MONTANA STATE UNIVERSITY

Winter wolf predation in an elk-bison system in Yellowstone National Park, Wyoming
by Rosemary Jaffe

Abstract:
Winter kill rates and prey selection of gray wolves (Canis lupis) were studied in the upper Madison drainage of Yellowstone National Park, Wyoming. Elk (Cervus elaphus) and bison {Bison bison) formed the ungulate preybase in the study system and a single wolf pack used the study area as its winter territory. Daily ground telemetry, snow tracking, and necropsies were used to acquire data from mid-November through May, 1998—1999 and 1999—2000. During the two winters 108 wolf kills were located. Wolves preyed primarily on elk and showed the strongest selection for calves, which comprised half the diet (n=56). Thirty cow elk ranging in age from 1 to 15 (mean=9.9) and 8 bulls ranging in age from 1 to 10 (mean=5.1) were also killed. Although bison were more abundant than elk, only one adult and 13 calf kills were found. Prey switching was apparent during the first year of the study. By late March, no elk calf kills were found while cow and bull elk and bison calves were killed at an increased rate. An analytical method was developed to estimate smoothed kill rates across time using a moving window average and a weighting scheme to account for undetected kills. This technique indicated that 30% of the wolf kills were undetected. Estimated kill rates (kills/100 wolf days) nearly doubled from fall to spring each year, and were approximately twice as high the first year (11.8) as the second year (6.5) of study. Two factors that likely influenced kill rates were confounded between winters. Snow conditions were severe the first year and mild the second, and the wolf pack increased from 7 to 13 wolves between years. Offtake from the calf elk population was an estimated 20-25%, the highest among prey types. Though offtake was not consequential for adult elk or bison, recruitment of calf elk into the adult population may be affected by wolf predation, particularly during years of light snowpack when few calves would normally succumb to winter undemutrition. The new methodology reduced variability and improved kill rate estimation, providing new insight into wolf-ungulate dynamics in the Rocky Mountain ecosystem.

WINTER WOLF PREDATION IN AN ELK-BISON SYSTEM

IN YELLOWSTONE NATIONAL PARK, WYOMING

by

Rosemary Jaffe

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

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
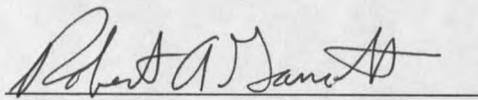Bozeman, Montana

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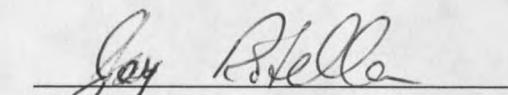
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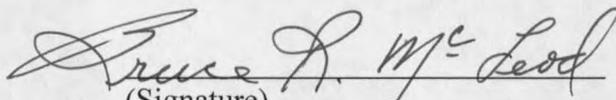
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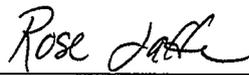
This thesis is dedicated to Morris Jaffe for inspiring my passion for the wild, and Ardyce Corneau Jaffe for teaching me grace, patience, and tenacity through example.

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ABSTRACT

Winter kill rates and prey selection of gray wolves (*Canis lupis*) were studied in the upper Madison drainage of Yellowstone National Park, Wyoming. Elk (*Cervus elaphus*) and bison (*Bison bison*) formed the ungulate preybase in the study system and a single wolf pack used the study area as its winter territory. Daily ground telemetry, snow tracking, and necropsies were used to acquire data from mid-November through May, 1998—1999 and 1999—2000. During the two winters 108 wolf kills were located. Wolves preyed primarily on elk and showed the strongest selection for calves, which comprised half the diet (n=56). Thirty cow elk ranging in age from 1 to 15 (mean=9.9) and 8 bulls ranging in age from 1 to 10 (mean=5.1) were also killed. Although bison were more abundant than elk, only one adult and 13 calf kills were found. Prey switching was apparent during the first year of the study. By late March, no elk calf kills were found while cow and bull elk and bison calves were killed at an increased rate. An analytical method was developed to estimate smoothed kill rates across time using a moving window average and a weighting scheme to account for undetected kills. This technique indicated that 30% of the wolf kills were undetected. Estimated kill rates (kills/100 wolf days) nearly doubled from fall to spring each year, and were approximately twice as high the first year (11.8) as the second year (6.5) of study. Two factors that likely influenced kill rates were confounded between winters. Snow conditions were severe the first year and mild the second, and the wolf pack increased from 7 to 13 wolves between years. Offtake from the calf elk population was an estimated 20-25%, the highest among prey types. Though offtake was not consequential for adult elk or bison, recruitment of calf elk into the adult population may be affected by wolf predation, particularly during years of light snowpack when few calves would normally succumb to winter undernutrition. The new methodology reduced variability and improved kill rate estimation, providing new insight into wolf-ungulate dynamics in the Rocky Mountain ecosystem.

