



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
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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.

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IN YELLOWSTONE NATIONAL PARK, WYOMING

by

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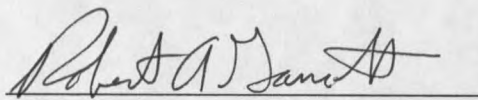
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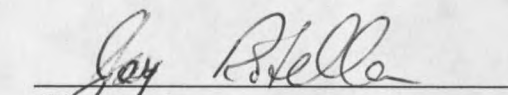
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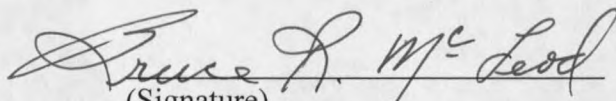
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This thesis is dedicated to Morris Jaffe for inspiring my passion for the wild,
and Ardyce Corneau Jaffe for teaching me grace, patience, and tenacity through example.

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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 (*Pseudotsuga menziesii*), and whitebark pine (*Pinus*

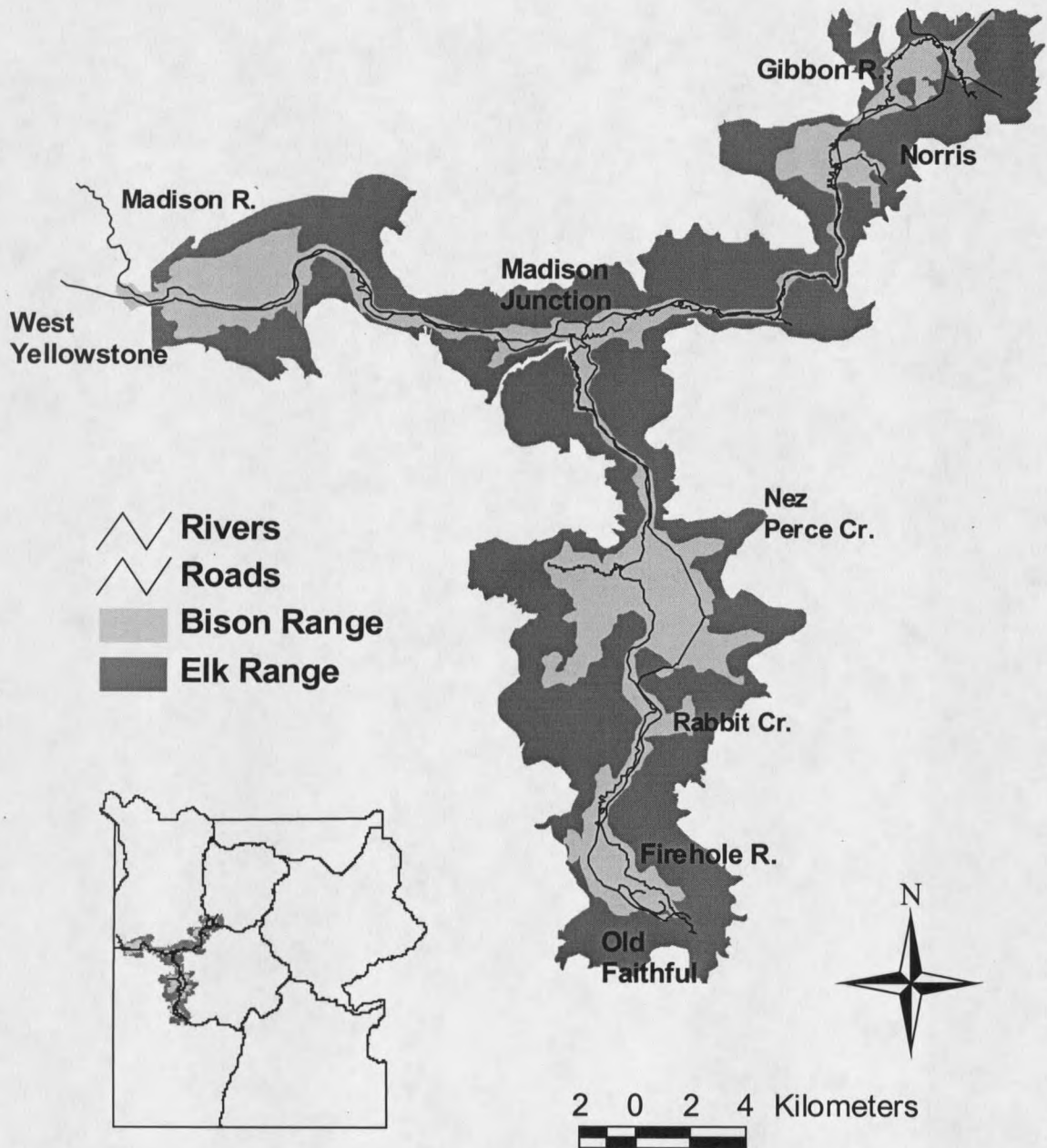


Figure 1. Study area in the Upper Madison drainages of Yellowstone National Park, Wyoming. The bison winter range (light area) was entirely contained within the elk winter range (dark area), as delineated by Ferrari (1999).

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 1993*b*, 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 (≥ 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 at 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:

$$\hat{K}_i = \frac{\sum_{j=1}^{P_k} X_{kj} E_{kj}}{\sum_{j=1}^{P_k} E_{kj}} \quad \text{and,} \quad \hat{D}_i = \frac{\sum_{j=1}^{P_k} Y_{kj} W_{kj}}{\sum_{j=1}^{P_k} W_{kj}}$$

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:

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

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 $i+k$ 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

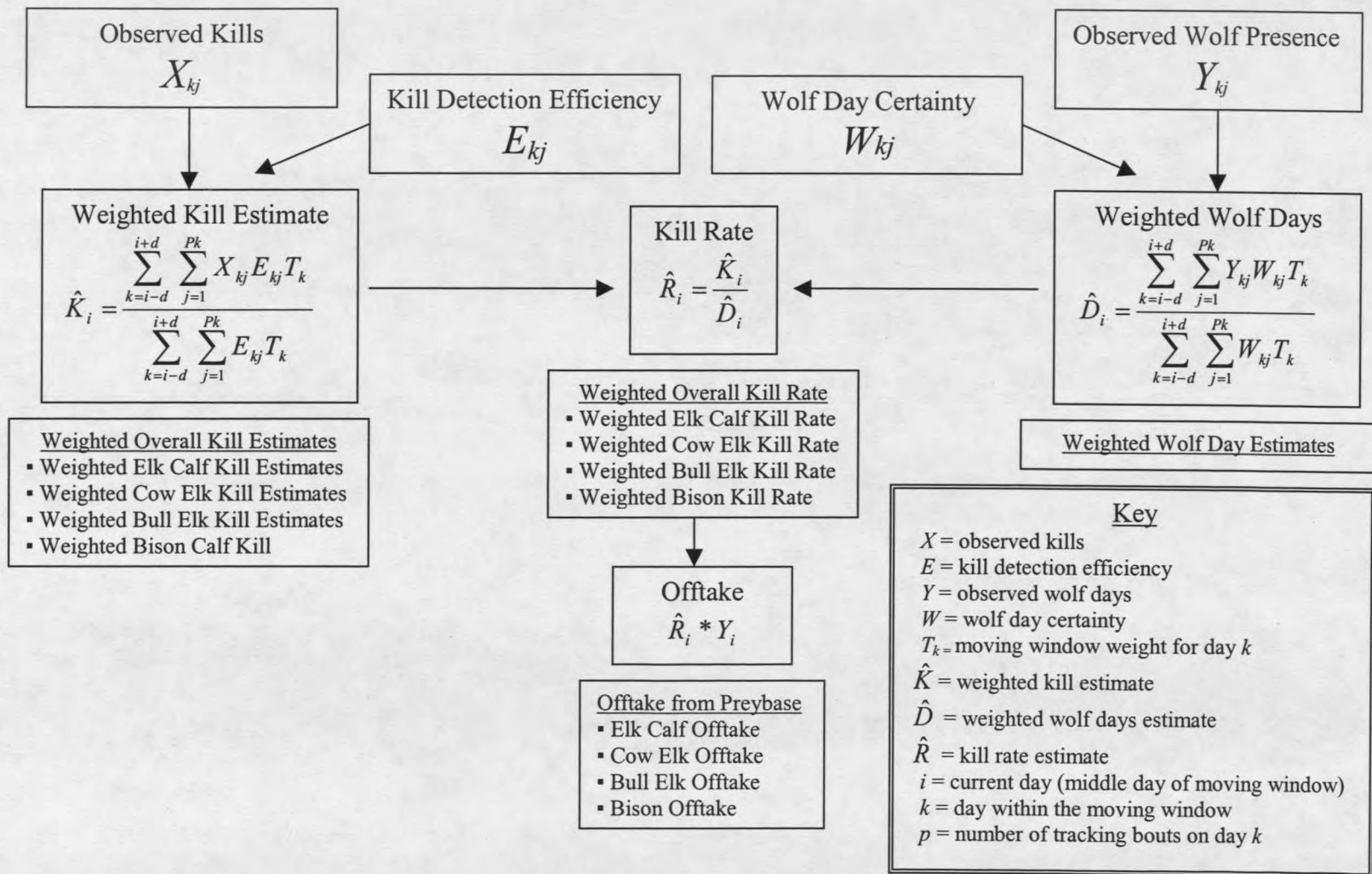


Figure 2. Method for estimated kill rate calculations and offtake using a moving window average and weighting scheme to adjust for difficulty in locating wolves and their kills daily. Triangular weights, T_k , are used to smooth data to better detect trends.

one day and repeated. As the center day (i) moves forward by one day, the last day of the previous window ($i-2$) is dropped, and the new day on the leading edge of the window is included ($i+2$). The sequence of weights 1,2,3,2,1 (the numbers in parentheses) remains constant according to their position in the window and are multiplied by the new set of daily kill rate estimates in the window (the numbers above the parentheses). Daily estimated kill rates are then averaged across the days in the window, so in this example the average kill rate for Day 1 is 0.1499, Day 2 is 0.1719, and Day 3 is 0.0201.

After calculating kill rates for the Nez Perce pack (Mathworks 1999), I tested the robustness of the method by varying the kill detection efficiency weights of 0.8 and 0.2 to 0.9 and 0.1, and 0.7 and 0.3. Estimated offtake was calculated by multiplying average weighted moving window daily kill rates (kills/100 wolf days) by observed daily wolf days on the study area. Although data from only the Nez Perce pack were used in the kill rate calculations, I used wolf day data from all wolves present on the study area in the offtake calculations to account for all wolf predation pressure on the ungulate populations in the study system. I assumed all wolves using the study area killed at the same per capita rate as the Nez Perce pack. The data were divided into pre-denning and denning seasons because the Nez Perce pack's behavior changed, from strong pack cohesion during the pre-denning season to making forays between the study area and the den located off the study area in varying numbers during the denning season. This, combined with diminished spring snow tracking conditions to locate kills, rendered the data from the denning season less reliable than pre-denning data. Total estimated offtake of elk according to sex and age class was subtracted from the initial population estimates for

each field season. Bison were excluded from this summary because maximum numbers in the winter population peaked during March due to migration, and mortalities occurred while numbers increased prior to the peak.

		<u>Day 1</u>			
		0.1429			
	0	(3)	0.2857		
0	(2)		(2)	0	
(1)				(1)	
<i>i-2</i>	<i>i-1</i>	<i>i</i>	<i>i+1</i>	<i>i+2</i>	
		<u>Day 2</u>			
		0.2857			
		0.1429	(3)	0	
	0	(2)		(2)	0
	(1)				(1)
	<i>i-2</i>	<i>i-1</i>	<i>i</i>	<i>i+1</i>	<i>i+2</i>
		<u>Day 3</u>			
			0		
			0.2857	(3)	0
		0.1429	(2)		(2) 0.1429
		(1)			(1)
		<i>i-2</i>	<i>i-1</i>	<i>i</i>	<i>i+1</i> <i>i+2</i>

Figure 3. Example of triangular weights (in parentheses) used with calculations of kill rates using a 5-day moving window average. The smoothing weights are multiplied by the set of daily kill rate estimates in the window (the numbers above the parentheses). The average kill rate for Day 1 is 0.1499, Day 2 is 0.1719, and Day 3 is 0.0201.

