK + ELK ² + LSLP + SWE + SNOW ²	16	1391.1	5.9	0.027
VEG + EDG + EDG ² + RD + RD ² + LRIV + ELV + ELV ² + LSLP + SNOW + SNOW ²	14	1393.5	8.3	0.008

† VEG = vegetation class, EDG = distance from edge, RD = distance from road, LRIV = log of distance from river, ELV = elevation, ELK = elk density, BD = bison density, LSLP = log of slope

* number of estimated parameters

relationship for this variable. The location of wolf kill sites showed a definite pattern of selection for meadow complexes and geothermal areas and avoidance for both burned and unburned forest classes. However, for wolf kills sites, the selection for geothermal areas was four times greater than that for meadow areas, which is an interesting contrast to the results of movement models where meadows were strongly favored.

The results of our exploratory analyses on wolf kill site data resulted in several competing models (Table 7). Given our data, the best approximating model included vegetation type, distance from edge, distance from road, distance from river, elevation, elk density, bison density and SWE. Once again, the second best model differed only in how we incorporated our distance to edge variable. Removal of various covariates resulted in models that had, in general, poorer performance. Models including both prey covariates received 77% of the weight. In contrast, models that were missing either one or both prey covariates received only 23% of the weight. As was the case with our

movement response variable, no first order interactions were included as effects in our best approximating model.

A priori analyses of the relationship between kill sites and movement data showed a clear distinction among models (Table 8). However, based on 95% confidence intervals for coefficient estimates, our certainty of having captured the true nature of the relationship was quite low. Confidence intervals included 0 for all covariates except distance from edge. We again tested for multicollinearity and found that the variance inflation factor was 2.33. Thus, other than the fact that kills occurred closer to edges, we could not differentiate between kill sites and movement vectors.

Table 8. Ranking of a priori hypothesized models concerning the effects of prey density and habitat features on the location of wolf kill sites versus the locations of wolf movements in the Madison-Firehole study area in Yellowstone National Park, Wyoming.

Model ^{†‡}	k*	AICc	ΔAICc	Coefficient (SE)	
Prey Suite					
ELK	2	1575	235	ELK = 0.20 (0.31)	
ELK + BD	3	1575	148	ELK = 0.17 (0.31)	BD = 0.37 (0.23)
Habitat Suite					
EDG	2	1574	210	EDG = -1.59 (0.53)	
VEG	4	1569	68	Burn = -1.82 (0.16)	Unburned = 0.13 (0.20)
				Meadow = -0.13 (0.21)	Thermal = 0.47 (0.21)
Combined Suite					
ELK + EDG	2	1566	193	ELK = 0.17 (0.31)	EDG = -1.59 (0.53)
VEG + ELK	5	1568	70	Burn = -2.37 (0.40)	Unburned = -0.92 (0.19)
				Meadow = 0.32 (0.21)	Thermal = 1.71 (0.22)
				ELK = 0.01 (0.30)	
VEG + ELK + BD	6	1568	41	Burn = -2.06 (0.45)	Unburned = 0.15 (0.20)
				Meadow = -0.17 (0.21)	Thermal = 0.61 (0.24)
				ELK = -0.60 (0.41)	BD = 0.35 (0.23)
ELK + BD + VEG + EDG	7	1556	0	Burn = -3.41 (0.65)	Unburned = 0.18 (0.20)
				Meadow = -0.07 (0.21)	Thermal = 0.64 (0.24)
				ELK = -0.60 (0.41)	BD = 0.37 (0.23)
				EDG = -1.53 (0.53)	

[†] ELK = elk density, BD = bison density, EDG = distance from edge, VEG = vegetation class

[‡] Model weights were not calculated for a priori models due to the magnitude of difference (ΔAICc values) between the best approximating models and all other models. As such, the model weight for each best approximating model is 1, while model weights for all other models are zero.

* number of estimated parameters

DISCUSSION

Over the past decade there has been a dramatic increase in the amount of literature pertaining to broad-scale habitat selection patterns, range expansion and the geographic distribution of wolves (Mladenoff et al. 1995, Massolo and Meriggi 1998, Corsi et al. 1999, Glenz et al. 2001). While these studies are important for conservation of the species, they offer little insight on the potential impacts wolf recovery will have on the systems to which they return. Of the finer scale studies that have been conducted, most have dealt with movement rates or movement patterns as they pertain to wolf home ranges (Ciucci et al. 1997, Merrill and Mech 2000, Jedrzejewski et al. 2001), yet very few have dealt with fine-scale selection (Kunkel and Pletscher 2001). By taking a fine scale approach, we gained insight on which landscape features have the largest effect on the places wolves chose to be. By studying fine-scale selection behavior, we provide an important step in understanding the potential effects wolf recovery can have on prey behavior and ultimately on predator-prey behavioral games.