INTRODUCTION

There is considerable debate about the influence of wolf predation on ungulate population dynamics (Boutin 1992, Van Ballenberghe and Ballard 1994). Attempting to determine the impacts of wolves on their prey has thus been a preeminent research theme (Peterson 1977, Fritts and Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Fuller 1989, Mech et al. 1998). The merits of various mathematical predator-prey models, including the concept of functional responses and relevant variables such as the rate of prey consumption and prey density, are contested in the literature (Messier 1994, Hayes et al. 2000). Abrams and Ginzburg (2000) suggest that to resolve the controversy surrounding these concepts, it is important to collect empirical data on numbers of prey killed and the abundance of both the predator and prey species in an environment, acknowledging that measurements of functional responses in nature are difficult to achieve and are therefore rare. Though most data used for developing theoretical predator-prey models has been collected on invertebrate populations (Eberhardt and Peterson 1999), recent attention has been devoted to large predators, and wolf-ungulate systems in particular (Messier 1991, Eberhardt 1997, Eberhardt and Peterson 1999, Hayes and Harestad 2000, Messier and Joly 2000).

Impacts of wolf predation on ungulate populations are frequently addressed by estimating kill rates and determining prey selection. For kill rates to be calculated, the number of wolves in the area of interest must be known, as well as the frequency of kills (Kolenosky 1972). Prey selection is dependent on prey abundance and the vulnerability

of individuals (Hayes et al. 2000). Vulnerability of prey has been studied at length in an attempt to sort out factors that may influence which individual animals are ultimately selected by predators, which can then affect kill rates. The relative susceptibility of an animal to predation is determined by physical and biological conditions. These complex relationships encompass considerations including species, sex, age, and physical condition of prey (Peterson et al. 1984, Huggard 1993a), prey density (Messier and Crete 1985, Messier 1991, Messier 1994), and the availability of alternate prey (Mech and Karns 1977, Peterson and Page 1983). Environmental factors such as elevation and open meadows far from cover (Kunkel and Pletcher 2000) may also influence the vulnerability of prey to capture by predators (Carbyn 1983, Carbyn et al. 1993). Snow has been identified as an abiotic factor that has particularly far-reaching effects by restricting movements and mobility (Formozov 1946, Fuller 1991), impacting escape and access to forage (Mech et al. 1971, Parker et al. 1984). Combined, these factors shape the wolf-ungulate dynamic within varying ecosystems.

The reintroduction of gray wolves to the Rocky Mountain region in 1995 and the natural colonization on the Northern Continental Divide has re-established the wolf-ungulate component to the Northern Rocky Mountain ecosystem. The gray wolf was considered extirpated from this region in the mid-1920s, with the last known wolf den recorded in 1923 in Yellowstone National Park (YNP), Wyoming (Weaver 1978). The return of wolves to the Northern Rockies stirred much controversy (Fritts et al. 1997), which continues. While there was strong public support for re-establishing wolf populations to YNP (McNaught 1987, Bath 1990), the effect of this predator on ungulate

populations remains a major concern. Apprehension about the potential effects of wolves on big game populations and livestock production at times conflicts with a keen interest in restoring and preserving large predators and their natural ecosystems. (Fritts et al. 1997). Understanding the influence wolf predation has on ungulate population dynamics in the Northern Rockies is, therefore, of particular importance.