Annual Snowpack

I used snow water equivalent (SWE) measurements, the amount of water contained in a column of snow (Farnes 1996), to evaluate the potential influence of snowpack on prey selection and kill rates. Automated SNOTEL sites near West Yellowstone, 2,042m, and on the Madison Plateau, 2,362m, were operated by the National Resources Conservation Service and recorded daily SWE measurements. These sites provided data from the valley floor and plateaus, respectively. Daily SWE measurements summed October 1 through the end of May each year were used as an index of snowpack severity.

RESULTS

Prey Abundance and Distribution

A total of 27 bison surveys were conducted throughout the study, 16 during 1998—1999 and 11 during 1999—2000. The bison population in the study area ranged from 464 to 921 in 1998—1999 and from 241 to 1168 in 1999—2000 due to migration, which peaked in late March both years (Figure 4). Bison represented 75% of the total estimated ungulate biomass during the first year of the study and 81% the second year (Table 1). The calf:adult ratio in the population ranged from 24:100 to 46:100 during 1998—1999 and 16:100 to 36:100 during 1999—2000. Bison were unevenly distributed throughout the 3 drainages of the study area. The Firehole drainage consistently contained the highest percent of the bison population during the study, with an overall average of 67%, the Madison drainage contained 22%, and Gibbon drainage, 11%. Bison numbers in the Gibbon drainage remained relatively constant, with most distributional shifts occurring between the Firehole and Madison drainages. The proportion of bison was highest in the Firehole drainage and lowest in the Madison drainage during the mid-winter months of February and March both years of the study, following patterns recorded previously by Bjornlie and Garrott (2001). Although collars were maintained on elk in all 3 drainages of the study area and the population was estimated, it was not possible to determine the distribution of elk within the study area. The fall 1998 elk population was estimated as 600 animals, including 59 bulls, 371 cows, and 170 calves (Figure 5), and an estimated 25% of the total ungulate biomass during the first year of the study (Table 1). In the fall of

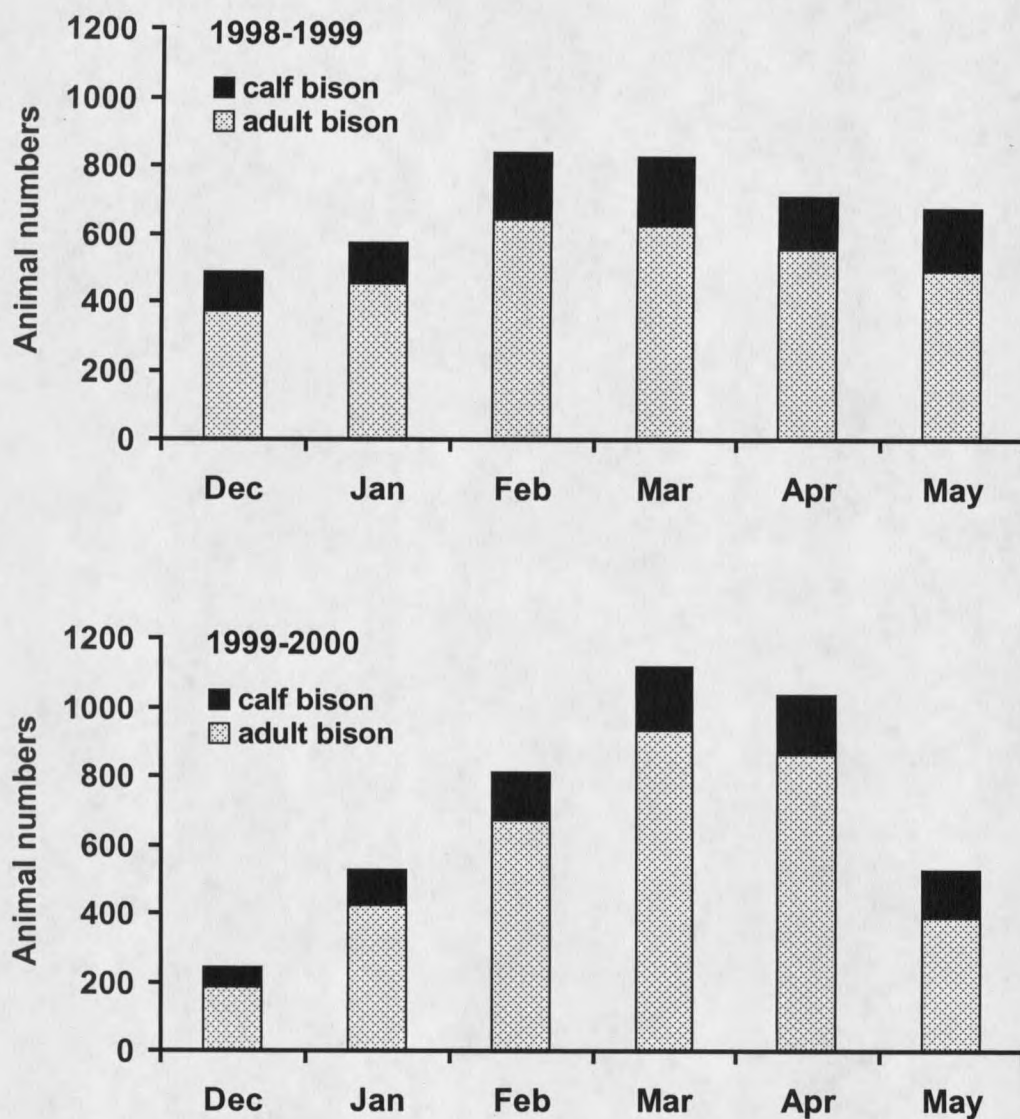


Figure 4. Temporal trends in bison abundance during the winters of 1998—1999 and 1999—2000 in the Upper Madison drainages of Yellowstone National Park, Wyoming. Census data on bison were collected December through May both years and averaged each month.

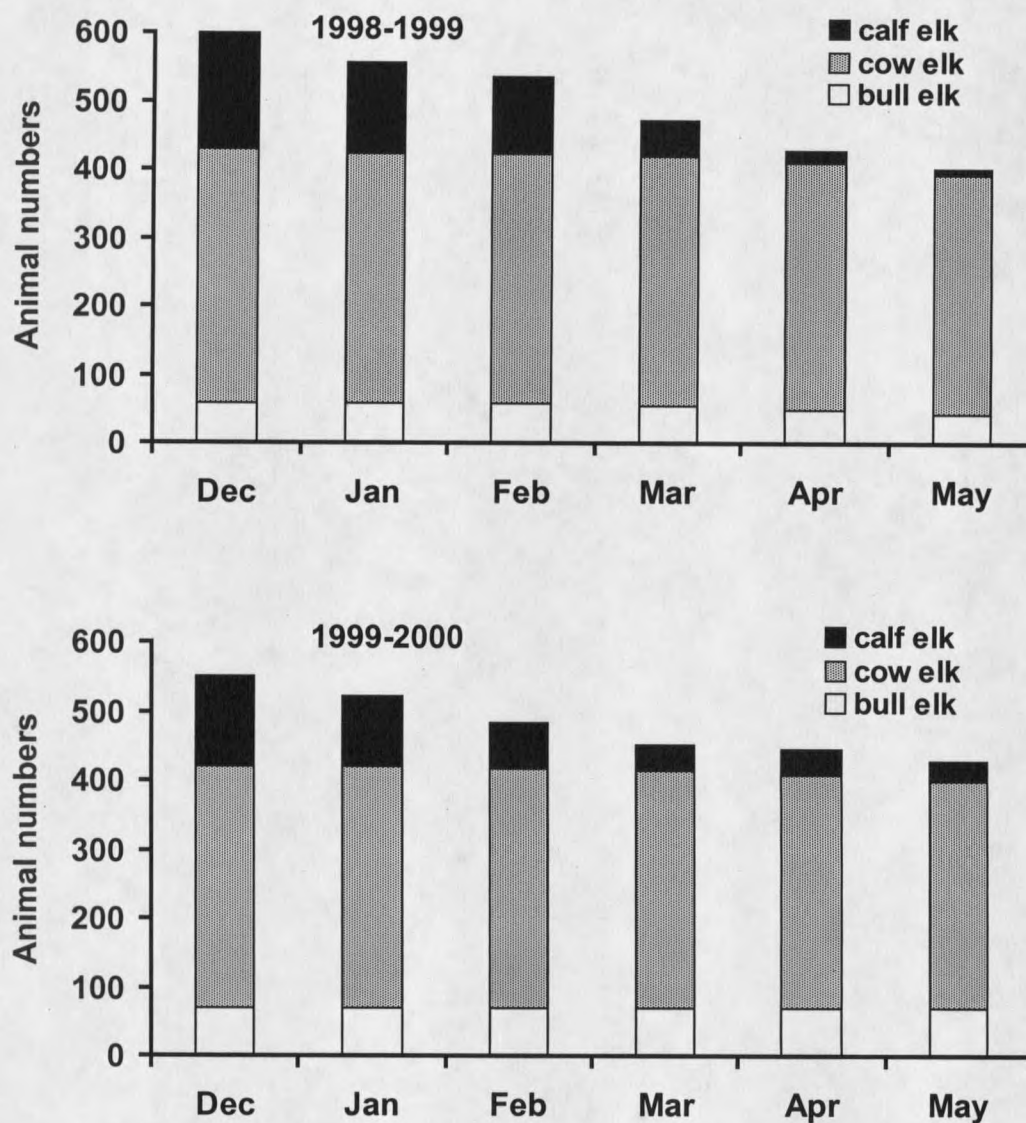


Figure 5. Temporal trends in elk abundance during the winters of 1998—1999 and 1999—2000 in the Upper Madison drainages of Yellowstone National Park, Wyoming. Elk abundance was calculated from mark-resight surveys in spring and fall, and calf-cow ratios throughout the winter of each year. November and December elk data were combined.

Table 1. Maximum number of individuals and biomass of prey available to wolves in the Upper Madison drainages of Yellowstone National Park, Wyoming, during the 1998—1999 and 1999—2000 field seasons. Elk estimates were calculated using spring and fall mark-resight surveys and fall calf:adult ratios from each year. Bison counts of peak migration were recorded in March during ground-based bison censuses.

Prey Type	1998-1999				1999-2000			
	No.	% of Ungulate Community	Biomass (kg)	% Biomass	No.	% of Ungulate Community	Biomass (kg)	% Biomass
Adult bison	675	44	337,500	68	982	57	491,000	77
Calf bison	246	16	33,456	7	186	11	25,296	4
Bull elk	59	4	16,933	3	70	4	20,090	3
Cow elk	371	25	87,556	18	350	20	82,600	13
Calf elk	170	11	19,710	4	132	8	15,306	2
Total	1521	100	514,835	100	1720	100	649,172	100

1999, there was an estimated population of 552 elk, with 70 bulls, 350 cows, and 132 calves, representing an estimated 19% of the total ungulate biomass during the second year. Calf:cow ratios decreased from 46:100 in December 1998 to 3:100 in May 1999, and 38:100 in December 1999 to 9:100 in May 2000. Combining these data provided an estimate of the relative availability of prey to wolves throughout each winter. There were far more bison than elk in the system, and calves were rare compared to adults in both species. Elk calves decreased most dramatically among all prey types.

Wolf Abundance and Distribution

The Nez Perce pack first established the study area as their winter territory during the 1997—1998 winter as a pair. The pack increased to 7 wolves in the spring of 1998, with 4 adults all fitted with radio collars and 3 pups. The Nez Perce pack numbered 13 at the beginning of the 1999—2000 field season, with 8 adults, 5 of which were collared, and 5 pups, however, one collared wolf left the pack in mid-February. Members of the Chief Joseph pack (5—6) used the study area during 1998—1999, and uncollared pairs and solitary wolves not associated with known packs were occasionally detected both winters.

