



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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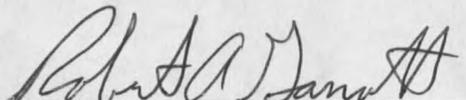
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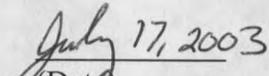
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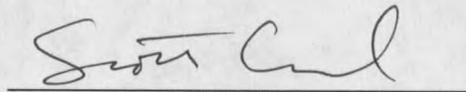
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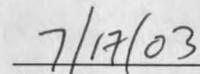
  
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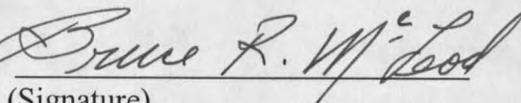
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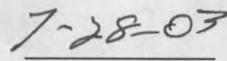
  
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## ABSTRACT

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 (*Lyacon 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).

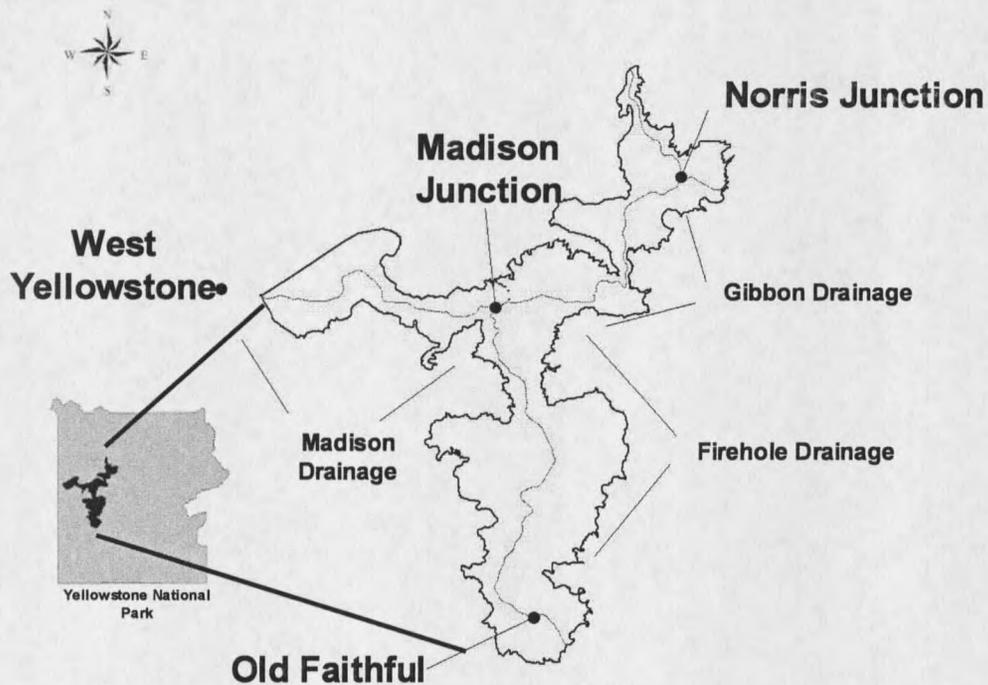


Figure 1. The Madison-Firehole study area was located in the western-central portion of Yellowstone National Park, Wyoming. The study area, defined by the wintering ranges for both the non-migratory Madison-Firehole elk herd and the migratory Central bison herd, was typified by three major river corridors 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 Garrott 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  $-180^{\circ}$  and  $180^{\circ}$ . 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<sub>c</sub> 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  $AIC_c$  ( $\Delta AIC_c$ ) 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  $\chi^2$  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.

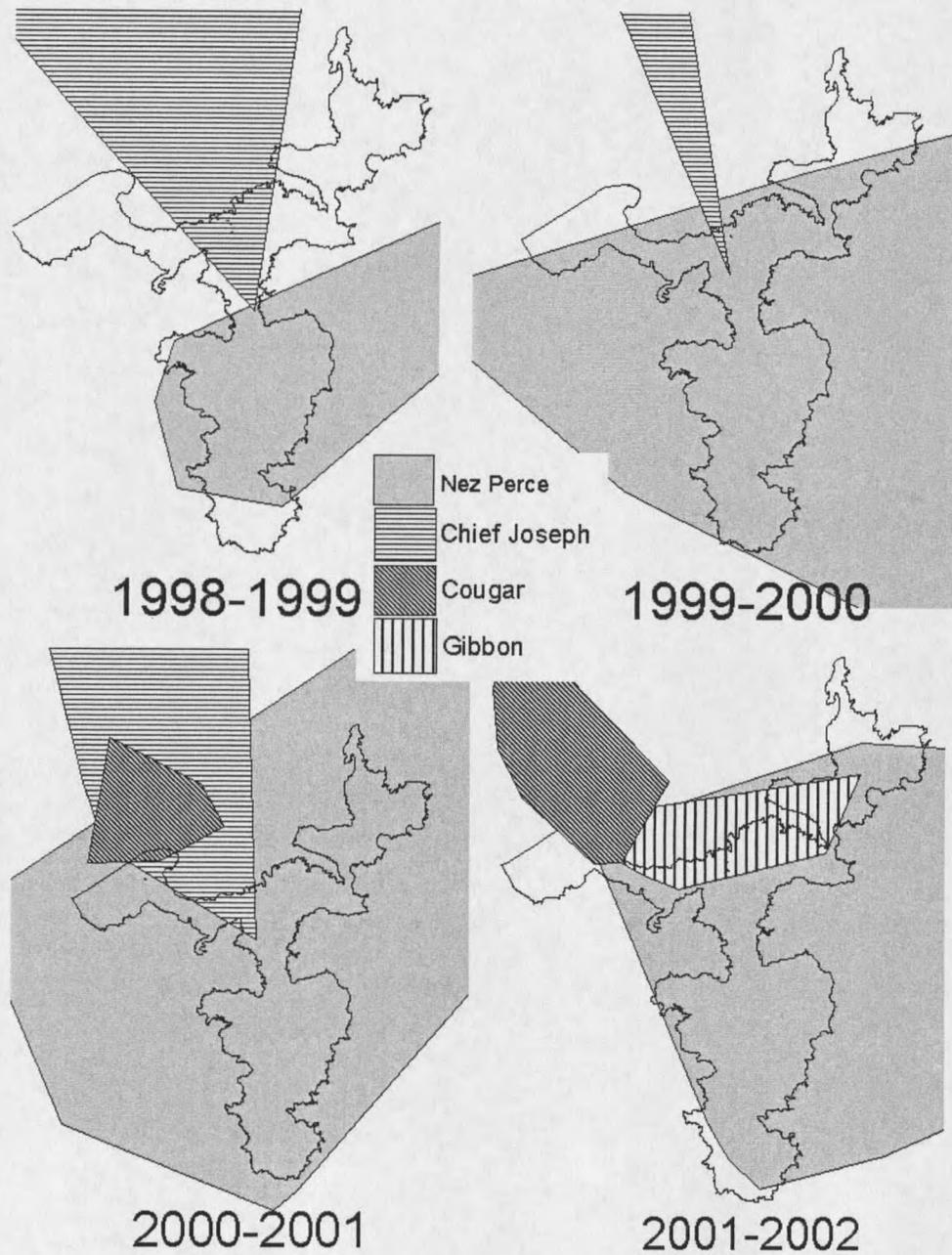


Figure 2. Minimum convex polygons are used to depict winter home ranges for all wolf packs that used the Madison-Firehole study area. All polygons were generated from aerial and ground based telemetry locations collected between 1 November and 30 April.























