The re-establishment of wolves to YNP provides a unique opportunity to study wolf-prey dynamics in the Rocky Mountain ecosystem. The goals of this investigation were to measure prey selection, kill rates, and offtake from ungulate populations by wolves. Specific objectives included: (1) estimating winter ungulate abundance and composition; (2) estimating the amount of predation ungulates were subjected to over time (wolf days); (3) describing prey selection patterns; (4) describing temporal patterns in kill rates, both within and between winters; and (5) estimating ungulate offtake by wolves according to species, sex, and age class. Understanding kill rates and prey selection of wolves is essential for understanding the impacts of wolves on ungulate populations. Natural resource professionals may use this information to assist in decisions about the management of both ungulate and wolf populations, and gain insights that can aid in evaluating the potential for reintroducing wolves to other ecosystems.

STUDY AREA

The study area consisted of approximately 27,000 hectares at elevations of 2250—2800 meters in the upper Madison River drainages of Yellowstone National Park, Wyoming. The area encompassed three drainages, the Firehole River north from Old Faithful and the Gibbon River west from the Norris Geyser Basin to their confluence at Madison Junction, and the upper Madison River to the western boundary of the Park (Figure 1). Extensive high plateaus carved by rivers resulted in steep canyons and open meadows where valleys broadened. Geothermal features warmed many low elevation meadows and streams, resulting in areas of reduced snow cover and free-flowing rivers with unique plant associations that continued photosynthesizing throughout winter (Despain 1990). The most extensive geothermal features were concentrated in the Upper, Middle, and Lower Geyser Basins of the Firehole drainage, and the Norris Geyser Basin in the Gibbon drainage.

Wet meadows and swales associated with the river systems were characterized by sedges (*Carex spp.*), common horsetail (*Equisetum arvense*), rushes (*Eleocharis flavescens*), and several species of grasses (*Agropyron spp., Deschampsia spp.*). Dominant species in the dry grassland meadows were Idaho fescue *(Festuca idahoensis)*, bluegrass (*Poa ssp.*) and sagebrush (*Artemisia spp.*) (Meagher 1973, Despain 1990). Most prominent of the contiguous forest communities was lodgepole pine (*Pinus contorta*), with scattered pockets of Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudosuga menziesii*), and whitebark pine (*Pinus*
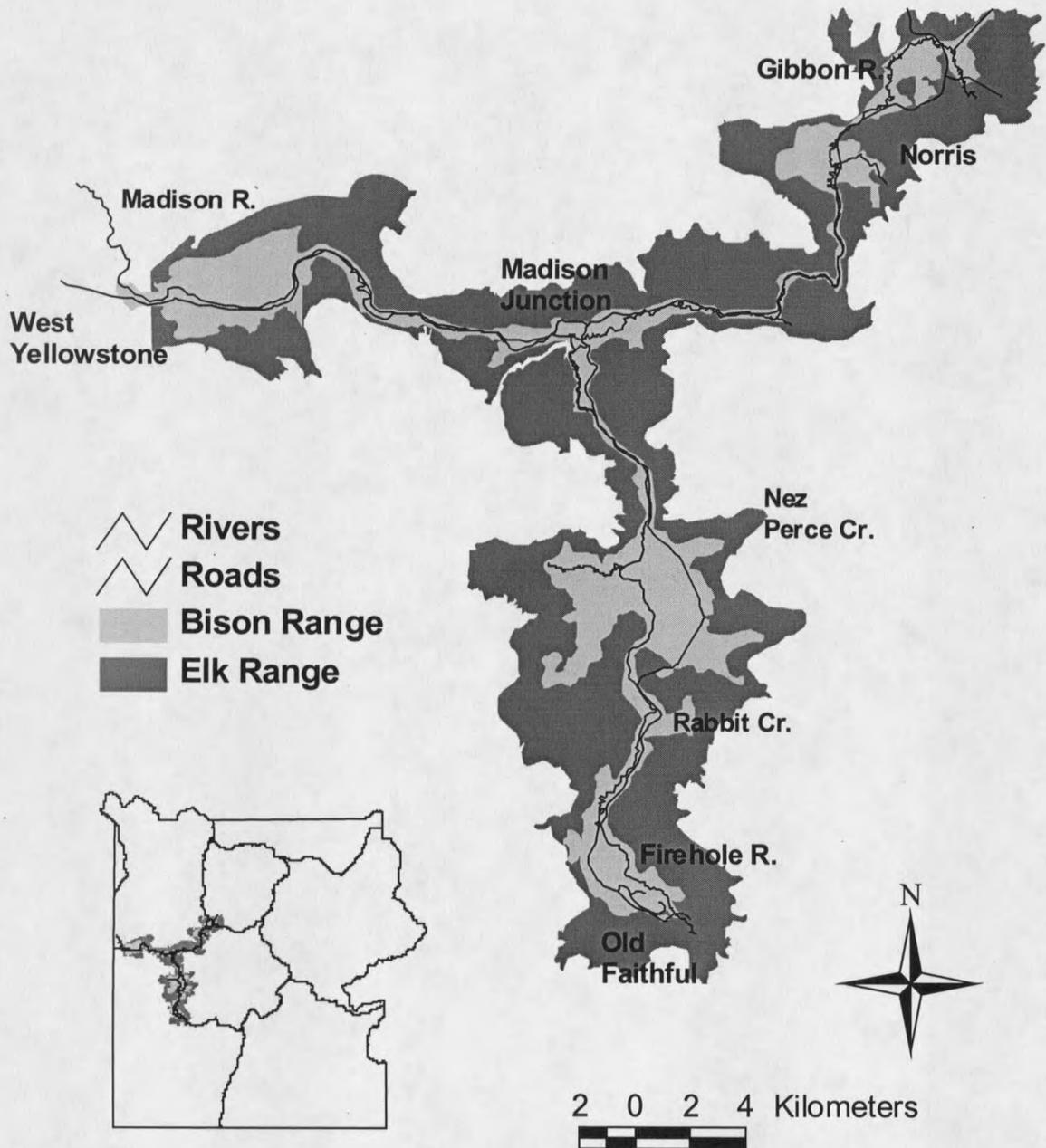
Figure 1. Study area in the Upper Madison drainages of Yellowstone National Park, Wyoming. The bison winter range (light area) was entirely contained within the elk winter range (dark area), as delineated by Ferrari (1999).