I detected wolves in the study area on 117 of the 173 days wolf presence was monitored during 1998—1999 (Figure 6). Total observed wolf days for the first field season was 787. The Nez Perce pack was detected in the study area on 111 days, including 110 days in the Firehole drainage and 1 day in the Gibbon drainage. The Chief Joseph pack moved through the study area twice, with 6 wolves for 2 days and 5 wolves for 3 days, for a total of 4 days in the Firehole drainage and 1 day in the Gibbon drainage. Uncollared pairs or solitary wolves were detected by tracks on 8 days in the Gibbon

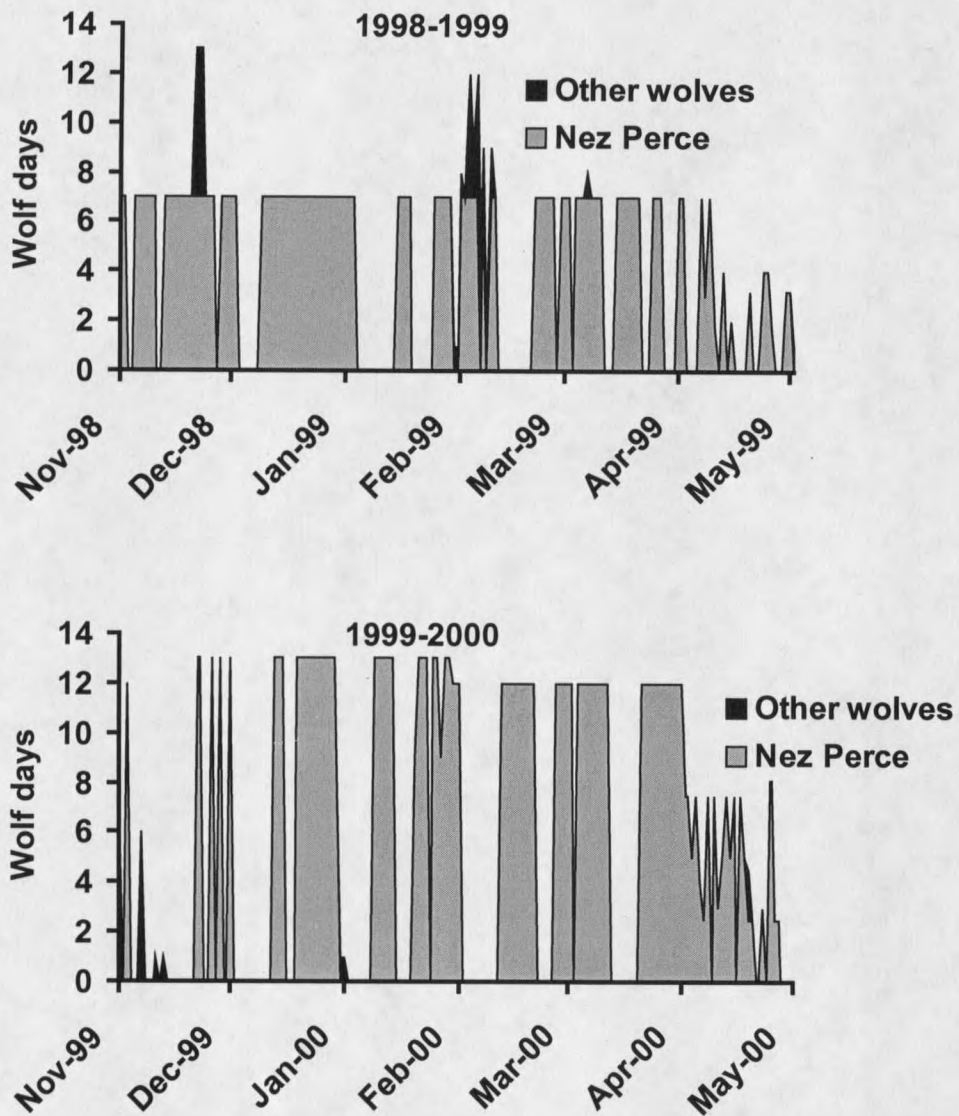


Figure 6. Temporal trends in wolf presence in the Upper Madison drainages of Yellowstone National Park, Wyoming. Data were collected during the 1998—1999 and 1999—2000 winters. “Other wolves” included members of the Chief Joseph pack and uncollared pairs and solitary wolves that briefly used the study area. Total number of observed wolf days during the 1998—1999 and 1999—2000 predenning seasons were 755 and 936, and 32 and 115 during the denning seasons, respectively.

drainage and 1 day in the Madison drainage. Effort was similar during 1999—2000.

Wolves were detected in the study area 102 of 171 days of monitoring, with a total of 1051 observed wolf days for the field season (Figure 6). The Nez Perce pack was detected on 96 days in the study area, including 88 days in the Firehole drainage, 10 days in the Gibbon drainage, and 1 day in the Madison drainage. The pack began using the study area later in 1999—2000 than the previous year, and wolves were rare until mid-January. Uncollared pairs or solitary animals were detected on 4 days in the Gibbon drainage and 2 days each in the Firehole and Madison drainages. Packs and uncollared wolves used the system simultaneously, but wolves seldom moved between drainages on a given day.

Based on telemetry locations, the area occupied by the Nez Perce pack during both winters of the study encompassed nearly the entire study area and extended roughly 30 km to the west and east. The pack killed prey primarily in the Firehole drainage and parts of the Gibbon drainage. Areas with the highest predation were Nez Perce Creek, Firehole Lake Drive, and along the Firehole River south of Rabbit Creek (Figure 7).

Wolf Kills

I located and recorded wolf travel routes on 84 days for a total of 307 km and 86 days for 321 km during 1998—1999 and 1999—2000, respectively. During both winters, a total of 108 definite (88) and probable (20) wolf kills (here after referred to as “kills”) were located (Table 2). Wolves killed primarily elk, with calf elk comprising approximately half the total number of wolf-killed ungulates located. During the 1998—1999 field season, 59 kills were located, including 30 elk calves, 11 cow elk, 6 bull elk, and 12 bison calves (Figure 8). A total of 49 kills were located during the winter of



Figure 7. Nez Perce pack 1998-1999 and 1999-2000 home range and spatial distribution of kills in the Upper Madison drainages of Yellowstone National Park, Wyoming. Kernel estimator uses kill site locations ($n=95$) with 5, 25, 50, and 75% probability polygons.

Table 2. Wolf-killed ungulates classified by species, sex, and age in the Madison-Firehole-Gibbon drainages of Yellowstone National Park, Wyoming. Data were collected during the winters of 1998—1999 and 1999—2000. Probable wolf kills are indicated with parentheses.

Year	Month	Elk				Bison			Total kills
		Bull	Cow	Calf	Total	Adult	Calf	Total	
1998- 1999	Nov	1	1	1(1)	3(1)	0	0	0	3(1)
	Dec	1	3	4	8	0	1	1	9
	Jan	0	2	7(1)	9(1)	0	1	1	10(1)
	Feb	0	1	15(2)	16(2)	0	1	1	17(2)
	Mar	0	2(1)	3(1)	5(2)	0	4(2)	4(2)	9(4)
	Apr	4(1)	2	0	6(1)	0	4(1)	4(1)	10(2)
	May	0	0	0	0	0	1	1	1
	Totals	6(1)	11(1)	30(5)	47(7)	0	12(3)	12(3)	59(10)
1999- 2000	Nov	0	0	0	0	0	0	0	0
	Dec	0	0	1	1	0	0	0	1
	Jan	0	1	2	3	0	0	0	3
	Feb	0	2	9(2)	11(2)	0	0	0	11(2)
	Mar	1	6	9(2)	16(2)	0	0	0	16(2)
	Apr	0	8(2)	5(3)	13(5)	0	0	0	13(5)
	May	1	2(1)	0	3(1)	1	1	2	5(1)
	Totals	2	19(3)	26(7)	47(10)	1	1	2	49(10)

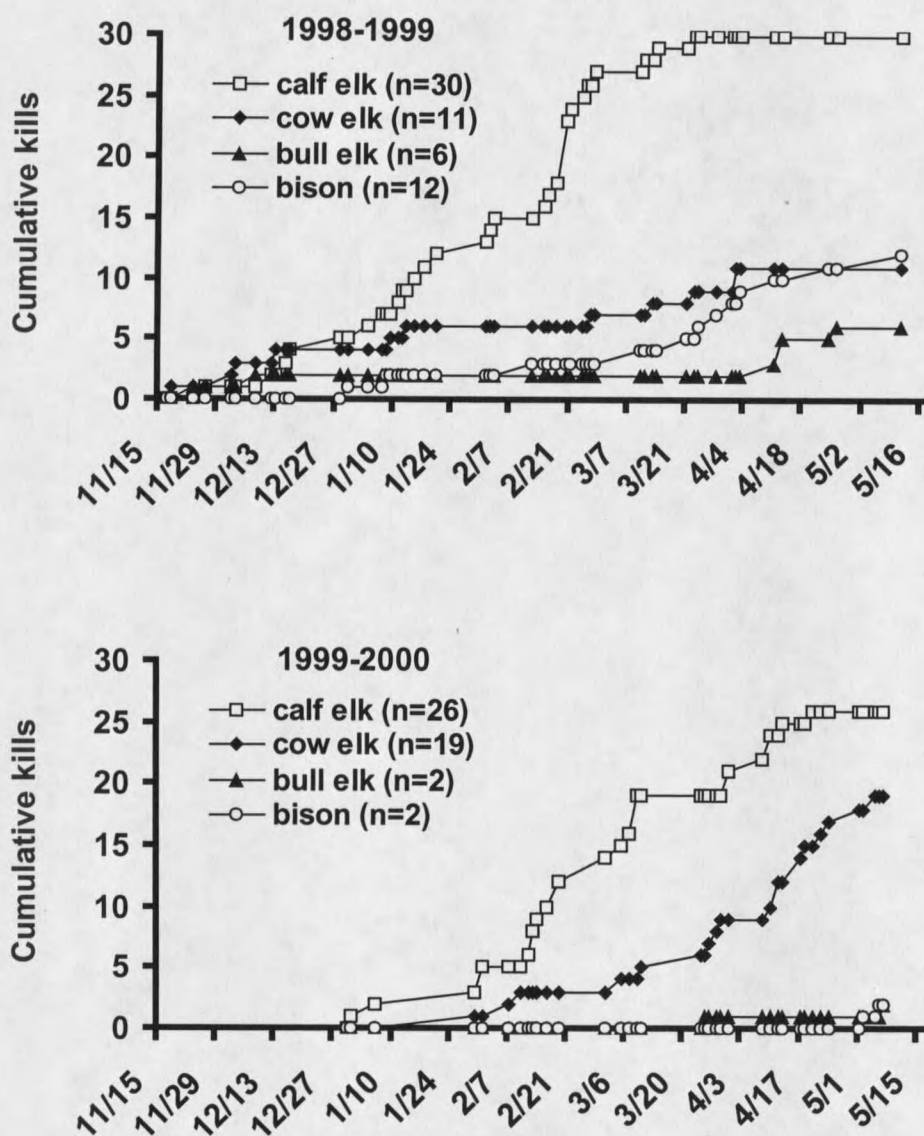


Figure 8. Temporal trends of prey killed by wolves classified by species, sex, and age class. Data were collected during daily snow tracking of wolves in the Madison-Gibbon-Firehole drainages of Yellowstone National Park, Wyoming, during the 1998—1999 and 1999—2000 field seasons.

1999—2000, with 26 elk calves, 19 cow elk, 2 bull elk, 1 bison calf, and 1 cow bison. Of the 37 adult elk killed that were aged by cementum annuli analysis, 54% were prime-aged, 1—9 years old ($n=20$), and 46% were old, 10-15 years old ($n=17$) (Figure 9). Mean age of cows killed was 10 years ($n=29$, $SD=4.4$) and bulls 5 years ($n=8$, $SD=2.9$).