Analysis of movement vectors clearly showed that wolves preferred to travel in meadows and geothermal areas. Meadow complexes in the Madison-Firehole study area were typically snow covered with thick wind crusts, while geothermal areas had little or no snow. We suspect wolves selected for vegetative communities in order to facilitate movement. This same conclusion was reached by Kunkel and Pletscher (2001), however, they also found that wolves traveled in areas where burned forest was more abundant. While we found that wolves avoided both burned and unburned forest, we suspect this difference was due to differences in burned forest stand structure between the study sites.

In our study area, most burned forest was typified by partially burned deadfall that greatly impeded movement.

Based on coefficient estimates, the strongest effect in our movement model was proximity to edge. Wolves showed a strong preference for traveling in close proximity to changes in vegetation/habitat type. Results from the chi-square analysis showed that wolves preferred to travel along hard edges, i.e. any edge that introduced structural change that could impede animal movements. Specifically, these hard edges included burned forest edges and river edges. Additionally, while we could not include geothermal areas in this analysis, we also consider them to be hard edges. Our interpretation of wolf preference for hard edges is that they selected for landscape features that increased their probability of making a kill when elk were encountered. Many chase sequences were observed where the initial wolf/elk encounter occurred in one habitat type and ended with a successful capture after crossing a hard edge. This relationship with hard edges was also observed for kill sites, indicating elk are more vulnerable under these conditions (see below). By selecting to travel in these areas, wolves maximized their encounter rates with more vulnerable elk. Recent research on African wild dogs (Creel and Creel 2002) and wolves (Hebblewhite and Pletscher 2001) has shown that some coursing canids typically encounter groups of prey at higher rates than what would be randomly expected. Prior to data collection, this relationship to edge was not expected. Based on results of predictive modeling, Mladenoff et al. (1995) expected wolf recolonization in northern Wisconsin to occur in areas with less edge. As was the case with selection for burned forest, we believe wolf response to this variable was specific to the different regions. On privately owned lands in Wisconsin, edges were

often associated with road corridors and were thus sites where wolves were likely to encounter human activity. In our study area, most edge structures are not associated with roads. We believe wolves preferred to travel along edges because they maximized encounter rates with more vulnerable elk.

Our best approximating movement model also showed that wolves preferred areas with higher elk and bison densities. However, based on coefficient estimates, the selection for elk density was surprisingly weak. A priori, we expected elk density to be the single strongest predictor. Other studies found that wolf movement rates and fine scale habitat selection patterns were influenced by the abundance and densities of their preferred prey species (Kunkel and Platscher 2001, Jedrzejewski et al. 2001).

Accordingly, we expected to observe a maximization of encounter rates, manifest through selection for high elk densities. Our explanation for the observed lack of selection is rooted in an interaction between two factors. The first of these is that, retrospectively, we suspect our method of projecting elk densities across the landscape was not as powerful as initially hoped. Based on research that paralleled our study, the influence of variation in the snowpack on winter elk movements is becoming more evident (A. Messer, unpublished data). Other studies have also shown that winter snow conditions affect movement and survival of elk (Sweeney and Sweeney 1984, Telfer and Kelsall 1984, Garrott et al. 2003). While our method of projecting elk densities would have been improved by detailed information regarding elk behavioral responses to snow and other landscape features, the method we used did capture over winter change in elk distribution from high snow, high elevation areas to low snow, low elevation areas.

The second interpretation of the relationship between wolf movement and elk density pertains to potential behavioral adaptations of elk. Work done on prey foraging behavior under predatory constraints has found that movement by prey greatly increases the probability of being detected by a predator (Daly et al. 1990, Boinski et al. 2000). However, these conclusions are only valid at very fine scales, i.e. predators must be relatively close to prey to detect movement. Recent theoretical work has focused on the movements of prey, as it pertains to predators, on a much larger scale (Mitchell and Lima 2002). Under conditions where wolves are not close enough to detect elk movements, yet assuming that wolves are capable of remembering where they last encountered elk, elk movement might be a viable predator avoidance technique. While we suspect that this behavioral adaptation of elk was occurring, our method of projecting elk densities was likely too coarse to detect this behavior. Elk movement as a mechanism for remaining elusive would be very dynamic. Movements among patches would occur over short time intervals and be spread among patches on fine spatial scales. Our method projected elk densities on broader spatial and temporal scales. Such a behavioral response by elk would manifest itself as a weak relationship between wolf movement and elk density.