albiculis) at higher elevations (Craighead et al. 1973, Despain 1990). Large-scale fires in 1988 burned 55% of the drainages, leaving a mosaic of burned and unburned forests at different stages of succession (Despain et al. 1989).

Winters were long and severe, with deep snowpack and cold temperatures. Data collected between 1968 and 2000 at National Resource Conservation Service SNOTEL sites located at Madison Plateau (2,362m) and West Yellowstone (2,042m) indicated snow typically began to accumulate by October, with snow depths commonly exceeding 91 cm in nonthermal areas (Eberhardt et al. 1998). On average, meltout began in the valleys in early April and 2 weeks later on the plateaus, ending in late May. Using averaged daily high and low temperatures, winter mean monthly temperatures in the valleys ranged from 2.5°C in October to -11.0°C in December and January, increasing to -4.2°C in March and 6.5°C in May.

Two ungulate species, elk and bison, were abundant in the study area. A non-migratory herd of approximately 600-800 elk (Eberhardt et al. 1998) remained within the study area year round (Craighead et al. 1973) where no hunting occurred. Bison migrated seasonally from their summer ranges in the Hayden Valley and Pelican Valley to the east of the study area to winter range in the Firehole, Madison, and Gibbon drainages during fall and early winter (Meagher 1973, Bjornlie and Garrott 2001). Between 250-1100 bison occupied the study area throughout the winters during the years of this study. Together, elk and bison formed the ungulate preybase for wolves in the study system.

The gray wolf was the primary predator of ungulates utilizing the Upper Madison winter range. Wolves were first released into the Firehole drainage in the spring of 1996

(Phillips and Smith 1996) and radio-collared wolves moved sporadically through the study area that first year. The Nez Perce pack established the Upper Madison drainages as its winter territory in 1997 and became the primary resident wolf pack in the study area. The Chief Joseph pack and other uncollared wolves occasionally moved through the area during the study. Other large predators found in the study area included the grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), and coyote (*Canis latrans*). Though grizzly bears were known as effective predators on neonate ungulates during early summer (Larsen et al. 1989, Ballard et al. 1991, Gasaway et al. 1992, Singer et al. 1997), I assumed their impacts were minimal during the winter months of my study since bears hibernated during most of the study period and elk calved during late May—June. Impacts on ungulate populations by black bear and coyote predation were also considered insignificant (Smith and Anderson 1996).