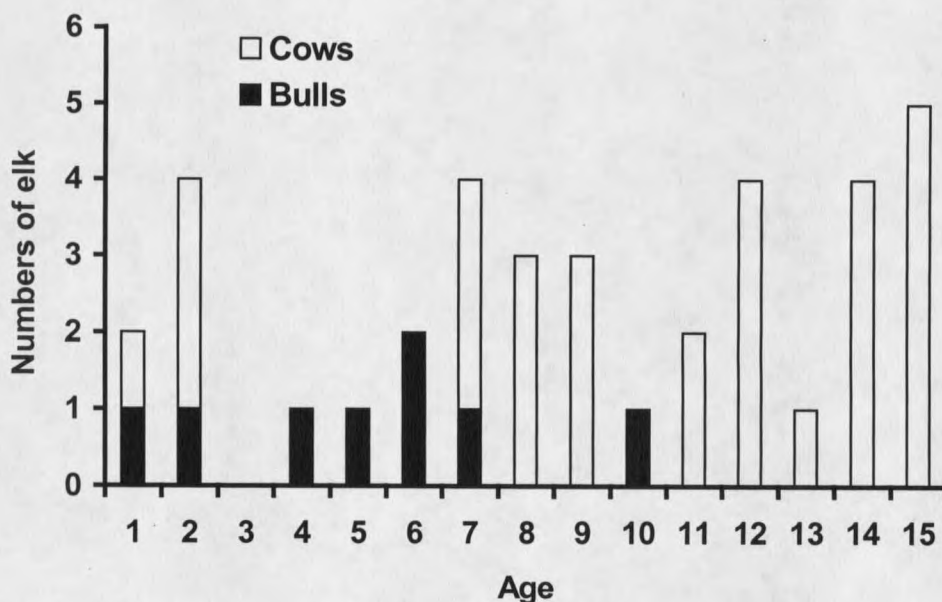


Figure 9. Ages of adult elk killed by wolves in the Madison-Firehole-Gibbon drainages of Yellowstone National Park, Wyoming. Data were collected during the winters of 1998—1999 and 1999—2000 ($n=37$).

Temporal trends of species, age, and sex of prey killed by wolves differed between winters. The wolves entered the study area in mid-November during 1998—1999 and January during 1999—2000 (Figure 8). Elk calves were killed until mid-March the first year and mid-April the second year of the study, and were the main prey for wolves during that time. During 1998—1999, wolves killed few cow and bull elk and

bison calves until March, then increased killing these prey types as they decreased killing elk calves. In contrast, bison and bull elk predation was negligible during the winter of 1999—2000, while cow elk became more important prey. Wolves began killing elk calves and cows concurrently during 1999—2000, and cow elk were killed more frequently throughout the winter compared to the previous winter. Percent of kills consumed by wolves at their initial feeding differed between the 2 years of the study as well. Average initial consumption of carcasses by wolves was 42% (n=27) and 75% (n=23) during 1998—1999 and 1999—2000, respectively.

Prey Selection

Selection among prey types varied both seasonally and annually (Figure 10). Wolves did not select their prey in proportion to all available prey types each month during December 1998—April 1999 (maximum $P < 0.005$), and January—April 2000 (maximum $P < 0.038$). During May 2000, evidence suggested that wolves selected all prey types in proportion to availability ($P = 0.45$). Though adult bison were consistently most available, they were very rarely preyed upon. In contrast, wolf selection for elk calves was far greater than availability and substantially higher than all other prey types both years of the study. The only exception was selection for bull elk during April 1999. Selection for calf elk increased steadily for the first 3 months after the onset of wolf predation each field season, then decreased and ended in March 1999 and April 2000. Peak selection for calf elk during 1998—1999 was approximately half of the peak selection during 1999—2000 due to fewer bison available during 1998—1999 compared to 1999—2000.

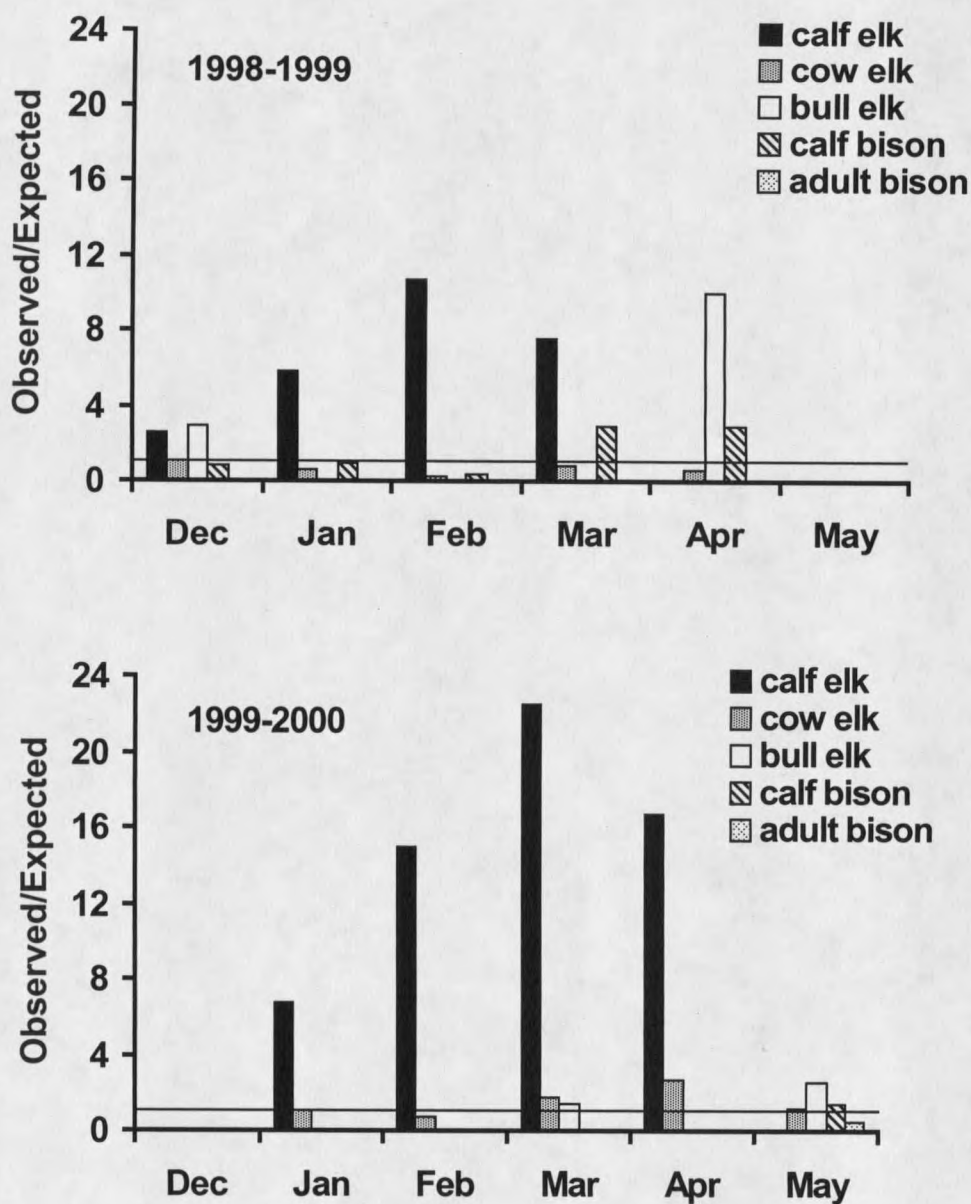


Figure 10. Use and availability of wolf prey types in the Upper Madison drainages in Yellowstone National Park, Wyoming. Observed/expected=1 (horizontal lines on graphs) indicates prey killed in proportion to availability, <1, less than expected, and >1, more than expected. Data were collected during the 1998—1999 and 1999—2000 winters.

When excluding bison from the analysis and considering only elk as prey, wolves did not select in proportion to availability of sex and age classes each month during February—April 1999 (maximum $P < 0.004$), and February—April 2000 (maximum $P < 0.002$). Evidence suggested that wolves selected elk prey types in proportion to availability during 2 months of 1998—1999, December ($P = 0.30$) and January ($P = 0.14$), and 3 months during 1999—2000, December ($P = 0.37$), January ($P = 0.15$), and May ($P = 0.54$). Temporal trends were similar in both prey selection analyses (Figure 11). However, peak selection, which differed strongly between years among all prey types, was nearly the same between years among only elk as prey.

Summary of Weights Used to Estimated Kill Rates

Smoothed estimated kill rates used weights with a 15 day moving window average. The distribution of weights used in kill rate calculations for kill detection efficiency in aggregate over the 2 field seasons were 1.0: 25%, 0.8: 10%, 0.2: 7%, 0.0: 58% (Figure 12). Wolf day weights in total for the 2 field seasons were 1.0: 70%, 0.8: 11%, 0.5: 11%, and 0.0: 8% (Figure 13). Estimated kills were highly variable and increased throughout winter until denning season, while estimated wolf days remained quite constant (Figure 14).

Estimated Kill Rates

Kill rates for the Nez Perce pack changed both within and between years (Figure 15). While estimated rates were highly variable both years, general trends indicate a fairly constant increase during both field seasons, nearly doubling from fall to spring,

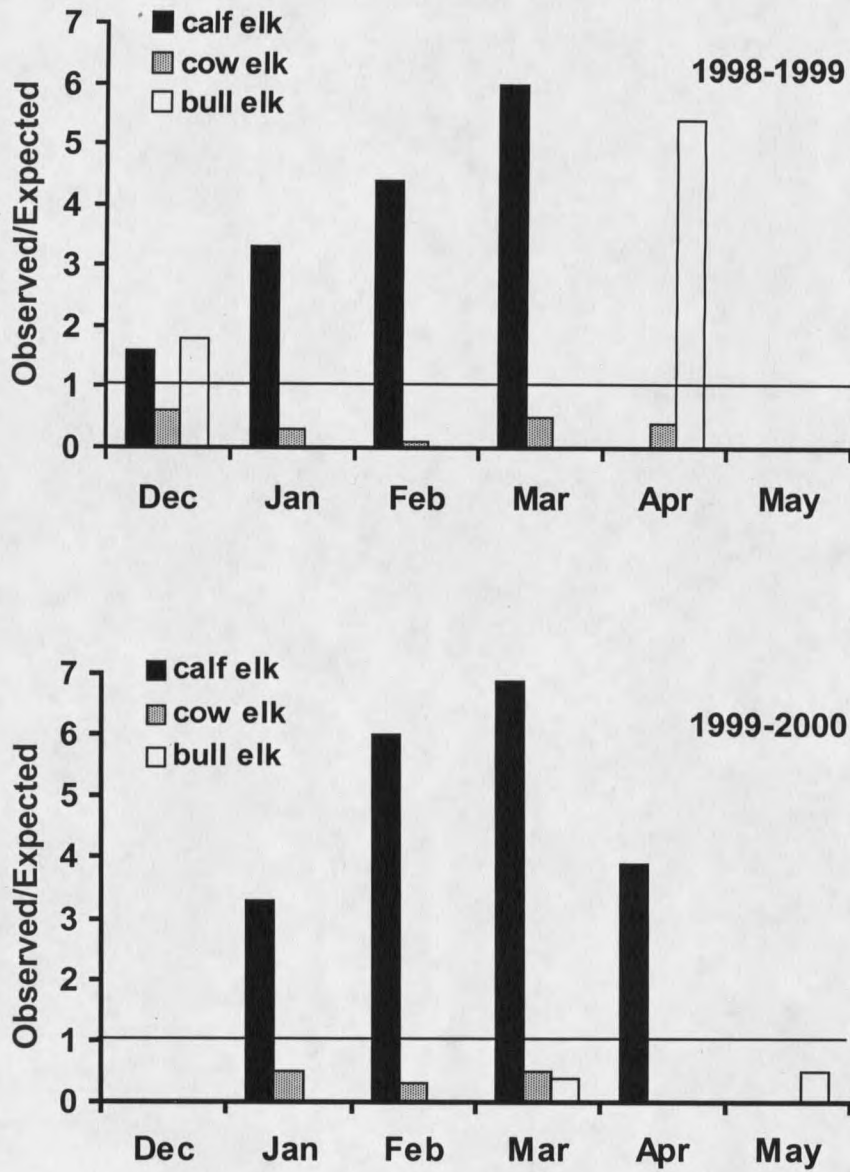


Figure 11. Use and availability of elk as prey in the Upper Madison drainages in Yellowstone National Park, Wyoming. Observed/expected=1 (horizontal lines on graphs) indicates prey killed in proportion to availability, <1, less than expected, and >1, more than expected. Data were collected during the 1998—1999 and 1999—2000 winters.