We analyzed wolf kill site data in order to gain biological insight as to where elk were most vulnerable to predation. By comparing kill sites to a systematic sample of points drawn from across the landscape, we were able to identify the conditions where elk had a higher probability of being killed. Our best approximating model established a clear trend between vegetation type and vulnerability. Elk were more vulnerable in geothermal settings and less vulnerable in burned forest, unburned forest and meadows. We also found that elk were more vulnerable to predation when they were in close

proximity to edges. As mentioned earlier, based on our chi-square analysis, wolf kill sites reflected selection for hard edges. Elk were likely more vulnerable to predation along hard edges because, if chased by wolves between vegetation/habitat classes, the switch in surrounding structure probably imposed a handicap on elk. This handicap would have been realized primarily in the form of greatly reduced escaping efficiency. For instance, when wolves chase elk through a burned forest, elk are forced to suddenly maneuver through a matrix of partially burned, downed timber. We suspect elk are instantly more vulnerable to predation under such conditions because any wrong or delayed decision would allow wolves to narrow gaps during a chase. A similar scenario exists if elk retreat to rivers to escape wolves. Mech (1970) reported that both moose (*Alces alces*) and elk have been documented to use water as a refuge from wolves. However, in our study area the rivers were often shallow enough for wolves to continue pursuit, rendering such an escape strategy ineffective. Under these conditions, features such as rivers and geothermal areas cease to be refuges for elk and essentially become environmental traps. Finally, a scenario unique to our study area concerns chase sequences in geothermal areas. When wolves encounter elk in geothermal areas, elk must attempt an escape. As such, they must exit the geothermal area and its snow-free landscape. By being forced to suddenly run through deep snow, we suspect elk are instantly more vulnerable to predation.

Analysis of kill sites versus movement vectors was performed to identify any selection patterns that wolves exhibited while traveling but not while killing. We identified three potential strategies that wolves could use while moving across the landscape. The first was that wolves selected for areas of high elk density, thereby

increasing elk encounter rates. However, we failed to detect a strong relationship of this nature through our movement analysis. The second strategy was that wolves maximized encounter rates with elk in areas where elk were more vulnerable to predation. Support for this scenario would have existed in the form of an inability on our part to distinguish between kill sites and movement vectors. Such a result would thus lend support to the argument that wolves selected areas where elk were most vulnerable. The third strategy was that wolves did not select for areas based on maximization of encounter rates with vulnerable elk. Based on the comparison of kill sites to movement data, support for this strategy would have existed in the form of noticeable differences between wolf kill sites and movement data. If wolf kill sites were easily distinguished from movement vectors, the wolves would not appear to be targeting areas of high elk vulnerability.

Based on model results, we were unable to detect any significant differences between kill sites and movement data. While ΔAIC_c values showed clear distinction among models, 95% confidence intervals spanned 0 for all coefficients except distance from edge. We interpreted this result as support for the strategy of selecting for areas where prey were most vulnerable. By selecting areas that were similar to those in which they had previously captured elk, wolves exploited the areas where elk were vulnerable.

Based on the results of this study, wolves clearly selected to travel in close proximity to edges as well as in geothermal areas. These were also the places where elk were most vulnerable to wolf predation. We believe such information sheds insight on the effects that predators may have on prey behavior. Through the identification of sites where elk are most vulnerable and by studying elk behavior in these areas, shifts in behavior should become evident. A recent line of literature has focused on the non-lethal

effects that predators have on prey. Such effects can potentially include elevated stress levels, shifts in foraging strategy, change in grouping behavior or the altering of movement patterns (Schmitz 1998, Brown et al. 1999). While we hypothesized that changes in elk movement patterns weaken the relationship between wolf movement and elk density, all of these potential responses reflect changes in the evolutionary stable strategy (ESS) for elk.

An ESS is a strategy for which, if followed by most members of a population, there is no other strategy that will result in higher reproductive fitness or survival (Maynard Smith and Price 1973). As such, elk should have one ESS for predator-free environments and a different ESS for systems where they are forced to deal with predators. Thus, we are forced to wonder if a shift in elk behavior occurred that delivered them from being naïve prey to vigilant prey. While such speculation is well beyond the scope of our study, we must wonder: did elk shift behavioral patterns simultaneously with wolf recovery to maintain an ESS, or was the length of time that wolves were absent insufficient for elk to develop an ESS for a predator-free environment? To address such a question would require a powerful behavioral model that reflects elk response to landscape variables under predatory and predator-free conditions.

Theories and modeling pertaining to predator-prey systems have evolved under a somewhat limiting paradigm. This paradigm focuses on the fact that predator behavior has been left out of predator-prey interaction models (Lima 2002). While the influence of predation risk on prey decision-making has been documented (Sih 1994), our knowledge of predator behavior has remained largely undeveloped. Due to this paradigm, predators have entered predator-prey models as a fixed risk component. We

thus attempted to explore the effects that prey and other landscape variables had on predator hunting behavior. Based on our results, we conclude that the incorporation of predator behavior into predator-prey interaction modeling is overdue. We have shown that prey are more vulnerable to predators under certain conditions, predators are capable of selecting for these conditions, and as such, the notion of fixed predation risk is largely inadequate. While the necessary steps to get past this paradigm will require much in terms of the data and knowledge we as ecologists will be expected to provide, theoretical modeling has already shown that spatial heterogeneity and mobility of both predators and prey play important roles in stabilizing enemy-victim systems (Hastings 1977, McCauley et al. 1993, Keeling et al. 2000). By studying and quantifying the behavior and spatial interactions between predators and prey, we can delve into the complexity of predator-prey races and incorporate biological insight into more accurate models of how the systems around us work.

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