METHODS

Field studies were conducted from mid-November through May for 2 consecutive winters for 183 and 184 days during 1998—1999 and 1999—2000, respectively. Data collected included wolf, elk, and bison abundance and distribution, and the species, sex, age, and frequency of wolf kills to analyze prey selection, kill rates, and offtake from prey populations. Data on snow conditions and condition of prey were collected to study factors potentially affecting prey vulnerability.

Prey Abundance and Distribution

I estimated winter bison and elk population sizes in the study area to estimate ungulate availability, determine wolf prey selection, and evaluate wolf offtake from prey populations. Ground-based censuses of the bison population were conducted every 10 days during 1998—1999 and every 14 days during 1999—2000, December through May. The bison winter range in the study area was divided into 72 units and 6 delineated travel routes that completely traversed all the units. Censuses were conducted by 3 crew members working independently during 2 consecutive days to locate all bison groups within each unit. For each bison group observed, the location was recorded on USGS 7.5-minute maps in Universal Transverse Mercator (UTM) coordinates, and sex and age composition was classified as calves, cows, and bulls when possible, otherwise as calves and adults (Ferrari 1999, Bjornlie and Garrott 2001).

I estimated the elk population occupying the study area at the onset of each winter field season by combining replicate Lincoln-Petersen population estimates from the

previous spring and replicate composition surveys conducted during the fall rut. Fifty-four radio collars were maintained on cow and calf elk on the study area during the 2 years of the study: 39 cows and 15 calves during 1998—1999 and 41 cows and 13 calves during 1998—1999. All surveys were conducted while traveling the road system using binoculars and a spotting scope in early morning and late evening when elk were most visible. A continuity-corrected Lincoln-Petersen population estimate was calculated for individual surveys (Chapman 1951) conducted on 10—13 consecutive days in spring (31 March—9 April 1998, 11—23 April 1999) when elk were aggregated in lower elevation meadows and after most winter mortality had occurred. The mean of the surveys was considered the estimate of the number of adult elk in the population entering the next winter (Rice and Harder 1977). Seven years of pre-wolf elk telemetry data showed no significant adult elk mortality from spring to the fall rut surveys (R.A. Garrott, unpublished data), and the wolves were absent from the study system during the snowless seasons both years of my study. Ten years of elk telemetry data in the Upper Madison drainages indicated that collared elk remained inside the study area year round (R.A. Garrott, unpublished data). Fall rut replicate composition surveys were conducted on 11—12 consecutive days in fall (26 September—7 October 1998, 25 September—5 October 1999) using the method described for spring surveys to determine the sex and age composition and estimate the increment to the population due to reproduction from the previous spring and summer. The proportion of cows and bulls in the adult population and calf:cow ratios were calculated and multiplied by the previous spring population estimate, which yielded the total elk population estimate and composition at the onset of winter. Monthly calf:cow

ratios (Thompson 1992:60) were calculated using a telemetry database maintained on elk

to adjust the early winter population estimate each month of the field season to account for

calf mortalities. The number of cow and bull elk carcasses detected each month by a 4-

person crew were considered the minimum adult elk mortality on the study area and used

to adjust monthly adult elk population estimates for mortalities throughout winter. Elk

biomass available to wolves was calculated by multiplying fall population estimates

classified by sex and age by the average weight of each class (Murie 1951:69. Bulls: 287

kg, cows: 236 kg: calves: 116 kg). March bison counts associated with peak migration

each year were used to calculate bison biomass in the same manner (Meagher 1973.

Adults: 500 kg, calves: 136 kg).

Wolf Tracking

I used ground-based telemetry to estimate the number and location of wolves

occupying the study area daily and detect fresh wolf trails in snow to ground-track and

locate kills. Movements of the Nez Perce pack were monitored by radio tracking 3—5

instrumented wolves and the Chief Joseph pack was detected using 1—2 instrumented

animals. The Nez Perce pack demonstrated strong pack cohesion during the pre-denning

season, as did the portion of the Chief Joseph pack that used the study area. I therefore

assumed tracks found in entirely different drainages than the packs used during a given

day were made by unmarked wolves which were not associated with either pack. The

linear configuration of the study area allowed most radio signals to be heard from the 3