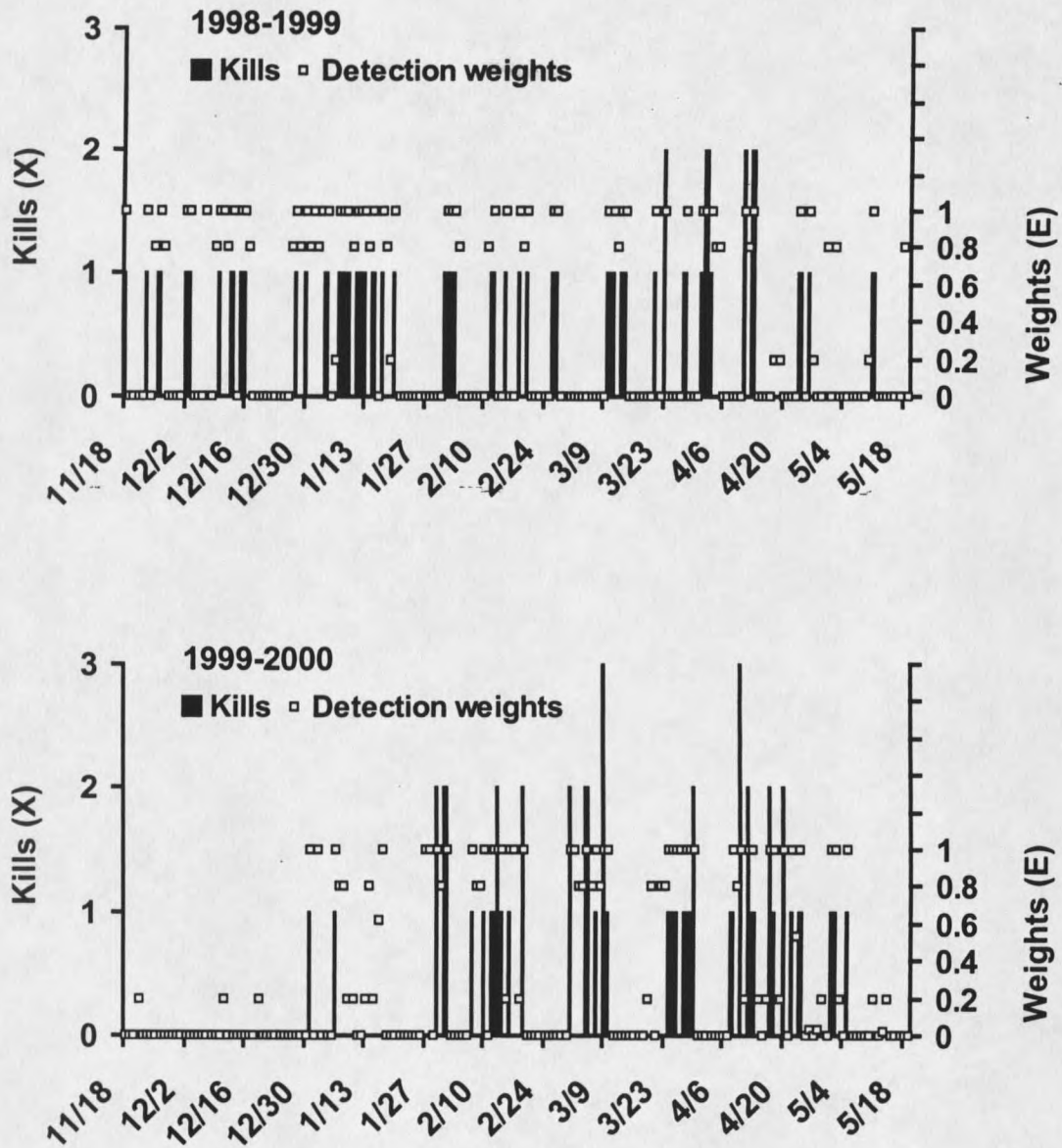


Figure 12. Distribution of observed kills for the Nez Perce pack and associated detection efficiency weights in the Upper Madison drainages of Yellowstone National Park, Wyoming. Wolf kill data were collected during the 1998—1999 and 1999—2000 winters. Weights were assigned according to daily snow tracking efficiency that varied due to tracking conditions and effort.

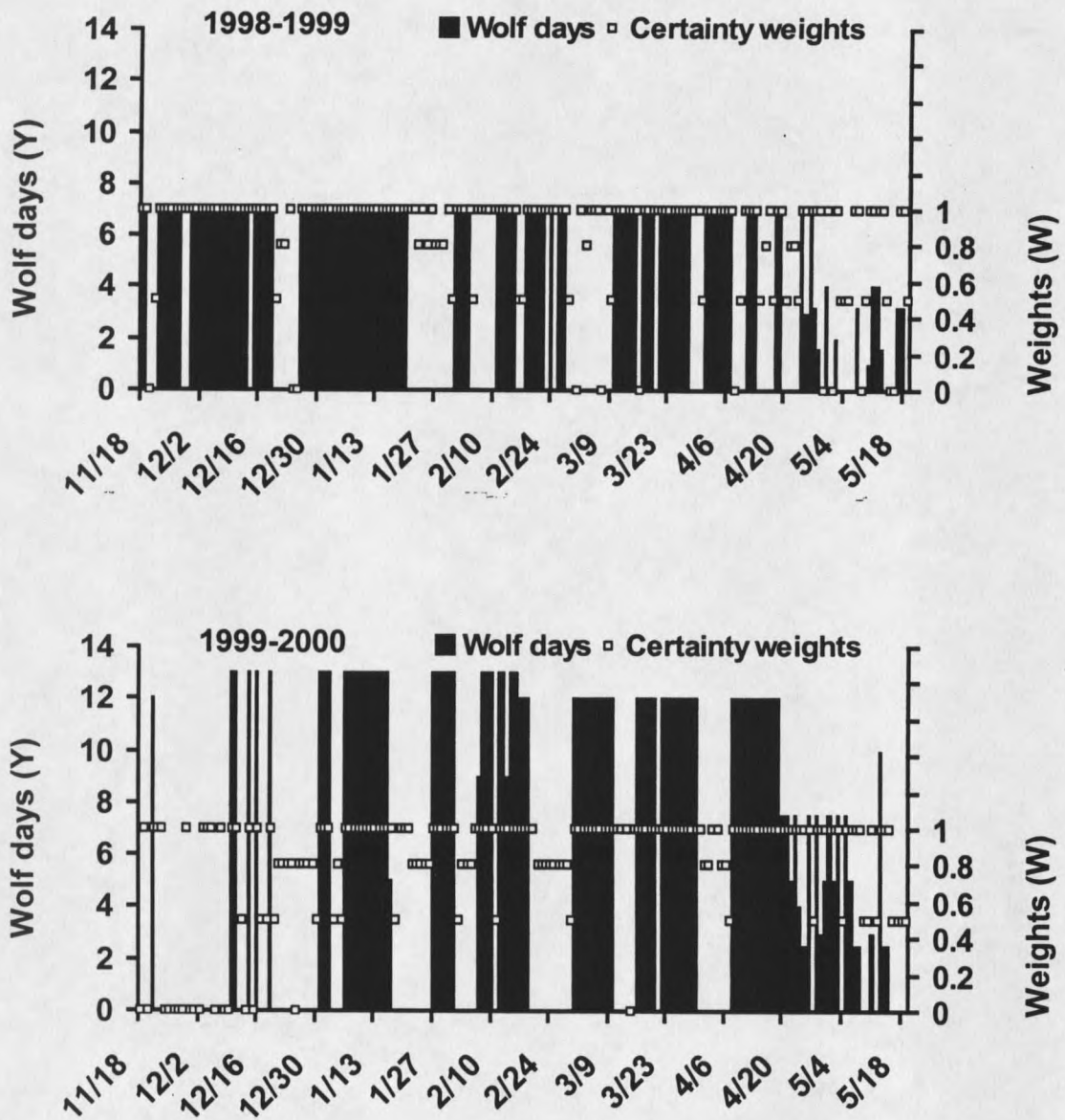


Figure 13. Distribution of observed wolf days for the Nez Perce pack and associated weights for certainty of detection in the Upper Madison drainages of Yellowstone National Park, Wyoming. Wolf presence data were collected during the 1998—1999 and 1999—2000 winters. Weights were assigned according to certainty of whether the Nez Perce pack was on or off the study area, which varied due to the difficulty in knowing the exact timing of the pack's movements.

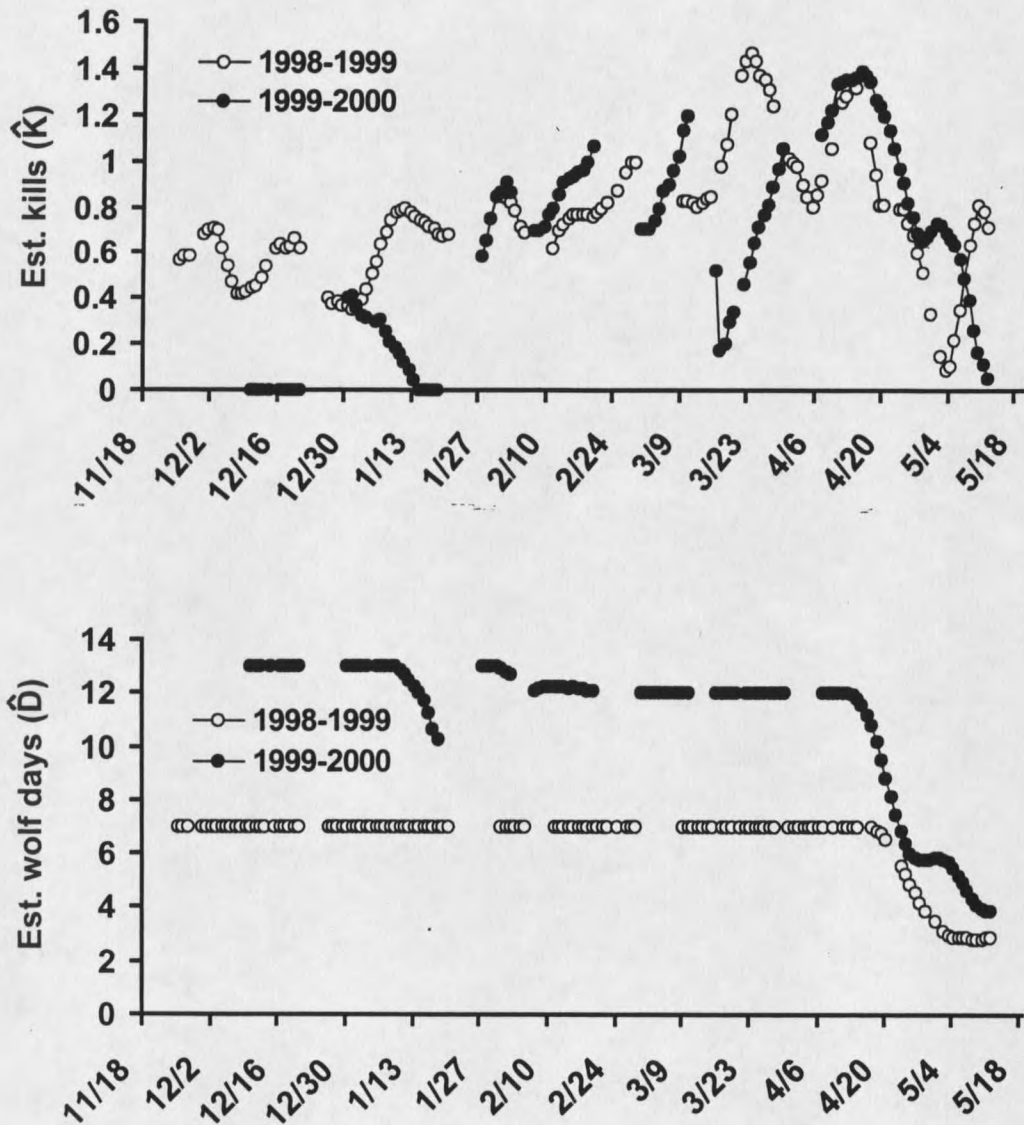


Figure 14. Estimated kills and wolf presence (wolf days) in the Upper Madison drainages of Yellowstone National Park, Wyoming. The study was conducted during the 1998—1999 and 1999—2000 winters. Estimates were calculated using a moving window average and a weighting scheme to adjust for the difficulty in locating all wolves and kills on the study area daily.

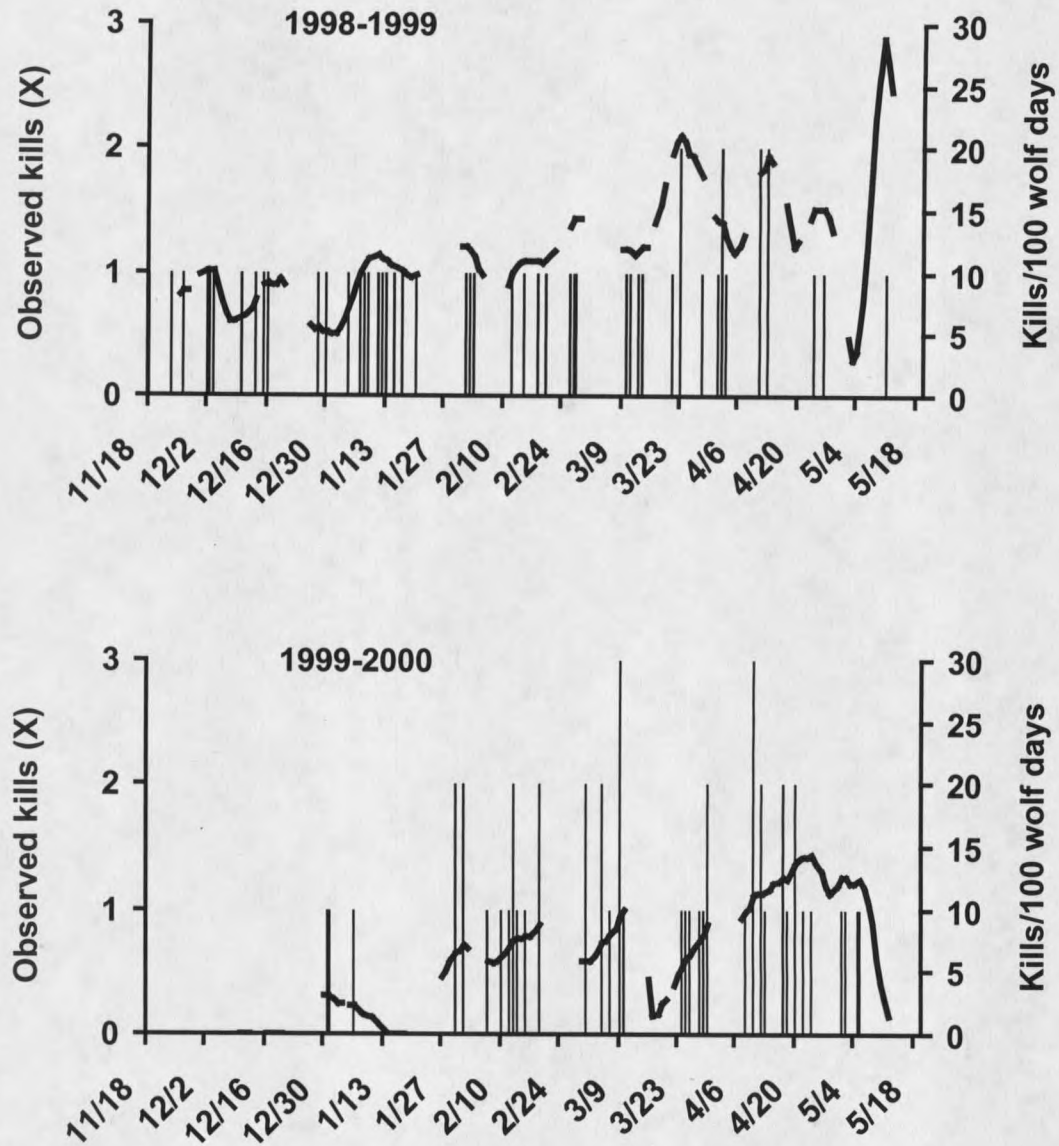


Figure 15. Weighted average kill rates for the Nez Perce pack using a 15-day moving window. Data were collected in the Upper Madison drainages of Yellowstone National Park, Wyoming, during November—May 1998—1999 and 1999—2000. Vertical lines are the observed kills and horizontal lines are the kill rates. Vertical lines are the observed kills and horizontal lines are the kill rates. Discontinuities in kill rates indicate the periods the pack was absent from the study area. Kill rates averaged across each winter are 11.8 and 6.5 kills/100 wolf days for the first and second year, respectively.

then dropping rapidly after peaking during denning season due to sporadic data.

Estimated kill rates were also nearly double during 1998—1999 compared to 1999—2000. Results from varying the weighting scheme for detection efficiency changed estimates of kill rates very little and demonstrated the weighting method was robust (Figure 16).

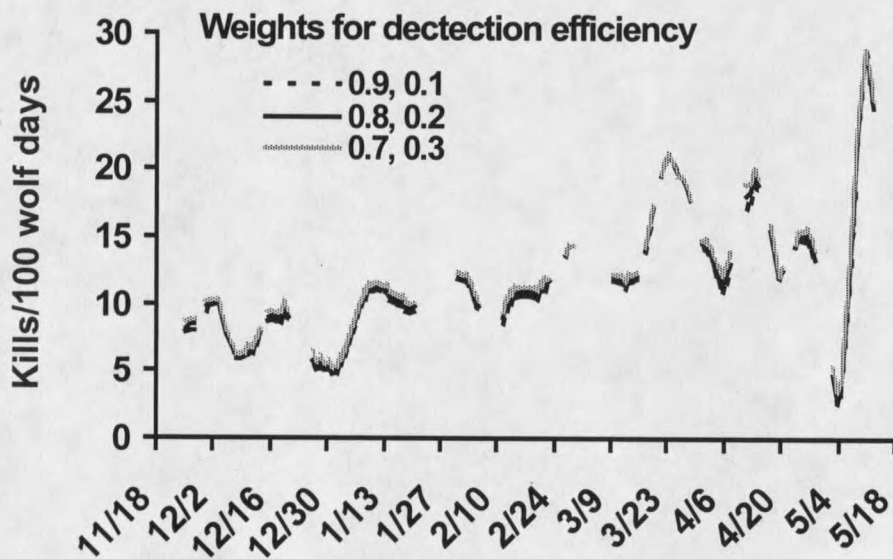


Figure 16. Robust test for the 1998—1999 weighted moving window average kill rates. Results were similar for 1999—2000. The wolf-ungulate study was conducted in the Upper Madison drainages of Yellowstone National Park, Wyoming.

Estimated Wolf Days and Offtake

The estimated number of wolf days on the study area was slightly higher than observed each year (Table 3). During 1998—1999, 199 tracking bouts yielded an estimated total of 836 wolf days, and 200 tracking bouts during 1999—2000 rendered 1186 estimated total wolf days. Estimated wolf offtake (kills) was also higher compared

Table 3. Observed and estimated weighted wolf days, total wolf kills, and kill rates in the Upper Madison drainages of Yellowstone National Park, Wyoming. Data were collected during the 1998—1999 and 1999—2000 winters, and the Nez Perce denning seasons began 27 April 1999 and 20 April 2000. Kill rates were calculated as kills/100 wolf days. Nez Perce estimated kill rates were averaged across each winter using a 15-day moving window average. Observed kill rates and estimated kill rates for all wolves were calculated by dividing kills by wolf days as they appear in the table.

	1998-1999		1999-2000	
	Observed	Estimated	Observed	Estimated
<u>Nez Perce</u>				
Wolf days				
Pre-denning	710	761	919	1051
Denning	31	44	113	130
Total	741	805	1032	1181
Kills	49	---	45	---
Kill rate	6.6	11.8	4.4	6.5
<u>All Wolves</u>				
Wolf days				
Pre-denning	755	793	936	1052
Denning	32	43	115	134
Total	787	836	1051	1186
Kills	59	84	49	66
Kill rate	7.5	10.0	4.6	5.6

to observed kills across the entire field seasons, 84 verses 59 during 1998—1999 and 66 verses 49 during 1999—2000, respectively. As a result of the estimation procedure, these differences indicated that approximately 30% of the kills made on the study area by wolves were undetected. Divided into pre-denning and denning seasons, the difference between estimated and observed offtake during the pre-denning seasons was 26% and 10% for the first and second winters, respectively, while denning season estimates were much higher, 63% and 52% (Table 4). Denning season offtake estimates were inflated

both years by highly variable kill rates due to the difficulty in locating kills during spring snow melt combined with the uncertainty of how many wolves were present on the study area each day as a result of pack fragmentation. The total estimated offtake of the first and second winters, 84 and 66, indicated an estimated difference of 21% difference between years. 1998—1999 offtake estimates of elk subtracted from the 1998 fall elk populations (Figure 5: 170 calves, 371 cows, 59 bulls) rendered 136 calves, 352 cows, and 50 bulls. Subtracting the 1999—2000 estimated offtake from the 1999 fall populations estimates of elk (Figure 5: 132 calves, 350 cows, 70 bulls) yielded 99 calves, 324 cows, and 69 bulls.

Table 4. Observed and estimated wolf kill composition in the Upper Madison drainages of Yellowstone National Park, Wyoming. Data were collected during the 1998—1999 and 1999—2000 winters. The Nez Perce denning seasons began 27 April 1999 and 20 April 2000, but 19 April 1999 and 13 April 2000 were used with estimated offtake to include all data influencing the 15-day kill rate window.

Season	1998-1999			1999-2000		
	NP ^a Obs ^c	All ^b Obs	All Est ^d	NP Obs	All Obs	All Est
Pre-denning						
Calf Elk	22	30	34	23	24	27
Cow Elk	11	11	19	11	12	13
Bull Elk	4	5	7	1	1	1
Bison	9	10	16	0	0	0
Total	46	56	76	35	37	41
Denning						
Calf Elk	0	0	0	2	2	6
Cow Elk	0	0	0	7	7	16
Bull Elk	1	1	2	0	1	0
Bison	2	2	6	1	2	3
Total	3	3	8	10	12	25
Total kills	49	59	84	45	49	66

^aNez Perce pack ^bAll wolves on the study area ^cObserved ^dEstimated

Condition of Prey

Body condition of prey differed within and between years. Forty-seven animals killed by wolves were examined for percent of bone marrow fat during 1998—1999 and 46 during 1999—2000. Approximately 60% of those had solid marrow (category 1) both years, however, solid marrow was evident in prey mainly November—February during 1998—1999 (Figure 17). In contrast, during 1999—2000, wolf-killed prey were found with solid marrow consistently throughout the field season. During the first field season, fat content in the marrow of calf elk began to decline in early January and gelatinous marrow was evident in late February. Cow and bull elk showed gelatinous marrow in early and mid-April, respectively. Bison calves began showing signs of marrow fat decline as early as the end of December and gelatinous marrow was evident by mid-March. During 1999—2000, decline in bone marrow fat began later than the previous year; calf elk showed signs of marrow fat decline early in February and gelatinous marrow was evident in early March. While cow elk had gelatinous marrow in the end of March, the 2 bull elk killed during the second spring had solid marrow, and only 1 of the 2 bison killed in May had gelatinous marrow.