major roads along the rivers (Figure 1). Radio signals for all collared wolves known to

frequent the study area were checked from these roads daily, with periodic scans for other

collared wolves associated with more distant packs. In addition, 3 other research crew members traveled daily in the backcountry of the study area and investigated wolf sign opportunistically. The starting point for each day's search for signals began with the last known location of wolves from the previous day. In the event that more than 1 pack occupied the study area simultaneously, packs or individuals were tracked on alternating days when they could not be reached on the same day. I estimated daily wolf locations using ground-based triangulation by employing a minimum of 3 azimuths for each wolf transmitter detected (White and Garrott 1990). I plotted the bearings on USGS 7.5-minute maps and recorded the center of the area delineated by the intersections of the azimuths as the estimate of the animals' location in UTM coordinates. Daily ground-based tracking was supplemented by an aerial tracking schedule maintained by NPS biologists (Smith et al. 2000). Weather-dependent flights were attempted daily mid-November—mid-December and during the month of March, and every 10—14 days during the rest of the year.

In order to locate wolf-killed prey, observers tracked recent wolf trails in snow (Kolenosky 1972, Peterson et al. 1984, Huggard 1993b, Ballard et. al 1997). A single person performed daily tracking during the winter of 1998—1999, and 2 observers tracked nearly daily during the 1999—2000 winter. On days 2 observers tracked, 1 observer began tracking where wolves or wolf trails were found the previous day, while the other observer hiked toward telemetry signals to find new wolf trails. Attempts were made to cover all wolf trails made in a 24-hour period to locate all kills. The vicinity of wolf locations and scavenger activity (ravens, eagles, coyotes, grizzly bears) was

searched for tracks and kills when the wolves left the area. Caution was taken to avoid approaching the wolves at distances <1 km to insure research activities did not influence wolf behavior.

I used the Minimum Convex Polygon Home Range estimator (*Animal Movement*, Hooge and Eichenlaub, 1997) to estimate the Nez Perce pack home range on a coarse scale. Using the fixed kernel estimator in *Animal Movement*, I also estimated the spatial distribution of wolf kills on the study area (least squares cross validation; Seaman and Powell 1996) with combined kill site data for the pack from both years of the study (n=95) and plotting probability polygons of 5, 25, 50, and 75% (grid size=155.5).

Identifying Wolf Kills and Prey Attributes

Necropsies were performed on all ungulate carcasses found on the study area to determine cause of death. The presence of blood or a hair trail and subcutaneous hemorrhaging on the hide or crushing of muscle was used as conclusive evidence of a kill. Subcutaneous hemorrhaging or punctures ($\geq$1 cm in diameter) on the throat, rump, or flanks, and crushing or punctures on the trachea or esophagus were diagnostic of predation by wolves (Banfield 1954, Mech 1970). I assigned the category of 'definite' when one or more of these traumas and wolf tracks were present a the kill site, and 'probable' when evidence of predation was present, wolves were known to be in the area and no other cause of death was apparent (Peterson et al.1984). When sign of both wolves and grizzly bears were present at a carcass, I assigned the category of probable and included these kills in analyses. Observations in south-central Alaska showed brown bears and wolves displace each other from their kills (Ballard 1982) and aerial

observations in YNP suggest grizzly bears often displace wolves from their kills (D.

Smith person. comm.). Definite and probable wolf kills were pooled for prey selection

analysis and kill rate calculations.

Species, sex, age, and condition of prey were recorded to determine prey selection

and identify potential factors contributing to prey vulnerability. The species of carcasses

was determined based on pelage, skulls, jaws, and bones. Sex was determined based on

the presence of antlers, horns, pedicels, and genitalia. Carcasses were categorized as

calves or adults based on carcass size and characteristic tooth eruption and replacement

patterns (Dimmick and Pelton 1994). Age of adult elk was determined through

cementum annuli analysis of incisor (I1 when possible) and/or canine teeth (Hamlin et al.

2000). To index the body condition of all ungulates found dead, bone marrow was

examined by sawing through the middle of the femur and the fat content was assessed

(Harder and Kirkpatrick 1994) according to 3 categories: (1) white and solid, (2) spotted

pink—red solid, and (3) gelatinous (Cheatum 1949). If a femur was not present, a

humerus was used. Carcasses were examined for jaw necrosis (Shupe et al. 1984) and

rated on a scale of 0-3 (none, slight, moderate, severe), arthritis, recorded as

presence/absence, and other apparent physical malady (i.e. broken bones, ticks, cysts).