Of the 37 adult elk examined for jaw necrosis in the field, 65% (n=24) showed signs of the disease. The youngest elk with necrosis was 4 years old, though no 3-year-old elk were found killed by wolves during the study. Of the 34 adults classified according to age and severity, 10 cows ranging 7—15 years old and a 5-year-old bull had severe jaw necrosis. Twenty-eight adult elk were examined for arthritis and 21% (6 cows) ranging 7—15 years in age showed sign of the disease, all of which also were

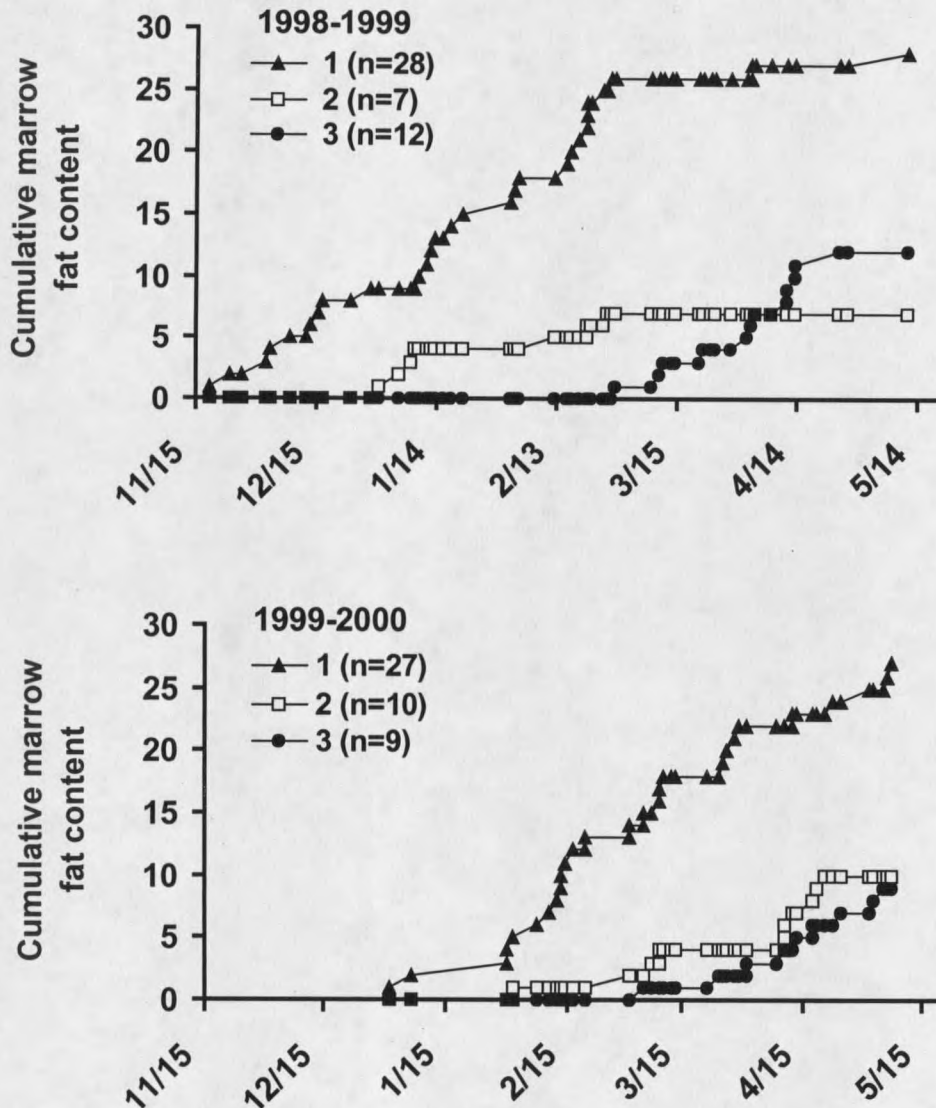


Figure 17. Cumulative categorical bone marrow fat content of prey killed during the 1998—1999 and 1999—2000 winters in the Upper Madison drainages of Yellowstone National Park, Wyoming. Categories were 1: white and solid, 2: spotted pink—red solid, and 3: gelatinous.

afflicted with jaw necrosis. Elk with other physical maladies that may have contributed to vulnerability to predation included a 9-year-old cow with a broken tibia previous to predation, a calf whose entire rear right leg was much larger than his left, and a 7-year-old cow with a deep abscess in her jaw and a deformed hoof. The only adult bison killed by wolves in the study had a broken molar which grew sideways.

Spatial and Temporal Snowpack Variation

Snow began to accumulate in late October at the Madison Plateau SNOTEL site and mid to late November at the West Yellowstone SNOTEL site, and continued increasing throughout the winter (Figure 18). Peak snow accumulation occurred in April

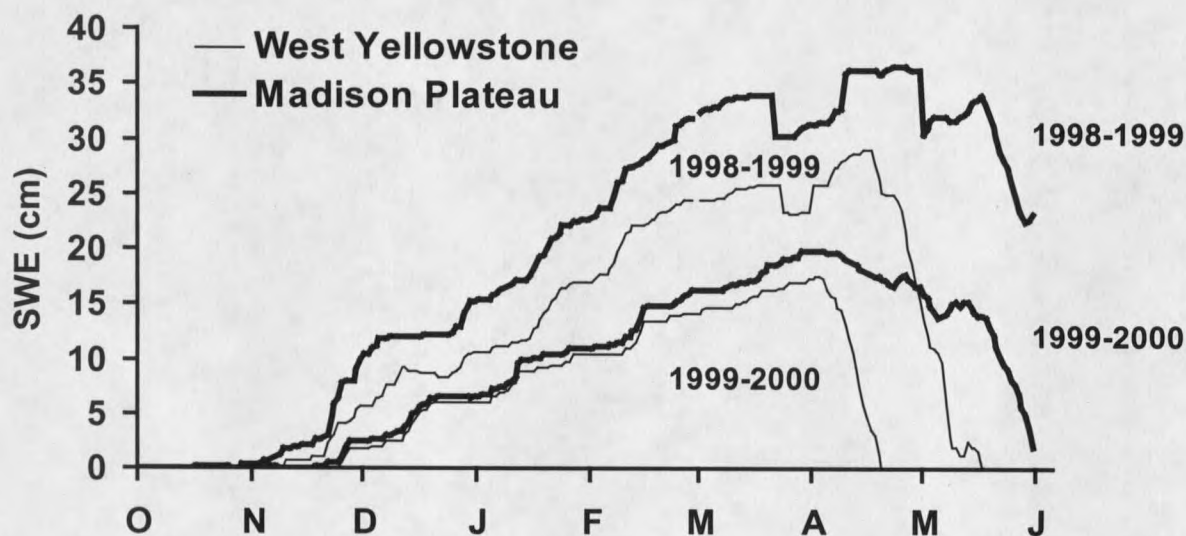


Figure 18. Temporal trends in snowpack, as indexed by snow water equivalent (SWE) measurements, recorded near West Yellowstone, Montana (2,042m), and on the Madison Plateau, Wyoming (2,362m).

followed by a period of rapid melting lasting 3—8 weeks. Snowpack at Madison Plateau was consistently greater than West Yellowstone and differed at both sites between years of the study. During 1998—1999, Madison Plateau peak SWE was 40% higher than the 31-year average (1968—1998) for peak SWE, and 24% lower than the 31-year average during 1999—2000. Peak SWE at West Yellowstone was 28% higher than the 31-year average during 1998—1999, and 23% lower than the 31-year average during 1999—2000.

DISCUSSION

Due to the difficulty in locating all kills and relocating wolves daily (Fritts and Mech 1981), most investigators have reported simply a minimum mean kill rate during a given time period and mean interval between kills (Fuller and Keith 1980, Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987, Carbyn et al. 1993, Ballard et al. 1997). While this practice has been useful, one has little information on what proportion of the kills were detected. Finding all kills and relocating wolves is difficult due to variable weather and tracking conditions, terrain and cover, and distances wolves are capable of travelling during a day. Included in the method of calculating kill rates for this study was a weighting scheme that accounted for variation in confidence of detecting kills on the study area each day. By weighting daily detection efficiency (giving less weight to data with less effort/certainty) and using a moving window average, the proportion of undetected kills was estimated. Using this technique, I estimated that approximately 30% of the kills that occurred during the 2 winters of the study and 25% during the pre-denning seasons were undetected. Although the weighting scheme performed well for the pre-denning season, further work to estimate kill rates during the denning season is necessary. Spring snow melt made locating kills difficult and the Nez Perce pack was fragmented during the denning season resulting in low efficiency in locating both wolves and their kills. Thus, kill rates and the associated offtake estimates for the denning seasons must be viewed with caution.

Kill rates for the Nez Perce pack differed both within and between years. Rates

increased throughout both winters, nearly doubling from fall to spring, and were roughly double the first year compared to the second. Rates were also highly variable within, as well as between winters. Increasing kill rates over winter found in the Upper Madison drainages were also observed in Riding Mountain National Park, Manitoba (Carbyn 1983), and northeastern Minnesota (Mech 1977). This trend was likely due to the increase of snowpack throughout winter that depleted body reserves and condition of ungulates as winter progressed. In high-elevation winter ecosystems, snow is the most important abiotic factor that impacts the survival of many species (Formozov 1946). Reduced forage availability and increased energy requirements deplete ungulate body condition, while ability to escape is diminished because movement is impeded (Parker et al. 1984). As snowpack increases during winter, prey concentrate in the areas where snow levels are reduced (Stelfox and Taber 1968). Cow bison also actively abandon their calves weakened by winter hardship (Van Camp 1975), leaving them with no protection. Combined, these factors increase vulnerability of ungulates to wolf predation as winter proceeds, which is reflected in kill rates.

The difference in kill rates between years may have been influenced by 2 factors, severity of winter snowpack and pack size, both of which differed between winters. Snow conditions were severe the first year and mild the second relative to the long-term average, which may have influenced predator-prey dynamics. Ungulates began depleting the last of their fat reserves earlier during the first winter than the second, evident in the bone marrow fat of wolf-killed prey in the study. While vulnerability of prey due to snowpack likely contributed to rates of predation, no significant relationship between

snow depth and kill rates was found in nonmigratory packs in Alaska (Dale et al. 1995). Conditions in the snow layers may be more influential in contributing to predation of ungulates than snow depth (Parker et al. 1984), and further examination is warranted.

In addition to snowpack severity, wolf pack size may have impacted kill rates each year of the study. The Nez Perce pack was comprised of 7 wolves during 1998—1999 and had consistently higher kill rates per wolf than when the pack numbered 13 with double the number of adults capable of hunting during 1999—2000. Pack size was inversely related to kill intervals in several studies (Fritts and Mech 1981, Messier and Crete 1985, Ballard et al. 1987, Thurber and Peterson 1993, Dale et al. 1995, Hayes and Harestad 2000, but see Ballard et al. 1997). A reason for higher kill rates during 1998—1999 when the Nez Perce pack numbered only 7 may be satiation achieved with less of the prey consumed during the initial feeding and subsequent loss to scavengers, also suggested by Thurber and Peterson (1993). Increased vulnerability of prey during the more severe winter may have also made hunting easier during the first winter. The pack hunted and fed at night during the first year, then rested by daylight while scavengers fed on the carcasses. The wolves often returned the next day to carcasses to feed on what remained. The second year, the pack consumed more of the carcasses on average during initial feedings than the first year, 75% versus 42%. Wolves in Riding Mountain National Park abandoned carcasses when half consumed by small packs in mid to late winter when kill rates were high (Carbyn 1983). A negative correlation between winter severity and carcass utilization was also reported in wolf studies in Algonquin Provincial Park (Pimlott et al. 1977) and northeastern Minnesota (Mech et al. 1971). Prey size may

also influence this dynamic. More cow elk and fewer calves were killed the second year compared to the first, so though kill rates differed between years, biomass consumed may have been similar. While both pack size and snowpack severity may have contributed to the higher kill rates observed during the first year of the study compared to the second, these factors are confounded during the 2 years of this study, so it is not possible to ascertain their relative influence on wolf kill rates. Research in this system is ongoing and additional years of study should provide more data to help elucidate the important drivers in this predator-prey dynamic.

To directly compare kill rates of this study with other studies, I averaged pre-denning observed Nez Perce pack kill rates for each winter. Average kill rates in the Upper Madison drainages were 6.8 elk and bison/100 wolf days during 1998—1999 and 4.9 during 1999—2000. These rates were similar to rates found on the Northern Range, YNP (Mech et al. 2001), 7.2 and 3.6 ungulates (elk, moose, mule deer, bison)/100 wolf days during March 1997 and 1998, respectively. YNP wolf kill rates were generally higher than most other wolf-ungulate systems studied, which may indicate high rates for re-establishing wolf populations compared to those that are established. In southwestern Quebec and northwest Alaska, average wolf kill rates ranged 0.4—4.6 moose and caribou/100 wolf days (Messier and Crete 1985, Dale et al. 1995, Ballard et al. 1997). Calculated in the metric of days/kill/pack, average observed kill intervals for the Nez Perce pack during the pre-denning seasons were 2.19 during 1998—1999 and 2.11 during 1999—2000. Other studies describe a wide range of intervals during different parts of winter for varied prey. Where moose were the primary prey, intervals ranged from 2.5—

43.0 (Mech 1966, Fuller and Keith 1980, Peterson et al. 1984, Thurber and Peterson 1993), moose or caribou, 1.2—6.2 (Burkholder 1959, Stephenson 1978, Ballard and Spraker 1979), elk or moose, 2.7—14.0 (Carbyn 1983), and bison or moose, 6.8 (Carbyn et al. 1993).

Not only were kill rates variable in the study system, but the use of prey types by wolves also differed within and between years. Prey switching was apparent during only the first year of the study. When elk calves, the primary prey, became scarce in mid-March, wolves increased their use of cow and bull elk and bison calves. By early April, no elk calf kills were found while kills of the other 3 prey types were located at an increased rate. The second year of the study, however, there was no evidence of prey switching, though wolves used calf elk more in early winter and cow elk more in late winter—spring. The same shift was also evident in Riding Mountain National Park where elk were the primary prey (Carbyn 1983), while in northwest Alaska, wolves switched from selecting caribou to moose when caribou migrated out of wolves' territories (Ballard et al. 1997).

During both years of the study, the species, sex, and age classes of animals killed by wolves were not proportional to the availability of each prey type within the study area, demonstrating non-random prey selection (Eaton 1974). Bison were the most abundant prey species available to wolves and concentrated in the Firehole drainage where wolf activities were highest both winters. Adult bison were rarely preyed upon, but represented 44% and 57% of the total prey population and 68 % and 77% of the total biomass during the first and second year, respectively. Calf bison were less available

than adult bison and cow elk, but killed in slightly higher proportion than availability during the first spring. Bison calves became more vulnerable as winter severity increased and were abandoned by their dams during the most severe months of winter (Van Camp 1975). During the first year of the study when snow conditions were harsh, bison calves were observed alone or in small groups without adults, left highly vulnerable to wolf predation. Thirteen wolf-killed calf bison were located during the study, 12 the first year and 1 the second, reflecting the differences in snowpack between years.

Wolves in this study showed strongest selection for elk, particularly calves. While calf elk were less available than bison and cow elk both years of the study, half of all wolf kills were calf elk. In other studies, moose calves (Fuller and Keith 1980, Peterson et al. 1984, Ballard et al. 1987) and elk calves (Carbyn 1983) were selected disproportionately higher than were present in the population during winter, indicating high calf vulnerability. This vulnerability was also evident in Africa. Cheetahs, leopards, wild dogs (Schaller 1972), and hyenas (Kruuk 1972) showed strong selection for wildebeest calves, and Thompson's gazelle fawns were highly vulnerable to hyena (Kruuk 1972) and cheetah (Schaller 1972) predation. Decline in condition throughout winter likely caused increased calf elk selection during the first three months of wolf predation both winters, while subsequent declining numbers of calf elk in the population likely led to a drop in selection thereafter. Condition of prey is an important factor in prey vulnerability, for which bone marrow fat is a measure. Cook et al. (2001) found that femur marrow fat values <90% in elk indicate <6% body fat. Thus, any loss of bone marrow fat indicates poor condition (McCullough and Ullery 1983, Mech and

DelGiudice 1985, Cook et al. 2001), while low levels indicate acute nutritional deprivation (Ratcliffe 1980, Depperschmidt et al. 1987, Harder and Kirkpatrick 1994). Marrow fat reserves in calf elk showed evidence of depletion by early January during the first winter, 1 month sooner than the second winter, while adult elk first showed a decline in marrow fat in April both years of the study. Most wolf-killed moose calves on the Kenai Peninsula (Peterson et al. 1984) and in south-central Alaska (Ballard et al. 1987) were also in poor condition by January while fat depletion in bone marrow of adult moose killed by wolves was evident after February.

Although calf elk were most selected by wolves on the study area, wolves also used adult elk. Cow elk, the second most abundant prey type both years of the study, were generally killed less than or in proportion to availability both winters. Bulls were the least available ungulate prey type on the study area and killed in higher proportion than availability only during April 1999. The use of cow elk as prey by wolves increased 42% from the first year to the second, which may have been due to the nearly doubled number of wolves in the Nez Perce pack the second year. Studies in Africa have shown that for carnivores that hunt communally, hunting group size and prey size are correlated (Kruuk 1972, Creel and Creel 1995). In contrast, wolf use of bull elk decreased by 66% from the first year to the second. Bulls generally deplete their fat stores during the rut and enter the winter with low fat reserves (Flook 1970). Their post-rut condition combined with the harsh snow conditions of the first year likely rendered bulls more vulnerable to predation the first winter than the second, which was relatively mild. Disease may also have been a factor that influenced the vulnerability of adult elk to

predation. Necrosis was found in 65% of adult elk in the Upper Madison drainages that were examined for the disease, as young as 4 years old. In Denali, 36% of moose preyed on by wolves had necrosis, whereas only 2% of wolf-killed caribou had the disease (Mech et al. 1995). The youngest cow elk found in this study afflicted with arthritis was 7 years old, and 21% of all wolf-killed adult elk had the disease. Similarly, wolf-killed moose with arthritis were reported as young as 6—8 years old in cows on Isle Royale (Peterson 1977) and the Kenai Peninsula (Peterson et al. 1984) and 5 years of age in bulls in Denali (Mech et al. 1995). In contrast, no cows less than 14 years old in Denali were found with the disease (Mech et al. 1995). Ages of adult elk in the Upper Madison drainages preyed on by wolves also differed from other studies, with higher numbers of prime-aged elk killed by wolves in the study system than senescent elk. More than half of the adult elk taken by wolves ranged from 2 to 9 years old, and bulls were mostly younger than cows. While wolves selected senescent elk, prime-aged elk were also vulnerable to wolf predation. Similarly, Mech et al. (2001) found among wolf-killed adult elk on the Northern Range, YNP, the mean age of bulls was 5—6 and cows was 13—15. Studies in Riding Mountain National Park (Carbyn 1983) and on the Kenai Peninsula (Peterson et al. 1984), however, found wolves preyed most heavily on the senescent ungulates (>11.5 years old).

The combined effects of variable kill rates and differing numbers of wolves between years were reflected in the offtake from the preybase, which differed by year. The estimated number of animals removed from the Madison-Firehole elk population by wolves was 21% higher the first year compared to the second, 84 and 66, respectively.

Offtake estimates are a function of the estimated daily kill rates, the numbers of wolves in each pack, as well as the timing and duration of pack presence on the study area each winter. Hence, the lower offtake the second year of the study was partially due to the larger pack size and movement of the Nez Perce pack. Wolves remained on their summer range outside the study area longer during the second year, becoming a persistent presence on the study area 2 months later than the first year, while elk stayed in high elevation terrain later than the previous year. The pack made more frequent and longer forays off the study area during the second year than the first resulting in 18% less time spent on the study area. This may have been partially due to elk concentrating in low elevation areas of reduced snow accumulation later in winter. Though pack size nearly doubled from the first winter to the second, observed wolf presence increased by only 25%, and the smaller pack the first year had a higher offtake per wolf than the larger pack the second year. Spatial dynamics between predator and prey were therefore important, effecting offtake.

The proportion of offtake by wolves from the preybase in the Upper Madison drainages also varied according to prey type and year. Observed offtake of bison calves was 5% and 0.5% of the maximum calf bison population during 1998—1999 and 1999—2000, respectively, and only one adult bison was killed during the 2 years of the study, which was inconsequential relative to the Upper Madison bison population. I used observed rather than estimated bison offtake because all bison calf kills were located on snowless thermal areas which were visited regularly by 3 research crew members in addition to daily wolf tracking activities, and the portions of the Upper Madison

drainages in which bison wintered were consistently well covered by research staff. It is therefore likely that nearly all bison calf kills were located. Bison offtake on the study area should thus be treated differently than elk offtake.

Because elk kills were not as obviously located as bison kills, I used estimated offtake of elk to account for undetected kills. The proportion of estimated offtake from the elk preybase was 5% and 8% for cows, 15% and 1% for bulls, and 20% and 25% for calves for the first and second winters, respectively. Pre-wolf research in the Upper Madison drainages since 1991 indicated prime-aged cow elk survival was very high (R.A. Garrott, unpublished data), thus a substantial proportion of the cow elk kills were probably additive. Pre-wolf recruitment, however, indicated high variability in over-winter calf survival and annual recruitment that was strongly correlated with severity of winter snowpack. I therefore speculated that there was a potential for wolf predation on calves the first year of the study, when snowpack conditions were harsh, to be at least partially compensatory. Total offtake was lower in the second year of the study, when snowpack was considerably reduced and over-winter starvation mortality would be expected to be low, suggesting wolf predation had a higher potential to be substantially additive. Though offtake was not significant for the adult elk or bison populations during the study, wolf predation may affect the recruitment of calf elk into the elk population, particularly during years of lighter snowpack.

The long-term effects of the wolf reintroduction on the elk and bison populations in the Upper Madison drainages are yet unknown, as this predator-prey system is still developing. During this study, only 1 wolf pack utilized the study system in primarily 1

of the 3 drainages for parts of each winter. Thus, a large proportion of the ungulate preybase was not significantly affected by wolf predation. Considerable potential exists for the expansion of wolf presence into the other 2 drainages by the expansion of current packs' territories and/or new packs establishing in areas currently not occupied by wolves. There is also potential for bison to become a more important component of the wolf preybase because of the high proportion of biomass bison represent in the preybase and capacity wolves show to kill bison. In Wood Buffalo National Park, bison are the primary prey for wolves and wolf predation on the bison population is significant (Carbyn et al. 1993). Two packs in YNP, including Nez Perce, presently prey on bison (Smith et al. 2000) and with time, wolves may develop effective bison hunting techniques and render bison important prey.

The ungulate preybase and daily wolf presence on the study area were quantified in this study, and daily ground tracking proved effective in obtaining information on kills. Attaining these empirical data contributes to knowledge of predator-prey systems and may assist in providing insights into theoretical questions of modeling these systems. The method developed during this study offers a robust approach to the difficult problem of calculating kill rates and offtake from prey populations. The important variables are often inter-dependent and difficult to measure. Some factors, such as locating all kills and wolves daily, cannot be measured with complete accuracy. In data analysis and model building, independence between variables is often assumed. Clearly, certain predation variables are not necessarily independent. Whether wolves ate yesterday will likely influence whether they attempt to eat today. The technique of using a moving

window average incorporates data that influences the kill rate calculated for current day from the surrounding days. This methodology therefore accounts for some of the lack of independence in predation data. The study of within season trends is also possible using this method through generating smoothed kill rates across time. In this study, the proportion of undetected kills is estimated, which removes the assumption used in current models that all kills are located and demonstrates how variable kill rates are. Capturing this variability sheds new light on the way predator-prey systems function and incorporates more of the complexity inherent in predator-prey systems into the modeling process. By identifying and quantifying more of the variability in predator-prey systems, the model is improved and the level of uncertainty is reduced over current models. This is a first step in better estimating kill rates and modeling what drives them. The application of this new approach to the recently re-established wolf population in the Rocky Mountain ecosystem helps give additional insight into wolf-ungulate dynamics and the potential impacts of wolf predation on ungulate populations.

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