To calculate kill rates, it was necessary to approximate the date of each kill based on

combined knowledge of wolf movements, carcass temperature, and the extent tissues

were dehydrated at the time of necropsy. I also estimated the percent of carcasses

consumed by wolves when kills were fresh and little sign was evident from other species

scavenging. To examine temporal trends of prey killed by wolves classified by species, sex, and age, I included kills made by all wolves on the study area.

Prey Selection Analysis

I used the Fisher Exact Test (PROC FREQ; SAS Institute 1990) to evaluate the relative use and availability of prey by wolves, or 'prey selection', comparing the observed composition of ungulate wolf kills made on the study area (i.e. use) with the estimated composition of ungulates occupying the study area (i.e. availability). Two analyses were conducted for each month, December through May, for both years of the study: first, a comparison of wolf kills across all prey types, and second, a comparison of wolf kills restricted to only elk. If a monthly kill count was <3, it was not used in analysis, so data for May and December 1998 were excluded. And while counts of 3 kills were used, the P-value was recognized as sensitive to change, whereas P-values for sample sizes of >5 were less sensitive to change (Dupont 1968).

Estimating Kill Rates and Offtake

A daily kill rate, R, may be expressed as the kills per day, K, divided by the daily number of predators, D. However, it is difficult to determine K and D exactly, so a kill rate must be estimated, where the estimator $\hat{R}$ is defined as

$$\hat{R} = \frac{\hat{K}}{\hat{D}}$$

and $\hat{K}$ and $\hat{D}$ are the estimated number of kills and wolves present on the study area during a given time, respectively. The general form for estimates of both K and D are similar:

$$\hat{K}_i = \frac{\sum\limits_{j=1}^{Pk} X_{kj} E_{kj}}{\sum\limits_{j=1}^{Pk} E_{kj}} \qquad \text{and,} \qquad \hat{D}_i = \frac{\sum\limits_{j=1}^{Pk} Y_{kj} W_{kj}}{\sum\limits_{j=1}^{Pk} W_{kj}}$$

where X_{kj} is the number of kills observed on a given day (k) during a given tracking bout (j), and E_{kj} is a subjective measure of detection efficiency for the same tracking bout. I used tracking bouts as units because tracking was performed in more than one place in the study area during a day. For the majority of days, there was 1 tracking bout. The $X_{kj}E_{kj}$ product is summed across the number of tracking bouts (P_k) during a given day. Likewise, $\hat{D}_i$, the weighted number of wolf days, is the product of Y_{kj}, the observed number of wolf days on a given day (k) during a given tracking bout (j), and W_{kj}, a subjective weight corresponding to certainty the wolves were on the study area. The summed products for $X_{kj}E_{kj}$ and $Y_{kj} W_{kj}$ are then divided by the sum of E_{kj} and W_{kj}, respectively, which by definition yields the weighted average (Neter et al. 1993:754).

Prey types included in the analyses for kill rates were calf and adult elk, and calf bison. Adult bison were excluded because only 1 was killed during the 2 years of the study. I used all information available from ground and aerial telemetry, snow tracking, and opportunistic sightings of wolf sign to estimate the number of wolves present in the study system each day, Y. Numbers of collared wolves detected, counts from clear trails that showed the number of wolves present, and numbers of wolves seen were recorded. Because the Nez Perce pack was the only pack that occupied a winter range in the study area, data for only the Nez Perce pack were used in the kill rate calculations. When all radio collars in the Nez Perce pack were detected together during the pre-denning season

(mid-November—mid-April), I assumed all members of the pack were present due to strong pack cohesion during that time, evident from ground and aerial tracking. During the denning season (mid-April—May), the alpha female was subtracted from the pack size because her den was outside the study area both years of the study and her transmitter was not detected after 26 April 1999 and 19 April 2000 during the first and second field seasons, respectively. The pack fragmented during the denning season and portions of the Nez Perce pack used the study area in different numbers and combinations of individuals, apparent from radio signals detected. I therefore estimated wolf days during the denning season on days counts of animals could not be determined from tracks by assigning a proportion of the uncollared wolves in the pack based on each collared animal detected via radio signals only. This estimation method was also applied during the pre-denning season when collared wolves were divided on the study area. Zero wolf days were assigned when no radio signals were detected on the study area.

Because kills are not always detected and wolf days cannot be known exactly, I developed a weighting scheme to adjust the daily data to better estimate kill rates and offtake. Weights were assigned according to daily wolf activity rather than observer activity. Confidence in locating kills each day varied due to tracking conditions and effort. When the pack was cohesive, the wolves typically stayed and consumed their prey at kill sites, thus limiting predation to 1 kill site per day. Evidence from snow tracking showed that multiple kills made by all wolves on the study area (n=16) were located within 1km of each other. I therefore assumed 1 kill site per tracking bout and assigned a weight of 1.0 for bouts when kills were detected, regardless of tracking effort and

perceived efficiency. To adjust for detection efficiency on days I found no kills, I assigned one of the following weights: 0.8 to days I covered most tracks and had good knowledge of the movement patterns of the pack, and 0.2 on days I located few tracks and knew little about wolf activity that day. I assigned a weight of 0.0 when either the wolves were absent from the study area or no field effort occurred.

Certainty of whether the Nez Perce pack was on the study area varied due to the difficulty in knowing the exact timing of the pack's movements off and on the study area. To adjust wolf presence estimates for this certainty, like kills, I assigned weights, referred to as wolf day certainty, to the daily estimated number of wolf days. Telemetry coverage of the study system was excellent and pack cohesion was strong during the pre-denning season. I therefore assigned the weight 1.0 when I detected all Nez Perce pack radio signals on the study area or had knowledge of where the wolves were off the study area during the pre-denning season. For consecutive days I checked radio signals and heard none and had no knowledge of where the pack was, I assigned 0.8, assuming the wolves were in a cohesive pack somewhere off the study area. On days the Nez Perce pack either entered or left the study area, I assigned a weight of 0.5 to reflect the uncertainty of what proportion of the day the pack was on the study area. I assigned 0.0 when no field effort occurred. Days that were assigned weights of 1.0 and 0.8 when the pack was off the study area were excluded from calculations of the kill rates because I had no knowledge of wolf predation activity on those days.

A moving window average was used to obtain smoothed estimates of daily kill rates across the entire field season to better define temporal patterns and trends.

Modifying the weighted average for estimated daily kills and wolf days to incorporate a

moving window average results in:

$$\hat{K}_i = \frac{\sum_{k=i-d}^{i+d} \sum_{j=1}^{Pk} X_{kj} E_{kj} T_k}{\sum_{k=i-d}^{i+d} \sum_{j=1}^{Pk} E_{kj} T_k} \qquad \text{and,} \qquad \hat{D}_i = \frac{\sum_{k=i-d}^{i+d} \sum_{j=1}^{Pk} Y_{kj} W_{kj} T_k}{\sum_{k=i-d}^{i+d} \sum_{j=1}^{Pk} W_{kj} T_k}$$

where $\sum_{k=i-d}^{i+d}$ is the sum of the estimated daily kill rates across the days in the window

(Figure 2). First, the number of days in the window, or window width, is chosen. Then

d, the number of days before and after the current day, i, is calculated by subtracting 1

from the window width and dividing by 2 (i.e. the window width = $2d+1$). The window

is then moved across time by successively increasing i by 1 day to calculate moving

window averages. I used a large window of 15 days to smooth the data and better show

temporal trends. To further smooth the continuous kill rate curve, for each window of 15

days, I incorporated a triangular weighting scheme with the daily estimated kill rates.

Using a large window allows trends to be identified, but daily kill rates can still be quite

variable and difficult to discern when days within the window are equally weighted.

Using triangular weights further smoothes the daily rates, allowing trends to be more

easily recognized. The triangular weights (T_k) are integer weights that decrease

uniformly with distance in time from the center day (i), which has maximum weight $d+1$.

Mathematically, day $i\pm k$ has the weight $d+1-k$. Each daily weighted kill rate estimate

within the window is multiplied by a weight corresponding to that day's position in the

window. An example ($d=2$) is as follows (Figure 3). Each window is moved forward by